# REVISION OF THE GENUS XIPHOCEPHALUS AND DESCRIPTION OF XIPHOCEPHALUS ELLISI N. SP. (APICOMPLEXA: EUGREGARINIDA: STYLOCEPHALIDAE) FROM ELEODES OPACUS (COLEOPTERA: TENEBRIONIDAE) IN THE WESTERN NEBRASKA SANDHILLS

# R. E. Clopton

Division of Science and Technology, Peru State College, Peru, Nebraska 68421

ABSTRACT: Xiphocephalus is revised, clarifying diagnosis of the epimerite complex, gametocyst, and oocyst. Xiphocephalus ellisi n. sp. (Apicomplexa: Eugregarinida) is described from Eleodes opacus (Coleoptera: Tenebrionidae) collected from Keith County in the Sandhills of western Nebraska. Measurements are means in micrometers. Developing trophozoites solitary; epimerite a complex of terminal epimerite and intercalating diamerite; epimerite elongate, ensiform, with transverse basal tumidus, length 2–3 times width of basal tumidus; width approximately half that of basal tumidus; tumidus toroidal, concavoconcave in anterioposterior axis; diamerite roughly cylindrical, no longitudinal fold apparent, length approximately twice width. Association late, frontal, isogamontic. Protomerite depressed ovoid, length 84.1, width 114.9, anterior distance to widest point 50.8. Protomerite—deutomerite septum clearly marked and constricted, width 99.3. Deutomerite narrowly obovoid, length 1,094.0, maximum width 197.0, anterior distance to widest point 137.8, equatorial width 163.3. Total length 1,204.4. Nucleus ellipsoid, length 64.9, width 42.2; typically with 2–3 polysomal endosomes. Gametocysts roughly spherical, length 376.1, width 348.2, wall paperlike, papillated, dehiscing by simple rupture, releasing oocysts in coiled chains, epispore packet absent, gametocyst residuum present. Oocysts brown to black, broadly deltoid, gibbous in lateral aspect, slightly keeled in dorsal aspect, length 9.7, height 8.5; with terminal protuberances and a single, central, spherical residuum.

The family Stylocephalidae comprises 15 genera and 90 species united by the form and color of the oocyst and the structure and development of the gametocyst. Known species are described primarily from tenebrionid beetles. The genera Lepismatophila Adams and Travis, 1935, and Colepismatophila Adams and Travis, 1935, are reported only from Thysanura and their oocysts are aberrant, thus it is not clear that their placement among Stylocephalidae is correct. Stylocephalus Ellis, 1912, and Xiphocephalus Théodoridès, 1963, are among the most speciose genera in the family, encompassing over half of the family's known diversity. At least 2 generic definitions of Xiphocephalus are currently in use, and although Xiphocephalus have been reported in Old World tenebrionid beetles from Europe (Blanchard, 1905; Théodoridès, 1954; Tuzet and Ormières, 1955, 1956), Africa (Théodoridès et al., 1965), and India (Devdhar and Amoji, 1977; Patil and Amoji, 1985), no type or voucher specimen is available to support a named species. No species is reported from the Nearctic, but little survey activity among Nearctic Stylocephalidae has been reported since Xiphocephalus was erected.

During an on-going biotic survey of the gregarine parasites of North American insects, a heretofore unknown gregarine species was discovered in populations of *Eleodes opacus* (Say, 1824) (Insecta: Coleoptera: Tenebrionidae: Eleodiini) in the Sandhills region of western Nebraska. The gregarine populations recovered are taxonomically distinct from known gregarine species and represent a new species of *Xiphocephalus* Théodoridès, 1963.

The taxonomy of Stylocephalidae is confused and chaotic but exemplifies the fundamental, generalized problem of gregarine taxonomy. Gregarine taxonomic diagnosis usually depends upon comparative morphometric analysis. The utility of such a comparison depends upon the developmental stability of the measurements chosen and the degree to which such measurements actually reflect the complex shape of the organism. The current system of gregarine morphometric analysis utilizes a rudimentary character set that inadequately describes gregarine

shape. Additionally, ontogenetic stages (trophozoites, sporonts, and gamonts) are not always readily discriminated. Measurements can be taken from all 3 stages separately, but usually measurements are reported from mixed populations, accentuating developmental variation and exacerbating an already difficult task.

