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Two New Menosporine Gregarines, *Hoplorhynchus acanthatholius* N. Sp. and *Steganorhynchus dunwoodyi* N. G., N. Sp. (Apicomplexa: Eugregarinorida: Actinocephalidae) from Coenagrionid Damselflies (Odonata: Zygoptera)

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ABSTRACT. *Hoplorhynchus acanthatholius*, n. sp. is described from *Enallagma civile*, the Civil Bluet damselfly. Trophozoites are solitary, lie in the mesenteron between the peritrophic membrane and the epithelium, and attain a maximum length of 850 μm. Epimerite ovoid to broadly ovoid; anterior margin bearing eight equidistant retroarcuate hooks; attached to protomerite by means of a vermicular stalk. Protomerite ovoid; deutomerite narrowly obvoid. Gametocysts spherical; diam 300 μm, sporulating by simple dehiscence in 48–72 h. Oocysts are characteristic of Menosporinae: smooth, biconical, crescentic, uniform in size and shape. *Steganorhynchus dunwoodyi*, n. g., n. sp. is described from the damselfly *Ischnura verticalis*. The genus is characterized by an epimerite comprising an ovoid papilla enclosed in a retractable, globular sheath, borne on a long vermicular stalk. Trophozoites are solitary, lie in the mesenteron between the peritrophic membrane and epithelium, and attain a maximum length of 605 μm. Protomerite very broadly ovoid; deutomerite obvoid. Gametocysts spherical; diam 258 μm, sporulating by simple dehiscence in 48–72 h. Oocysts are characteristic of Menosporinae: smooth, biconical, crescentic, uniform in size and shape. The population dynamics of *H. acanthatholius* and *S. dunwoodyi* among damselfly populations in five Nebraska localities are presented.

Supplementary key words. *Enallagma civile*, gregarine, *Ischnura verticalis*, parasite, parasitism, population dynamics, Sporozoa.

THE family Actinocephalidae is a cosmopolitan group comprising well over 250 protist species parasitic in a variety of arthropods, primarily insects and centipedes [19]. The group is apparently specious on a global scale, but the New World actinocephalid fauna is relatively small. Clopton [5] noted this pattern of new world paucity is "... more likely a result of insufficient survey work rather than true faunistic poverty." Known gregarine parasites of North America odonates are all members of Actinocephalidae. They have been assigned to five genera across three subfamilies: *Geneiorhynchus* and *Actinocephalus* (Actinocephalinae) [8, 22], *Prismatospora* and *Nubenocephalus* (Acanthosporinae) [7, 10] and *Domadracunculus* (Menosporinae) [5]. All of these species are reported from temperate zones. No gregarine parasite is known from the New World tropical or subtropical odonates. These observations suggest that a substantial gregarine fauna remains undiscovered in the intestines of New World odonates.

During a study of host/parasite interfaces of gregarines and odonates in southeastern Nebraska, two distinct gregarine forms were collected consistently from two coenagrionid damselfly species, *Enallagma civile* Hagen, 1861 and *Ischnura verticalis* Charpentier, 1840 (Odonata: Zygoptera). One form displays the general characters of *Hoplorhynchus*, but is separated from known species by a unique suite of epimerite characters. The second gregarine form shares the general characters of Menosporinae, but possesses a suite of characters clearly distinct from known menosporine genera. The unique form of these gregarine populations prompted the present proposal of two new species and a new genus of menosporine gregarines. Their basic parasite population biology is also discussed.

MATERIALS AND METHODS

Adult damselflies were collected from *E. civile* and *I. verticalis* populations from Oak Lake (section 14, T 10 N, R 6 E), Lancaster County, Nebraska; and Dunwoody Pond (section 32, T 15 N, R 37 W), Beckius Pond (section 1, T 14 N, R 38 W), Nevins Tank of the Sillison Ranch (section 11, T 14 N, R 36 W), and Lake Ogallala (section 2, T 14 N, R 38 W), Keith County, Nebraska. A total of 776 adults were dissected and examined for parasites during May–August 1991 to provide parasite morphometric and population dynamics (prevalence, mean intensity, and abundance) data. The data presented here are derived from the following samples: parasite population dynamics, 268 *I. verticalis* adults and 253 *E. civile* adults; parasite morphometrics, 94 *I. verticalis* adults and 161 *E. civile* adults. A smaller sample of naiads (n = 94) was collected from the same locations, dissected and examined for parasites. Species determinations for zygopteran naiads are based on the proportions and lengths of various body parts, the number and placement of important setae and the shape, tracheation, and marking of the caudal gills. Body proportions, lengths and setal numbers are unstable in first–fourth instar nymphs [12]. Growth associated variance also confounds many caudal gill characters. The problem is often exacerbated by the fragility of the gills themselves and the variability of regenerated caudal gills among very young instars [27]. As a result, it is only feasible to make positive species identifications in late nymphal instars and only such nymphs are included in this study. All measurements reported here are from parasites of adult damselflies in an effort to avoid confounding data from several host and parasite populations.

