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CLITELLOCEPHALUS AMERICANUS N. GEN., N. SP. (APICOMPLEXA: EUGREGARINIDA: GREGARINIDAE) FROM *CRATACANTHUS DUBIUS* (COLEOPTERA: CARABIDAE: HARPALINAE) IN THE NEBRASKA SANDHILLS AND *CLITELLOCEPHALUS OPHONI* N. COMB. (APICOMPLEXA: EUGREGARINIDA: GREGARINIDAE) FROM *OPHONUS PUBESCENS* (COLEOPTERA: CARABIDAE: HARPALINAE) IN SÈTE, FRANCE

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ABSTRACT: *Clitellocephalus americanus* n. gen., n. sp. (Apicomplexa: Eugregarinida: Gregarinidae) is described from *Cratacanthus dubius* (Coleoptera: Carabidae) collected from Keith County in the Sandhills of western Nebraska. *Clitellocephalus ophoni* n. comb. is redescribed using original type material from *Ophonus pubescens* (Coleoptera: Carabidae) collected in Sète, France. *Clitellocephalus* n. gen. is distinguished by a deltoid epimerite with an internal anterior obconoid structure and a basal toroidal vacuole, which is retained in gamonts. Protomerites are broadly elliptical to cylindrical; deutomerites are narrowly obovate. Association is precocious, caudofrontal, and biassociative, with the satellite protomerite engulfing the posterior end of the primite deutomerite to form an interlock. Gametocysts are spherical. Sporoducts are present but reduced and irregular in number. Oocysts are dolioform, dehiscing in chains. The species described herein are differentiated by their overall size and relative proportion of cellular structures.

Cratacanthus dubius (Beauvois, 1811) Dejean, 1829 (Coleoptera: Carabidae: Harpalinae: Harpalini) is the type species of a monotypic Neartic genus of carabid beetles. They are small animals, usually less than 15 mm, characteristically encountered under dung pats and fallen timber in the Nebraska Sandhills. During an ongoing biotic survey of the gregarine parasites of North American insects, a heretofore unknown gregarine species was discovered in populations of *C. dubius* in the southern Sandhills of western Nebraska. These gregarines are taxonomically distinct from the known gregarine species and represent a new species. At a generic level they are distinct from the known genera but have a strong morphological affinity for *Gregarina ophoni* Tuzet and Ormières, 1956.

Gregarina ophoni was described from the populations of the European strawberry ground beetle, *Ophonus pubescens* (Müller, 1776) (Coleoptera: Carabidae: Harpalinae: Harpalini), collected in Sète, France, in the early 1950s. Additional topotype specimens were collected and confirmed by the late Rene Ormières as recently as 1967. The description of the newly discovered gregarine species from *C. dubius* is accompanied by a redescription of *G. ophoni*, using type and homotype materials from Ormières' personal research collection. The descriptions presented herein use the extended gregarine morphometric set introduced by Clopton (1999), apply these characters only to mature or invariant stages, erect a new genus, and propose a new species and a new combination within that newly erected genus.

MATERIALS AND METHODS

Cratacanthus dubius adults were collected from beneath cattle dung pats in 3 localities in Keith County, Nebraska (Table I). Beetles were transported to the laboratory at Cedar Point Biological Station (CPBS), divided into lots of 4–6 individuals each, and held in 250-ml glass culture dishes 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). Permanent parasite preparations were made using wet smears of gregarines and host gut tissues fixed in ethanol, formalin, and acetic acid, stained with either Semichon's acetocarmine or Harris hematoxylin and eosin–xylol, and mounted in Damar balsam (Spectrum Laboratory Products, Inc., Gardena, California), as described by Clopton (1996, 1999, 2000).

Gametocysts were extracted from the collected feces and either transferred dry or with distilled water or 2.5% potassium dichromate to individual glass microvials (BioQuip Products, Gardena, California). Vials were sealed with white silicon stoppers, and gametocysts were held for maturation and dehiscence. Oocyst structure and dimensions were taken from fresh preparations of oocysts in agar monolayer mounts (Clopton, 1999, 2000).

The observations on gregarines infecting *O. pubescens* were taken from permanent microscope preparations prepared by Ormières. The research and survey collections of Ormières are now held in the author's private collection. The collection includes 12 slides of gregarines that Ormières identified as *G. ophoni* recovered from *O. pubescens* taken in Sète, France, between 1955 and 1973: the single-type slide upon which the original description was based; a 9-slide series collected in September 1967; 1 slide collected in March 1968; and a single slide prepared in June 1973. Three of the slides in the 1967 series appear to be stained using the periodic acid–Schiff reaction. The remainder are stained with carmine, presumably Semichon's acetocarmine as per Ormières' standard protocol (Tuzet and Ormières, 1956).

Observations were made using an Olympus B-Max 50 compound microscope with ×20, ×40, and ×100 universal planapochromatic objectives and with either phase contrast condensers or differential interference contrast prisms. Digital photographs were taken with an Olympus DP-11 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 the digitized images of preserved specimens using Image-Pro Express® v 4.0 image analysis software (Media Cybernetics, L.P., Silver Spring, Maryland). Drawings were made using digitized images of live and fixed specimens. Photographic plates were processed and assembled using Adobe® Photoshop® 5.5 software (Adobe Systems, Inc., San Jose, California).