The developmental stability of morphometric characters is a critical issue for gregarine taxonomy. Measurements taken from sporonts and gamonts are relatively stable because these are mature specimens. Measurements taken from trophozoites or mixed populations are inherently nondiscriminating because they are based on a changing population; the resulting morphometrics are confounded by continuous developmental variation within a single gregarine taxon (see Watwood et al., 1997). These problems have led to a gregarine systematic that is at best in a state of chaotic flux, e.g., Stylocephalus, and at worst impenetrable and untenable, e.g., Gregarina. The description presented herein alleviates these problems by utilizing an extended morphometric character set for gamonts of Stenophoricae, restricting analysis of continuous morphometric characters to mature or invariant stages, and standardizing discontinuous epimerite characters. In addition to introducing a more rigorous gregarine taxonomic protocol, this work revises the generic definition of Xiphocephalus and proposes a new species within the genus.

# **MATERIALS AND METHODS**

Eleodes opacus (Say, 1824) adults (n = 34) were collected from beneath cattle dung pats surrounding the stock tank at Beckius' Windmill, approximately 2 km north of Roscoe, Keith County, Nebraska, between 15 June and 28 July 1997. Locality coordinates were determined with an Eagle Explorer Global Positioning Satellite locator. Beetles were transported to the laboratory at Cedar Point Biological Station, divided into lots of 4-6 individuals each, and held in 250-ml glass culture dishes (Carolina Culture Dishes, Carolina Biological Supply Company, Burlington, North Carolina) with damp filter paper. All beetles were held for at least 6 hr for gametocyst shedding and then either preserved as permanent specimens or examined for gregarine infection within 48 hr of collection. Beetles were eviscerated and their alimentary canals dissected in insect muscle saline (Belton and Grundfest, 1962).

TABLE I. Described Xiphocephalus species, synonyms, and host records.

Xiphocephalus africanus (Théodoridès, Desportes, and Jolivet, 1965) Corbel, 1971

=Stylocephalus africanus Théodoridès, Desportes, and Jolivet, 1965 ex. Erodius granipennis Fairmaire; Kénitra\*, Morocco

Pimelia grandis Klug; Tutti Island†, Shembat†, Khartoum†, Sudan

Pimelia platynota Fairmaire; Kénitra\*, Morocco

Pimelia rotundipennis Kraatz; Kénitra\*, Morocco

Pogonobasis raffrayi Haag; Burrit, Khartoumt, Sudan

Prionotheca coronata Olivier; Tutti Island†, Shembat†, Khartoum†, Sudan

Thriptera crinita Klug; Shembat<sup>†</sup>, Khartoum<sup>†</sup>, Sudan Zophosis trilineata Olivier; Saint Louis<sup>‡</sup>, Senegal

Xiphocephalus ellisi n. sp.

ex. Eleodes opacus (Say); Keith County, Nebraska, USA Xiphocephalus gladiator (Blanchard, 1905) Corbel, 1971

- =Stylocephalus gladiator Blanchard, 1905
- =Stylocephalus gladiator Watson, 1916
- ex. Elenophorus collaris Linnaeus; Nîmes§||, France

Xiphocephalus gonocephali Patil and Amoji, 1985

ex. Gonocephalum depressum Fabricius; Dharwar#, Karnatakata, India

Xiphocephalus karnatakaensis (Devdhar and Amoji, 1977) Levine, 1984

- =Stylocephalus Xiphocephalus karnatakaensis Devdhar and Amoji, 1977
- ex. Gonocephalum hoffmannseggi Stevens; Dharwar¶, Karnataka, India

Xiphocephalus latipes Patil and Amoji, 1985

- ex. Scleron latipes (Guérin-Meneville); Dharwar#, Karnataka, India Xiphocephalus phaleriae (Tuzet and Ormières, 1955) Corbel, 1971
- =Stylocephalus phaleriae Tuzet a..d Ormiéres, 1955
- ex. Phaleria cadaverina Fabricius; Sète\*\*, France

Xiphocephalus reitterae Patil and Amoji, 1985

- ex. Scleron reitteri Gebien; Dharwar#, Karnataka, India
- Xiphocephalus serpentula (Devdhar and Amoji, 1977) Levine, 1984
  - =Stylocephalus Xiphocephalus serpentula Devdhar and Amoji, 1977
  - ex. Gonocephalum hoffmannseggi Stevens; Dharwar¶, Karnataka, India
- \* Corbel, 1971.
- † Théodoridès et al., 1965.
- ‡ Théodoridès and Jolivet, 1982.
- § Blanchard, 1905.
- || Théodoridès, 1954.
- # Patil and Amoji, 1985.
- ¶ Devdhar and Amoji, 1977.
- \*\* Tuzet and Ormières, 1955, 1956.