Parasites were measured as fresh preparations in water. No more than 10 parasites were measured from each host, reducing the effects of osmotic distortion in morphometric data. Specimens for permanent mounts were fixed in AFA (alcohol, formalin, and acetic acid), washed in 70% ethanol, stained with Semichon's acetocarmine, dehydrated with ethanol, cleared in xylene, and mounted in Canada Balsam. Measurements and ratios reported here are from living trophozoites (see Clopton et al. [6] and Richardson & Janovy [22]) and are presented in micrometers as range values with embedded means followed by the standard deviation in parentheses. Morphometric data presented here are taken from parasite population samples collected from Oak Lake, Lancaster County, Nebraska. Protomerites and deutomerites were measured at their widest points.

Individual adult damselflies were isolated abdomen down in 5-ml test tubes with 1 ml of water and left overnight for fecal collection. Frass was examined for the presence of gametocysts. Hosts that shed gametocysts were dissected to determine the gregarine species present. Gametocyst and oocyst measurements are reported from hosts with single parasite species infections. Gametocysts were held in water for sporulation and dehiscence. Oocysts were measured in both fresh preparations and air-dried

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Giemsa-stained smears. The type of measurements taken from oocysts are shown in Fig. 1. Oocyst morphology and measurements were uniform regardless of preparation method. Camera lucida drawings were made from preserved gregarines. All observations were made with an American-Optical Spencer binocular compound microscope with 15× wide field eyepieces, 10× and 40× objectives, and a Silge & Kuhne Ortho-Illuminator B. Terminology for parasite population parameters is consistent with Margolis et al. [20]. Levine's uniform terminology for Apicomplexa [18] is used in this paper with the exception that the term trophozoite is used for all parasites with an epimerite as explained by Richardson & Janovy [22]. Terminology for shapes of planes is consistent with that suggested by the Systematics Association Committee for Descriptive Biological Terminology [2, 3] and forms the basis for derivation of terminology for shapes of solids used in these descriptions. Other anatomical terminology is consistent with that of Torre-Bueno [25].

RESULTS

Hoplorhynchus acanthatholius n. sp.

Diagnosis. Eugregarinida Léger, 1892, sensu strictu Levine, Corliss, Cox, Deroux, Grain, Honigberg, Leedale, Loeblich, Lom, Lynn, Merinfeld, Page, Poljansky, Sprague, Vavra, and Wallace, 1980; Septatina Lankester, 1855, sensu strictu Levine, Corliss, Cox, Deroux, Grain, Honigberg, Leedale, Loeblich, Lom, Lynn, Merinfeld, Page, Poljansky, Sprague, Vavra, and Wallace, 1980; Actinocephalidae Léger, 1892, Menosporinae sensu strictu Léger, 1892: oocysts axially asymmetric (crescentic), without spines or thickenings at their poles; with the characters of the genus *Hoplorhynchus* Carus, 1863 sensu lato Levine, 1988 [19]: Epimerite long, terminating in a flattened bulb bordered by digitations anteriorly; oocysts ellipsoid, a little curved.

Trophozoite. (Fig. 2–4) Protomerite very broadly ovoid, posterior margin depressed, anterior margin nearly apiculoid and joining stalk of epimerite; length (LP) 28.8–**77.1**–140.0 (±22.7); width (WP) 25.0–**85.6**–180.0 (±30.6). Deutomerite narrowly obvoid, posterior margin acuminate, anterior margin depressed and variable in length with age; length (LD) 57.6–**303.9**–710.0 (±121.0); width (WD) 28.8–**101.1**–225.0 (±44.9); total length (TL) 86.4–**381.0**–850.0 (±140.3). Indices: LP:TL 0.14–**0.21**–0.33 (±0.37); LD:TL 0.67–**0.79**–0.86 (±0.04); LP:LD 0.16–**0.27**–0.50 (±0.64); WP:WD 0.58–**0.86**–1.11 (±0.10); (n = 117). Epimerite ovoid to broadly ovoid, posterior margin depressed, slightly cuculloid, anterior margin depressed with eight equidistant retroarcuate hooks, joined to protomerite by a vermicular stalk without a visible septum; length 28.8–82.0–144.0. Nucleus ellipsoid, typically mesad but often equatorial in anterior half of deutomerite; diam 40 μm. Trophozoites solitary.