Permanent parasite preparations were made with wet smears of gregarines and host gut tissues (Clopton, 1996). Wet smears were fixed for 3 min in AFA (ethanol, formalin, and acetic acid [Galigher and Kozloff, 1971]), washed in 70% ethanol, stained with either Semichon's acetocarmine (Semichon, 1924) or Heidenhain's hematoxylin (Galigher and Kozloff, 1971), dehydrated in ethanol, cleared with xylene, and mounted in Damar balsam (Galigher and Kozloff, 1971). Gametocysts were extracted from collected feces and transferred into individual wells of a Miniwell® assay plate (Nunclon Miniwell® minitray plate, 60 conical, flat-bottomed, 10-µl wells; Nunclon #439225, Nalge Nunc International Corp., Rochester, New York). 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 in agar monolayer mounts prepared as follows. Molten agar (1.5% solution) was pipetted onto a clean glass slide and 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. 5 µl) 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. The monolayer technique provides a uniform object plane well suited for light microscopy with dry or oil-immersion objectives.

Observations were made with an Olympus B-Max 50 compound microscope with 20×, 40×, and 100× universal planapochromatic objectives and either phase contrast condensers or differential interference contrast prisms. Digital photographs were taken with an AGFA ActionCam digital camera through the aforementioned microscope with either a green density filter (phase contrast condensers) or a neutral density filter (differential interference contrast prisms and condenser). Measurements were taken from digitized images of live specimens with BioScan® Optimas® v 4.1 image analysis software (BioScan Inc., Edmonds, Washington). Drawings were made with the use of digitized images of live and fixed specimens. Photographic plates were processed and assembled with Adobe® Photoshop® 4.0 software (Adobe Systems, Inc., San Jose, California).

Morphometric measurements taken were those depicted in Figures 1 and 2. Measurements (in micrometers) are presented as range values followed by means, standard deviations, and sample sizes in parentheses. Terminology for parasite ontogenetic stages and anatomy largely follows that proposed by Levine (1971). Filipponi (1949) recognized 2 distinct components comprising an epimerite complex in *Stylocephalus*: the terminal epimerite or holdfast proper and the diamerite, an intercalating neck or stalk between the epimerite and the protomerite. Filipponi's (1949) epimerite complex terminology is adopted herein. Terminology for shapes of planes and solids is consistent with that suggested by the Systematics Association Committee for Descriptive Biological Terminology (Anonymous, 1962). Additional terminology is derived from Harris and Harris (1994).

## **DESCRIPTION**

# Xiphocephalus Théodoridès, 1963

Stylocephalus (Xiphocephalus) Théodoridès, 1963 Stylocephalus Ellis, 1912, pro parte

#### **Revised diagnosis**

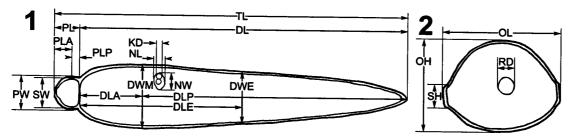
Eugregarinida Léger, 1892, sensu strictu Levine et al. (1980); Septatina Lankester, 1885, sensu strictu Levine et al. (1980); Stenophoricae Levine, 1984, sensu Chakravarty, 1960; Stylocephalidae Ellis, 1912, with the characters of the genus *Xiphocephalus* Théodoridès, 1963, amended as follows: epimerite complex elongated into a cylindrical, often filiform diamerite, expanding terminally to form the epimerite proper; epimerite elongated into a xiphoid process (including deltoid, ensiform, lanceolate, and gladiate forms), terminating in a sharp or rounded point; gametocysts papillate, with internal pseudocyst residuum; oocysts axially asymmetric, broadly deltoid, gibbous in lateral aspect, slightly keeled in dorsal aspect (including hat-, purse-, stone-, and seed-shaped of previous authors), emerging in chains.

#### Taxonomic summary

Type species: Xiphocephalus gladiator (Blanchard, 1905) Corbel, 1971.

# Remarks

Théodoridès (1963) defined 3 subgenera within Stylocephalus: Stylocephalus (Conicocephalus), Stylocephalus (Stylocephalus), and Stylocephalus (Xiphocephalus), using the specific form of the epimerite proper to distinguish each of the 3 taxa. He also noted strong correlation between the shape of the epimerite proper and the general form of the diamerite. Stylocephalus (Conicocephalus) is characterized by a broad, conical diamerite terminating in a distinctive nipple. Stylocephalus (Stylocephalus) is characterized by a cylindrical diamerite terminating in a simple sphere. Stylocephalus (Xiphocephalus) is characterized by a cylindrical, often filiform diamerite bearing a long, xiphoid, or lanceolate epimerite with a blunt or sharp apex. Corbel (1971) elevated S. (Xiphocephalus) to the generic level in his revision of the Stylocephalidae but focused his diagnosis on the filiform nature of the diamerite. He did not alter the position of S. (Conicocephalus). Subsequent authors



FIGURES 1, 2. Morphometric measurements for Stylocephalidae. 1. Trophozoite. 2. Oocyst. DL, deutomerite length; DLA, deutomerite length anteriad greatest width; DLE, deutomerite length at equator (½ DL); DLP, deutomerite length posteriad greatest width; DWE, deutomerite width at equator; DWM, deutomerite greatest width; KD, karyosome diameter; NL, nucleus length; NW, nucleus width; OH, oocyst height; OL, oocyst length; PLA, protomerite length anteriad greatest width; PLP, protomerite length posteriad greatest width; PW, protomerite width; RD, residuum diameter; SH, oocyst shoulder height; SW, width at protomerite—deutomerite septum; TL, total length.

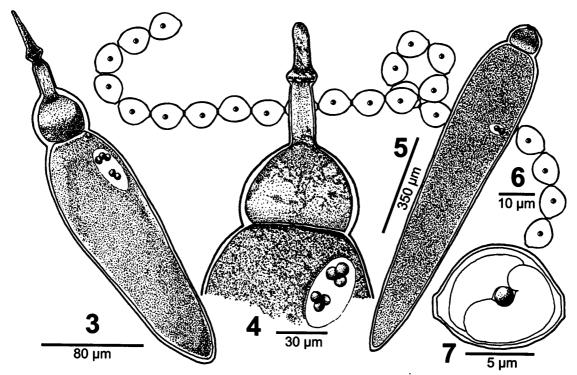
have confirmed the *Xiphocephalus* sensu strictu hypothesis, describing 5 (Devdhar and Amoji, 1977; Patil and Amoji, 1985) of the genus' 6 species since Corbel (1971) elevated *Xiphocephalus*. In addition, gametocyst structure and developmental pattern and oocyst structures are consistent among known species of *Xiphocephalus*. The genus is amended here to clarify the diagnostic intent of Théodoridès (1963) and to include known gametocyst and oocyst morphology. Described species of *Xiphocephalus* are presented in Table I.

# Xiphocephalus ellisi n. sp. (Figs. 3–12)

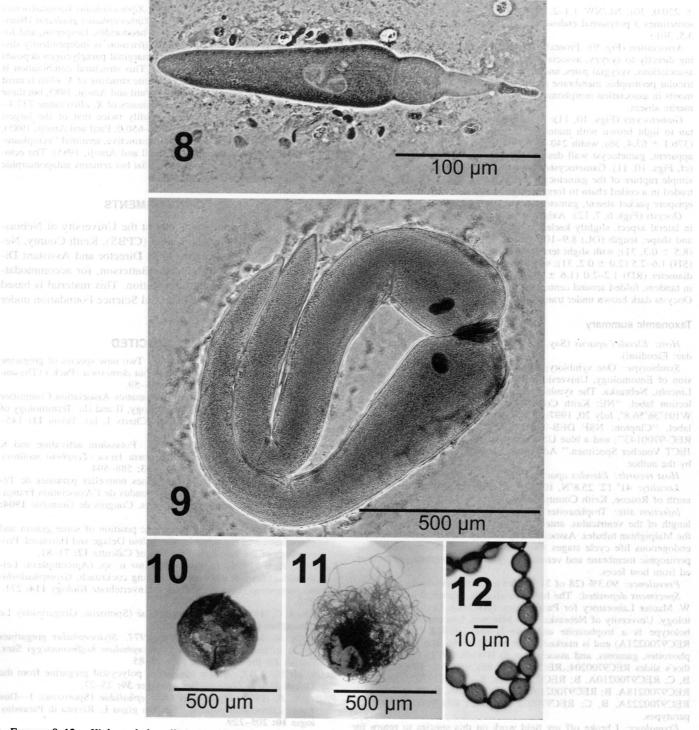
Trophozoite (Figs. 3, 4, 8): Developing trophozoites solitary (Figs. 3, 8), attached to host ventricular epithelium. Holdfast an epimerite complex of terminal epimerite and intercalating diamerite. Epimerite elongate, xiphoid (Figs. 3, 4, 8), ensiform, terminally obtuse, with transverse basal tumidus, narrowing anteriad, length 2–3 times width of basal tumidus, approximately equal that of diamerite; width approximately half that of basal tumidus, less than that of diamerite; enlarging posteriad at fusion with diamerite to form a basal tumidus; tumidus toroidal,