Association. Association late and ephemeral, leading directly to syzygy, latero-associative while caudally enrobed in the peritrophic membrane. Gamonts in association laterally fused, similar in shape to trophozoite but nearly twice as broad; epimerite absent.

Gametocysts. Spherical and white with gelatinous coat. Diameter approximately 300. Gametocysts held in water typically sporulated and dehisced by rupture within 48–72 h of collection.

Oocysts. (Fig. 1, 5) Axially asymmetric, biconical, crescentic, compressed in the plane perpendicular to the major axis, smooth (without spines), very uniform in size and shape. Figure 1 (A–D) indicates the dimensions measured. A, 7.5–**7.5**–7.5; B, 3.6–**3.6**–3.6; C, 11.7–**11.7**–11.7; D, 5.9–**5.9**–5.9 (n = 38).

Type host. *Enallagma civile,* Civil Bluet Damselfly; adults.

Type locality. Oak Lake, Lancaster County, Nebraska, USA (section 14, T 10 N, R 6 E).

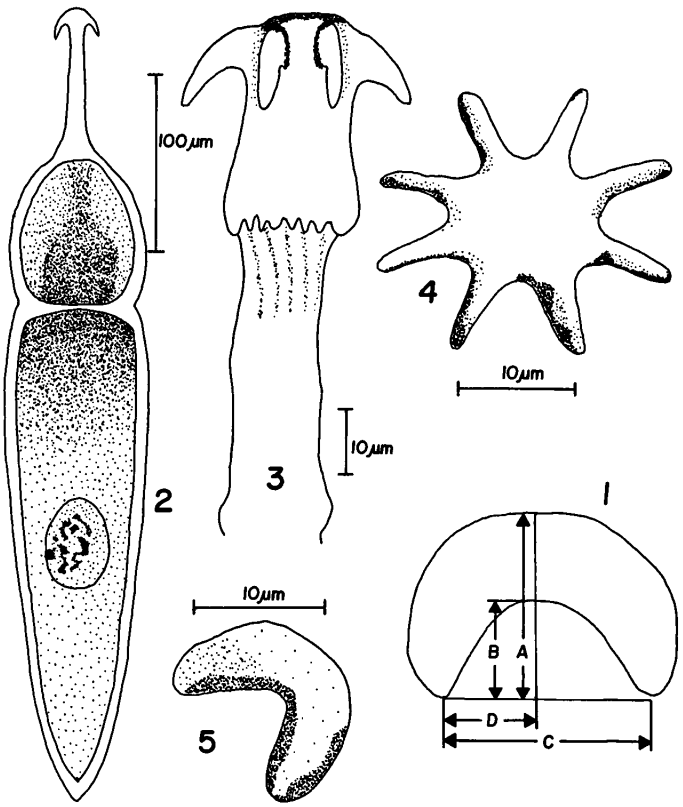

Fig. 1–5. *Hoplorhynchus acanthatholius* n. sp. **1.** Oocyst with dimensions measured. **2.** Trophozoite. **3.** Epimerite showing structural details. **4.** Epimerite en face. **5.** Oocyst.

Specimens deposited. Holotype and three paratypes (one slide USNM No. 82441) deposited in the United States National Museum Helminthological Collections, Beltsville, Maryland. The holotype has the following fixation artifacts: the nucleus is displaced slightly posteriad and there is swelling of the epimerite stalk.

Infection site. Anterior part of mesenteron between epithelium and peritrophic membrane.

Etymology. The specific epithet, *acanthatholius,* is derived from the Greek *akantha,* meaning a thorn or spine, and *tholia,* meaning a broad brimmed hat and is given to mark the nature of the epimerite.