concavo-concave in anterioposterior axis, width approximately twice length; diamerite roughly cylindrical, tapering anteriad with distinct constriction at junction with epimerite, little or no evidence of longitudinal folds, length approximately twice width; without visible septum at junction with protomerite but clearly differentiated by decreased density of cytoplasm. Protomerite broadly ovoid to very broadly ovoid. Protomerite—deutomerite septum clearly marked and constricted. Deutomerite obovoid to narrowly obovoid, Nucleus ellipsoid to broadly ellipsoid; with 2–3 distinct polysomal endosomes.

Gamont (Fig. 5): Protomerite depressed ovoid to very broadly ovoid, length (PL) 60.3-118.6 ( $84.1\pm15.0$ , 30), width (PW) 85.3-168.7 ( $114.9\pm21.2$ , 30), PL/PW 0.6-0.9 ( $0.7\pm0.1$ , 30), anterior distance to widest point (PLA) 33.0-71.9 ( $50.8\pm9.8$ , 30), posterior distance to widest point (PLP) 19.7-52.0 ( $33.2\pm9.0$ , 30), PLA/PLP 0.7-2.9 ( $1.6\pm0.5$ , 30), PLA/PW 0.3-0.5 ( $0.4\pm0.0$ , 30), PLP/PW 0.2-0.4 ( $0.3\pm0.1$ , 30). Protomerite-deutomerite septum clearly marked and constricted, width (SW) 67.8-139.4 ( $99.3\pm16.3$ , 30), PW/SW 0.9-1.3 ( $1.2\pm0.1$ , 30). Deutomerite obovoid to very narrowly obovoid, length (DL) 150.6-1.638.3 ( $1.094.0\pm313.4$ , 30), maximum width (DWM) 101.3-10.1



FIGURES 3-7. Xiphocephalus ellisi n. sp. 3. Solitary trophozoite. 4. Protomerite and epimerite complex of trophozoite, detail. 5. Gamont. 6. Oocyst chain. 7. Oocyst with central residuum and enfolding sporozoites.



FIGURES 8-12. Xiphocephalus ellisi n. sp. 8. Holotype, trophozoite (Semichon's acetocarmine under phase contrast). 9. Gamonts in syzygy (Semichon's acetocarmine under phase contrast). 10. Gametocyst with papillated epicyst wall, 24 hr. 11. Gametocyst dehiscence, 72 hr. 12. Chain of oocysts, each with a single central residuum (agar oocyst monolayer under differential interference contrast).

303.8 (197.0  $\pm$  45.4, 30), anterior distance to widest point (DLA) 49.8–419.0 (137.8  $\pm$  67.6, 30), posterior distance to widest point (DLP) 27.1–1,425.7 (956.1  $\pm$  281.7, 30), equatorial width (DWE) 113.1–255.6 (163.3  $\pm$  34.3, 30), anterior distance to equatorial plane (DLH) 349.8–830.2 (559.5  $\pm$  129.9, 30), DL/DWM 1.5–7.7 (5.5  $\pm$  1.1, 30), DWM/DWE 0.9–1.3 (1.2  $\pm$  0.1, 30), DLA/DWM 0.4–1.4 (0.7  $\pm$  0.2, 30), DLP/DWM 0.3–7.0 (4.8  $\pm$  1.2, 30), DLH/DWE 2.7–4.8 (3.5  $\pm$  0.6,