Remarks. The genus *Hoplorhynchus* is based almost entirely on the structure of the epimerite, "a flattened bulb bordered by digitations anteriorly" [4, 19]. Species in this genus are separated from one another by the relative shape of the flattened bulb and the number and form of digitations present [4, 14, 15]. Trophozoite shape, measurements and indices have been used to discriminate between species with similar epimerites [15]. *Hoplorhynchus acanthatholius* is similar in shape to *Hoplorhynchus orthetri* Hoshide, 1953 [14] but fully developed trophozoites are much smaller (850 μm and 1,850 μm respectively). In addition, the epimerite of *H. acanthatholius* bears eight equidistant retroarcuate hooks in contrast to a corona of 10–12 recurved hooks. Type hosts are in different suborders. In comparison to *Hoplorhynchus hexacanthus* Obata, 1953 [21], *H. acanthatholius* is much smaller with a larger LP:TL ratio (0.212 vs. 0.08–0.125) and an epimerite with eight hooks rather than six. *Hoplorhynchus acanthatholius* is also half the size of *Hoplorhynchus gracilis* Hoshide, 1954 [15] and has a different oocyst structure.

Table 1. Population dynamics of *Hoplorhynchus acanthatholius* infecting five populations of *Enallagma civile* in Nebraska.[a]

	Nevins Tank	Lake Ogallala	Oak Lake	Beckius Pond	Dunwoody Pond
Prevalence	0.67	0.47	0.60	0.31	0.24
Intensity	2–67	1–100	1–150	2–50	3–99
Mean					
Intensity	9.10 (14.09)	28.56 (29.81)	16.41 (24.31)	16.5 (22.83)	42.13 (35.21)
Abundance[b]	6.06 (12.21)	13.53 (24.38)	9.87 (20.46)	5.08 (13.90)	9.91 (24.33)
n (hosts)	30	38	138	13	34

[a] Where appropriate, standard deviations are presented parenthetically below means.

[b] The abundance of *H. acanthatholius* is not significantly different among collecting sites (ANOVA $F = 0.72$ [4,248], $\alpha = 0.05$).

Although similar in shape to those of *Hoplorhynchus ramidigitus* Sarkar and Haldar, 1980 [23], the oocysts of *H. acanthatholius* are more strongly concave. Trophozoite shape and epimerite structure differ markedly between these two species.

Association and syzygy of *H. acanthatholius* are nearly identical to that of *Nubenocephalus nebraskensis* Clopton, Percival and Janovy, 1993 [7]. No significant difference in the formation of associations or progression of syzygy was observed.

Enallagma civile adults were sampled from all five collecting sites. Cardinal indicators of *H. acanthatholius* population dynamics in five populations of Nebraska *E. civile* are presented in Table 1. *Hoplorhynchus acanthatholius* was recovered from *E. civile* naiads sampled from all five collecting sites.

This is the first gregarine from North American odonates assigned to the genus *Hoplorhynchus.*

Steganorhynchus n. g.

Diagnosis. Eugregarinida Léger, 1892, sensu strictu Levine, Corliss, Cox, Deroux, Grain, Honigberg, Leedale, Loeblich, Lom, Lynn, Merinfeld, Page, Poljansky, Sprague, Vavra, and Wallace, 1980; Septatina Lankester, 1855, sensu strictu Levine, Corliss, Cox, Deroux, Grain, Honigberg, Leedale, Loeblich, Lom, Lynn, Merinfeld, Page, Poljansky, Sprague, Vavra, and Wallace, 1980; Actinocephalidae Léger, 1892, Menosporinae sensu strictu Léger, 1892. Oocysts are axially asymmetric, biconical, crescentic, without spines or thickenings at their poles, compressed in the plane perpendicular to the major axis. The epimerite of *Steganorhynchus* is set on a long vermicular stalk, terminating in an ovoid papilla enclosed in a retractable globular sheath.

Etymology. The generic name is derived from the Greek, *steganos* meaning sheathed and *rhynchos* meaning snout and is given to mark the nature of the epimerite.

Remarks. *Steganorhynchus* is clearly a member of the family Actinocephalidae as defined by Levine [19] in that the epimerite is symmetrical, association is late and leads directly to syzygy, and the gametocysts are without sporoducts. The placement of this genus at the subfamily level is more problematic and requires a reconsideration of current subfamily diagnoses.