30), DWM/SW 1.3–2.5 (2.0  $\pm$  0.3, 30), DWE/SW 1.3–2.1 (1.6  $\pm$  0.2, 30). Total length (TL) 737.4–1,756.8 (1,204.4  $\pm$ 272.8, 30). Indices: PL/TL 0.1–0.1 (0.1  $\pm$  0.0, 30), PL/DL 0.1–0.5 (0.1  $\pm$  0.1, 30), PW/DWM 0.5–0.9 (0.6  $\pm$  0.1, 30), PW/DWE 0.6–0.9 (0.7  $\pm$  0.1, 30), DL/TL 0.1–1.0 (0.9  $\pm$  0.1, 30). Nucleus ellipsoid, typically abaxial; length (NL) 38.2–86.8 (64.9  $\pm$  11.6, 30), width (NW) 21.1–66.8 (42.2  $\pm$  10.5, 30), distance to protomerite–deutomerite septum (NDS) 24.9–981.5 (201.9

 $\pm$  220.0, 30), NL/NW 1.1–2.1 (1.6  $\pm$  0.2, 30); typically with 2 but sometimes 3 polysomal endosomes, diameter (KD) 11.9–26.5 (17.2  $\pm$  3.5, 30).

Association (Fig. 9): Frontal; isogamontic; late and ephemeral; leading directly to syzygy, associated pairs fusing laterally during syzygy; associations, syzygial pairs, and gametocysts located between host ventricular peritrophic membrane and posterior ventricular epithelium. Gamonts in association morphometrically similar to solitary gamonts; epimerite absent.

Gametocysts (Figs. 10, 11): White to opalescent in color, becoming tan to light brown with maturity; roughly spherical; length 285-480 (376.1  $\pm$  63.4, 36), width 240-470 (348.2  $\pm$  63.9, 36); no hyaline coat apparent, gametocyst wall desiccating to become paperlike, papillated (cf. Figs. 10, 11). Gametocysts mature within 48-72 hr and dehisce by simple rupture of the gametocyst walls (Figs. 10, 11). Oocysts are extruded in a coiled chain to form a single, tangled, sticky mass (Fig. 11); epispore packet absent, gametocyst residuum present.

Oocysts (Figs. 6, 7, 12): Axially asymmetric, broadly deltoid, gibbous in lateral aspect, slightly keeled in dorsal aspect, very uniform in size and shape; length (OL) 8.9-10.3 ( $9.7\pm0.3$ , 31), height (OH) 7.8-9.1 ( $8.5\pm0.3$ , 31); with slight terminal protuberances or shoulders, height (SH) 1.6-2.5 ( $2.0\pm0.2$ , 31); with a single, central, spherical residuum, diameter (RD) 1.2-2.0 ( $1.6\pm0.2$ , 31); octozooic, sporozoites resting in tandem, folded around central residuum. Extruded in chains (Fig. 7). Oocysts dark brown under transmitted light, black under reflected light.

### **Taxonomic summary**

Host: Eleodes opacus (Say, 1824) (Insecta: Coleoptera: Tenebrionidae: Eleodiini).

Symbiotype: One symbiotype specimen is deposited with the Division of Entomology, University of Nebraska State Museum (UNSM), Lincoln, Nebraska. The symbiotype is identified with 3 labels: a collection label, "NE: Keith Co.; Cedar Point Biol Stn, N41°12′25.8" W101°36′56.8", July 20, 1997: R. E. Clopton, coll."; a NSF deposition label, "Clopton: NSF DEB-9705179, NSF PROJECT VOUCHER, REC-9700143"; and a blue UNSM voucher label "RESEARCH PROJECT Voucher Specimen." Additional voucher specimens are retained by the author.

Host records: Eleodes opacus; adults.

Locality: 41° 12′ 25.8″N, 101° 36′ 56.2″W, Beckius Windmill, 2 km north of Roscoe, Keith County, Nebraska.

Infection site: Trophozoites and gamonts were observed along the length of the ventriculus, anterior to the ileum and the attachment of the Malpighian tubules. Associations primarily located in the ileum. All endogenous life cycle stages were observed between host ventricular peritrophic membrane and ventricular epithelium. Gametocysts collected from host feces.

Prevalence: 90.3% (28 of 31 beetles examined postmortem).