Léger [17] was the first worker to recognize family groups among the gregarines and established 10 families based on oocyst morphology. Among these families were the 3 taxa now constituting the subfamilies of Actinocephalidae: Actinocephalinae, Acanthosporinae and Menosporinae. Léger [17] recognized that each of these taxa was united by a unique oocyst morphology: axially symmetrical and without spines (Actinocephalinae); axially symmetrical and spined (Acanthosporinae); and, axially asymmetrical, crescentic and without spines, compressed in the plane perpendicular to the major axis (Menosporinae). The diagnoses of these taxa have expanded through the revisions of several authors. In his 1899 review of the Sporozoa, Labbé [16] combined the shared the epimerite and oocyst characters of *Menospora* Léger, 1892 and *Hoplorhynchus* Carus, 1863 to redefine Menosporidae. Ellis [9] chose to lump crescentic spores with biconical spores and redefined Actinocephalidae to include Menosporidae. Watson [26] recognized these oocyst differences and resurrected Menosporidae as a monotypic family diagnosed with the characters of the type genus, *Menospora.* Later authors returned *Hoplorhynchus* to the menosporids and propagated Watson's redefinition of Menosporidae even though her definition functionally synonymized Menosporidae and *Menospora.*

The current rank of Actinocephalinae, Acanthosporinae and Menosporinae within Actinocephalidae reflects the work of Grassé [13]; who adopted the definition of Menosporidae sensu Watson and placed *Hoplorhynchus* within Menosporinae. Levine [19] provides the latest review of the group. He retains Grassé's definitions and places both *Hoplorhynchus* and *Odonaticola* within Menosporinae. Although these reviews adopt Menosporinae sensu Watson, it is clear that Menosporinae sensu Léger is used as the functional definition of the taxon. Menosporinae sensu Watson is clearly equivalent to *Menospora* sensu Léger and is in error. Menosporinae sensu Léger (oocysts axially asymmetric, crescentic and smooth, compressed in the plane perpendicular to the major axis) is the correct functional definition and is adopted here.

The crescentic oocysts of *Steganorhynchus* unite this taxon with those of Menosporinae sensu strictu Léger, 1892. The four named genera of Menosporinae, *Menospora, Hoplorhynchus, Odonaticola* and *Domadracunculus* are separated by unique structure features of their epimerites. The epimerite of *Steganorhynchus* is fundamentally different from those of existing genera. *Menospora* possess a cupule bordered with recurved hooks [17], *Hoplorhynchus* possess a flattened bulb bordered anteriorly with digitations or spines [4], *Odonaticola* possess a hat-shaped or umbrelliform disk with a margin of petaloid spines [24], and *Domadracunculus* possess a distinctly pleated cup or sucker, without anterior digitations or a corona of hooks [5]. *Steganorhynchus* lacks epimerite hooks, digitations, spines or pleated suckers of any kind, distinguishing all existing genera from the new genus. The ovoid papilla enclosed in a retractable globular sheath is a fundamental epimerite structure unique to *Steganorhynchus* and diagnostic of the genus.

Steganorhynchus dunwoodyi n. sp.

Diagnosis. Actinocephalidae (Menosporinae) with the characters of the genus: epimerite set on a long vermicular stalk, terminating in an ovoid papilla enclosed in a retractable, globular sheath.

Trophozoite. (Fig. 6–8) Protomerite very broadly ovoid; length 48.0–**78.6**–105.6 (±13.3); width 57.6–**94.7**–153.6 (±18.1). Deutomerite obvoid; length 105.6–**272.4**–499.2 (±80.1); total length 163.2–**350.7**–604.8 (±90.0). The junction between the protomerite and deutomerite is broadly constricted. Indices: LP:TL 0.15–**0.23**–0.35 (±0.04); LD:TL 0.65–**0.77**–0.85 (±0.04); LP:LD 0.18–**0.30**–0.55 (±0.06); WP:WD 0.73–**0.89**–1.22 (±0.08); (n = 68). Epimerite an ovoid papilla enclosed in a retractable globular sheath, set on end of long vermicular stalk. Nucleus elliptoid, typically mesad in anterior half of deutomerite; diam 35.0. Trophozoites solitary.