Specimens deposited: The holotype slide is deposited in the Harold W. Manter Laboratory for Parasitology (HWML), Division of Parasitology, University of Nebraska State Museum, Lincoln, Nebraska. The holotype is a trophozoite on slide HWML 39724 (author's slide REC9700221A) and is marked by an etched circle. The remaining trophozoites, gamonts, and associations in HWML 39725 (28 slides, author's slides REC9700204; REC9700205; REC9700206; REC9700209A, B, C; REC9700210A, B; REC9700215A, B, C; REC9700216A, B, C; REC9700218A, B; REC9700221B; REC9700222A, B, C; REC9700229A, B) are paratypes.

Etymology: I broke off my field work on this species to return for the birth of my first child and completed the work during the first weeks of his life. The specific epithet is given in honor of my son, Ellis Teague Clopton, who followed me to Cedar Point Biological Station to collect beetles when he was 1 wk old.

# Remarks

Xiphocephalus ellisi is the first species of Xiphocephalus described from the New World. Gamonts of X. ellisi possess an ovoid to elongate ovoid deutomerite that is distinct from the serpentine deutomerites of Xiphocephalus serpentula Devdhar and Amoji, 1977, and Xiphocephalus gonocephali Patil and Amoji, 1985. The ensiform nature of the epimerite proper distinguishes X. ellisi from species with cordate (Xiphocephalus gonocephalus gonocephalus

ocephalus latipes Patil and Amoji, 1985; Xiphocephalus karnatakaensis Devdhar and Amoji, 1977) or gladiate (Xiphocephalus gladiator [Blanchard, 1905]; Xiphocephalus africanus Théodoridès, Desportes, and Jolivet, 1965) epimerites. Xiphocephalus africanus is independently distinguished by a diamerite with distinct marginal paraglycogen deposits bordering an agranular central channel. This structural combination is not observed among X. ellisi. The epimerite structure of X. ellisi is most similar to that of Xiphocephalus reitteri Patil and Amoji, 1985, but these taxa are morphometrically disparate. Gamonts of X. ellisi range 737.4–1,756.8, their average length being readily twice that of the largest reported gamont of X. reitteri (TL 545.0–650.0; Patil and Amoji, 1985). Xiphocephalus reitteri also possesses a distinctive, terminal "ectoplasmic tail" that is retained into syzygy (Patil and Amoji, 1985). The ectoplasmic tail does not occur among X. ellisi but remains autapomorphic for X. reitteri.

#### **ACKNOWLEDGMENTS**

I appreciate the use of facilities at the University of Nebraska's Cedar Point Biological Station (CPBS), Keith County, Nebraska. Special thanks to the CPBS Director and Assistant Director, John Janovy, Jr., and Mary Batterson, for accommodating my wife and new son at the station. This material is based upon work supported by the National Science Foundation under grant DEB-97-05179.

#### LITERATURE CITED

- ADAMS, J. A., AND B. V. TRAVIS. 1935. Two new species of gregarine protozoa from the firebrat, *Thermobia domestica* (Pack.) (Thysanura). Journal of Parasitology 11: 56-59.
- Anonymous. 1962. Report of the Systematics Association Committee for Descriptive Biological Terminology, II and IIa. Terminology of simple symmetrical plane shapes (Charts 1, la). Taxon 11: 145–155, 245–247.
- Belton, P., and H. Grundfest. 1962. Potassium activation and K spikes in muscle fibers of mealworm larva (*Tenebrio molitor*). American Journal of Physiology 203: 588-594.
- BLANCHARD, L. F. 1905. Deux grégarines nouvelles parasites de Ténébrionides des Maures. Comptes rendus de l'Association Française pour l'Avancement des Sciences, Congrès de Grenoble 1904: 923-928.
- CHAKRAVARTY, M. M. 1960. Systematic position of some genera and classification of the suborder *Cephalina* Delage and Hérouard. Proceedings of the Zoological Society of Calcutta 12: 71-81.
- CLOPTON, R. E. 1996. Leidyana migrator n. sp. (Apicomplexa: Leidyanidae) from the Madagacar hissing cockroach, Gromphadorhina portentosa (Insecta: Blattodea). Invertebrate Biology 114: 271–278.
- CORBEL, J. C. 1971. Les Stylocephalidae (Sporozoa, Gregarinida). Le Naturaliste Canadien 98: 1-39.
- DEVDHAR, M. J., AND S. D. AMOJI. 1977. Stylocephalus gregarines found in tenebrionid beetle, Gonocephalum hoffmannseggi Stev. Archiv für Protistenkunde 119: 75-85.
- ELLIS, M. M. 1912. A new species of polycystid gregarine from the United States. Zoologischer Anzeiger 39: 25-27.
- FILIPPONI, A. 1949. Studi sugli *Stylocephalidae* (Sporozoa): I—Due nuovi stilocefalidi parassiti di *Blaps gigas* L. Rivista di Parassitologia **10:** 205–229.
- GALIGHER, A. E., AND E. N. KOZLOFF. 1971. Essentials of practical microtechnique, 2nd ed. Lea and Febiger, Philadelphia, Pennsylvania, 531 p.
- HARRIS, J. G., AND M. W. HARRIS. 1994. Plant identification terminology: An illustrated glossary. Spring Lake Publishing, Payson, Utah, 198 p.
- LANKESTER, E. R. 1885. Protozoa. *In* The encyclopedia britannica, 9th ed., Vol. 19, T. S. Baynes (ed.). J. M. Stoddard Co., Ltd., Philadelphia, Pennsylvania, p. 831–865.
- Léger, L. 1892. Recherches sur les Grégarines. Tablettes Zoologique 3: 1-182.
- LEVINE, N. D. 1971. Uniform terminology for the protozoan subphylum Apicomplexa. Journal of Protozoology 18: 352–355.