Association. Association late and ephemeral, leading directly to syzygy, latero-associative while caudally enrobed in the paratrophic membrane. Gamonts in association laterally fused,

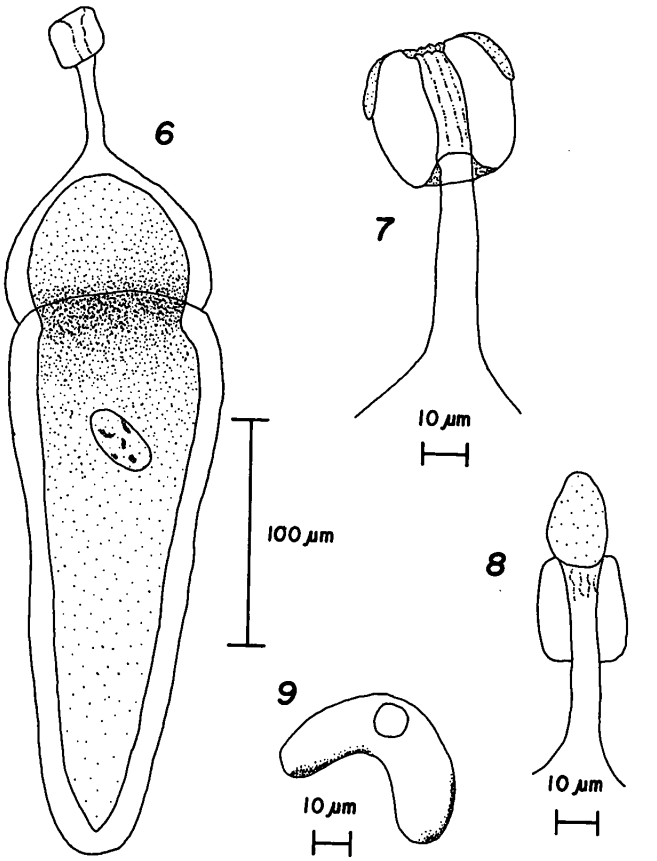

Fig. 6–9. *Steganorhynchus dunwoodyi* n. g., n. sp. 6. Trophozoite. 7. Sheathed epimerite (detail). 8. Unsheathed epimerite (detail). 9. Oocyst.

similar in shape to trophozoite but nearly twice as broad; epimerite absent.

Gametocysts. Spherical and white; diam approximately 258. Gelatinous coat increased diam to approximately 315. Gametocysts held in water typically sporulated and dehisced by rupture within 48–72 h of collection.

Oocysts. (Fig. 1, 9) Axially asymmetric, biconical, crescentic, compressed in the plane perpendicular to the major axis, smooth (without spines), very uniform in size and shape. Figure 1 (A, B, C, D) indicates the dimensions measured. A, 8.8–**8.8**–8.8; B, 4.4–**4.4**–4.4; C, 11.0–**11.0**–11.0; D, 5.5–**5.5**–5.5 (n = 40).

Type host. *Ischnura verticalis*, Common Forktail Damselfly, adults.

Type locality. Oak Lake, Lancaster County, Nebraska, USA (section 14, T 10 N, R 6 E).

Specimens deposited. Holotype (one slide USNM No. 82821) deposited in the United States National Museum Helminthological Collections, Beltsville, Maryland.

Infection site. Anterior part of mesenteron between epithelium and peritrophic membrane.

Etymology. The specific epithet, *dunwoodyi*, is given in honor of Mr. Dwayne Dunwoody who graciously gave the authors permission to collect on his property.

Remarks. Our interpretations of the retractable nature of epimerites of *S. dunwoodyi* are based on observations of living trophozoites, fixed specimens, and preliminary ultrastructural studies of the host-parasite interface. Epimerites of living and fixed specimens are commonly observed in one of two states:

Table 2. Population dynamics of *Steganorhynchus dunwoodyi* infecting three populations of *Ischnura verticalis* in Nebraska.[a]

	Nevins Tank	Oak Lake	Dunwoody Pond
Prevalence	0.37	0.23	0.07
Intensity	1–251	1–35	2–22
Mean			
Intensity	50.20 (45.43)	8.63 (5.95)	8.11 (2.62)
Abundance[b]	18.73 (63.49)	1.97 (10.09)	0.56 (6.53)
n (hosts)	67	70	131

[a] Where appropriate, standard deviations are presented parenthetically below means.

[b] The abundance of *S. dunwoodyi* is significantly different among collecting sites (ANOVA $F = 15.00$ [2,265], $\alpha = 0.05$).

with the epimerite papilla fully retracted into the basal fleshy sheath (Fig. 7); and, with the epimerite papilla fully exposed, leaving the basal sheath inverted around the epimerite stalk (Fig. 8). The process of retraction was not observed in living specimens, but epimerites from living and fixed specimens were often observed in intermediate retractile stages. Preliminary ultrastructural studies reveal the differential roles of the epimerite papilla and basal sheath in formation of the host-parasite interface. The papilla attaches and interdigitates with the epicytic folds of the host epithelial cell, forcing the anterior edge of the host cell to invaginate and envelop the epimerite papilla. The basal sheath of the epimerite spreads across the surface of the attachment and neighboring host epithelial cells, interdigitating with their epicytic folds (Percival, T. J. 1992. Tissue Level Interfaces of Four Actinocephalid Gregarines and Their Coenagrionid Hosts. Thesis. University of Nebraska, Lincoln, Nebraska.) We conclude that the functional epimerite holdfasts of *S. dunwoodyi* are composed of a turgid, apical papilla and a retractile, basal sheath. These distinct structures both play a similar role as holdfast, but they may serve unrelated absorptive functions.

Association and syzygy of *S. dunwoodyi* are nearly identical to that of *N. nebraskensis* [7]. No significant difference in the formation of associations or progression of syzygy was observed.

No specimen of *I. verticalis* was collected from Lake Ogallala or Beckius Pond. Cardinal indicators of *S. dunwoodyi* population dynamics in populations of *I. verticalis* collected from Nevins Tank, Oak Lake, and Dunwoody Pond are presented in Table 2. *Steganorhynchus dunwoodyi* was recovered from *I. verticalis* naiads sampled from all three collecting sites.

Steganorhynchus dunwoodyi is the type species of the genus *Steganorhynchus*.

DISCUSSION

Differences in the population dynamics of *H. acanthatholius* and *S. dunwoodyi* among the five sites studies are probably a result of differences in the ephemerality of the sample sites. Nevins Tank, Lake Ogallala and Oak Lake are permanent water sources and are present all year long. In contrast, Beckius Pond is a flood-water pond and Dunwoody Pond is an artificial pond managed for livestock use. Beckius Pond and Dunwoody Pond are subject to large variations in structure and water level, tending to be ephemeral and unpredictable from one season to the next. This ephemerality appears to depress populations of *I. verticalis* and their parasites. *Enallagma civile* populations have colonized all five sites and there is not a significant difference

in the abundance of *H. acanthatholius* among these populations. The decreased relative abundance and increased relative intensity of *H. acanthatholius* at Dunwoody Pond indicate the presence of a localized, high-risk transmission mechanism affecting small portions of the host population. We have not identified such a transmission mechanism, but previous studies have implicated prey species as mechanical vectors of gregarine oocysts [1]. We hypothesize that Dunwoody Pond contains a colonizing prey species that acts as an efficient mechanical vector of gregarine oocysts.

This work is part of a larger, on-going survey of the gregarine fauna of New World odonates. We hope that an intensive study of this group will allow us to address a series of larger questions regarding the nature of speciation within the parasitic group and coevolution of the host-parasite guild. Taxonomic survey is the first step in this more expansive study. The work presented here represents a significant contribution, increasing to eight the number of gregarines reported from the New World odonates [5, 7–10, 22]. The group remains largely enigmatic as a result of simple neglect, but focused survey will quickly expose the taxonomic diversity of the group in the New World. Our work with gregarines parasitizing odonates provides a case example. *Actinocephalus brachydactylus* Ellis, 1913, *Prismatospora evansi* Ellis, 1914, and *Geneiorhynchus aeschnae* Crawley, 1907 were all described in the 7 year period from 1907–1914. An hiatus of over 60 years passed before serious taxonomic survey work was reinitiated on gregarines of North American odonates: the remaining 5 known species have been described within the last 6 years. We also expect to see important biogeographical trends emerge as our recovery rate for Nearctic gregarine species increases. Among the gregarines parasitizing Nearctic odonates, only *G. aeschnae* has been confirmed as an Holarctic species. This species is reported from larval aeschnids in Michigan and Pennsylvania [8, 9], and from nine out of 22 larval aeschnids sampled in Bavaria, Germany [11]. As this survey progresses, we expect to recover additional species originally described from the Old World. It is likely that a diverse gregarine fauna remains to be discovered within the New World odonates. With increased taxonomic survey, we expect to expand our knowledge of the diversity, distribution, and relationships of Eugregarinorida.

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