- 1984. Nomenclatural corrections and new taxa in the apicomplexan protozoa. Transactions of the American Microscopical Society 103: 195-204.
- ——. 1988. The protozoan phylum Apicomplexa, Vol. 1. Chemical Rubber Company Press, Inc., Boca Raton, Florida, 203 p.
- ——, J. O. CORLISS, F. E. C. COX, G. DEROUX, J. GRAIN, B. M. HONIGBERG, G. F. LEEDALE, J. R. LOEBLICH III, J. LOM, D. LYNN, E. G. MERINFELD, F. C. PAGE, G. POLJANSKY, V. SPRAGUE, J. VAVRA, AND F. G. WALLACE. 1980. A newly revised classification of the protozoa. Journal of Protozoology 27: 37–58.
- PATIL, C. C., AND S. D. AMOJI. 1985. Eugregarine parasites of Coleoptera from the northeast region of Karnataka. VI. Xiphocephalus spp. found in tenebrionid beetles. Archiv für Protistenkunde 129: 191-197.
- SEMICHON, L. 1924. Procédeé de coloration et de regonflement des parasites animaux. Revue de Pathologie Végétale et d'Entomologie Agricole 11: 193-195.
- THÉODORIDES, J. 1954. Description complémentaire de Stylocephalus gladiator (L. F. Blanchard 1905) (Eugregarina Stylocephalidae). Annales de Parasitologie Humaine et Comparée 29: 33-36.

- ——. 1963. A propos du genre Stylocephalus Ellis, 1912 (Eugregarina Stylocephalidae). Comptes Rendus 88° Congrès des Sociétés Savantes (Clermont-Ferrand) 11: 679–682.
- ——, I. DESPORTES, AND P. JOLIVET. 1965. Grégarines parasites de coléoptères Ténébrionides de la région de Khartoum (République de Soudan). Bulletin de l'Institut Français d'Afrique Noire 27: 139-164.
- —, AND P. JOLIVET. 1982. Sur la présence de Stylocephalus africanus Théod., Desp. et Jolivet, 1965 (Eugregarina Stylocephalidae) chez un Zophosis (Col. Tenebrionidae) du Sénégal. Annales de Parasitologie Humaine et Comparée 57: 108.
- TUZET, O., AND R. ORMIÈRES. 1955. Sur quelques Grégarines parasites de Ténebrionides. Recueil des Travaux Zoologie des Faculté des Sciences de Montpellier 1: 57-64.
- ———, AND ———. 1956. Sur quelques Grégarines de la région de Sète. Annales de Parasitologie Humaine et Comparée 31: 317–330.

  WATWOOD, S. J. JANOVY, JR., E. PETERSON, AND M. A. ADDISON, 1997.
- WATWOOD, S., J. JANOVY, JR., E. PETERSON, AND M. A. ADDISON. 1997. Gregarina triboliorum (Eugregarinida: Gregarinidae) n. sp. from Tribolium confusum and resolution of the confused taxonomic history of Gregarina minuta Ishii, 1914. Journal of Parasitology 83: 502-507.