The morphometric measurements taken largely follow those proposed by Clopton (1999), although additional metrics particular to the genus under study are also presented herein. Measurements are presented in micrometers as mean values followed by range values, standard deviations, and sample sizes in parentheses. Terminology for parasite ontogenetic stages and anatomy largely follows that proposed by Levine (1971). 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).

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TABLE I. Sample size, number of infected individuals, and prevalence of *Clitellocephalus americanus* infecting *Cratacanthus dubius* from 3 sample sites in Keith Country, Nebraska, during July and August 1998.

Site	Location	Month	n	# Infected	Prevalence (%)
Ceder Point Biological Station	41°12′44.6″N, 101°39′45.2″W	July	52	1	1.9
		August	14	7	50.0
Nevens Ranch	41°12′25.8″N, 101°25′11.7″W	July	12	0	0.0
		August	3	2	66.7
White-Tail Creek	41°13′18.2″N, 101°37′09.7″W	August	17	12	70.6
All sample sites		July	64	1	1.6
		August	34	21	61.8
		Overall	98	22	22.5

DESCRIPTION

Clitellocephalus Clopton n. gen.

(Figs. 1–40)

Diagnosis

Eugregarinida Léger, 1892, sensu strictu Levine et al. (1980); Septatina Lankester, 1885, sensu strictu Levine et al. (1980); Gregarinicae Chakravarty, 1960; Gregarinidae Labbè, 1899, with characters of the genus *Clitellocephalus* n. gen.: epimerite deltoid, basal width at the site of attachment to protomerite roughly equal to protomerite width, with an internal anterior obconoid structure and basal toroidal vacuole, retained in gamont; protomerite broadly elliptical to cylindrical; deutomerite narrowly obovate; association precocious, caudofrontal, and biassociative, the satellite protomerite engulfing the posterior end of the primite deutomerite to form an interlock; gametocysts spherical, sporoducts present but reduced, irregular in number; oocysts dolioform, dehiscing in chains.

Taxonomic summary

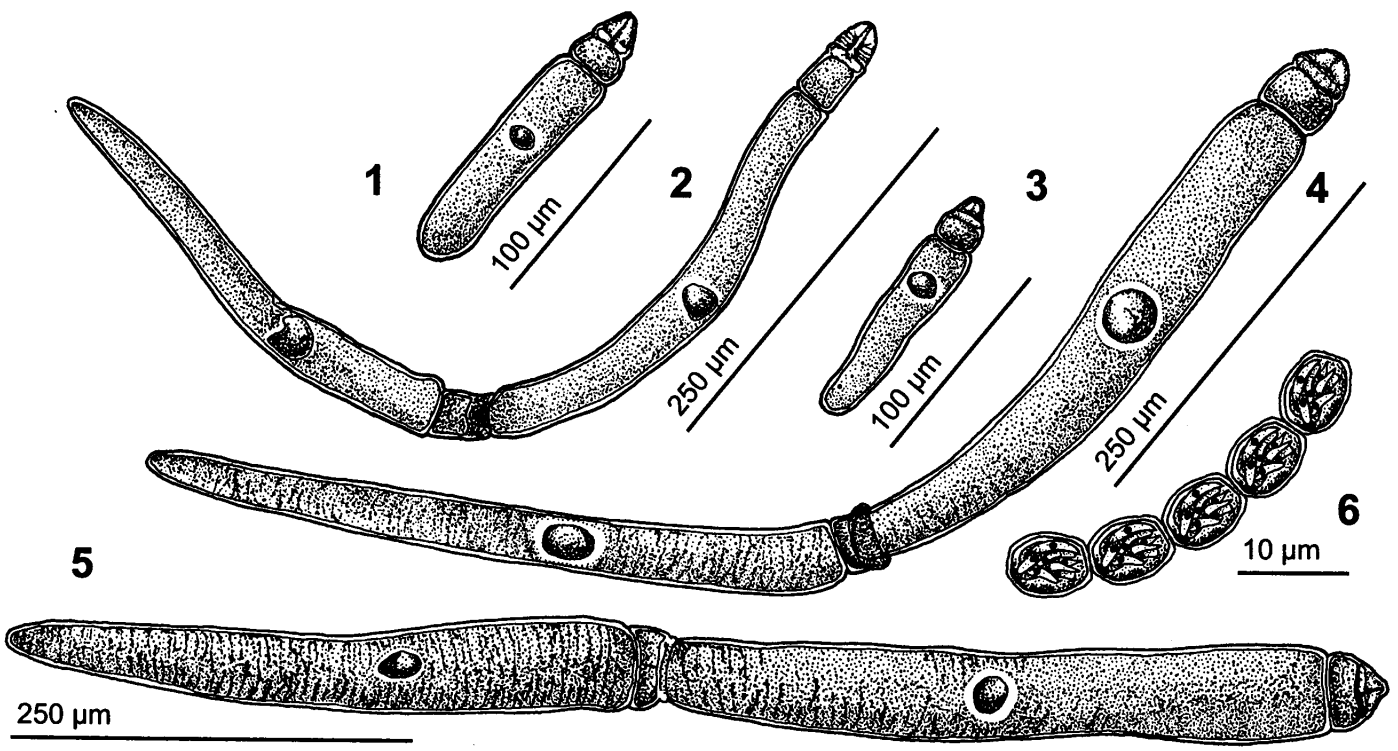
Type species: Clitellocephalus americanus n. sp.

Other described species: Clitellocephalus ophoni n. comb., syn. *Gregarina ophoni* (Tuzet and Ormières, 1956) Clopton.

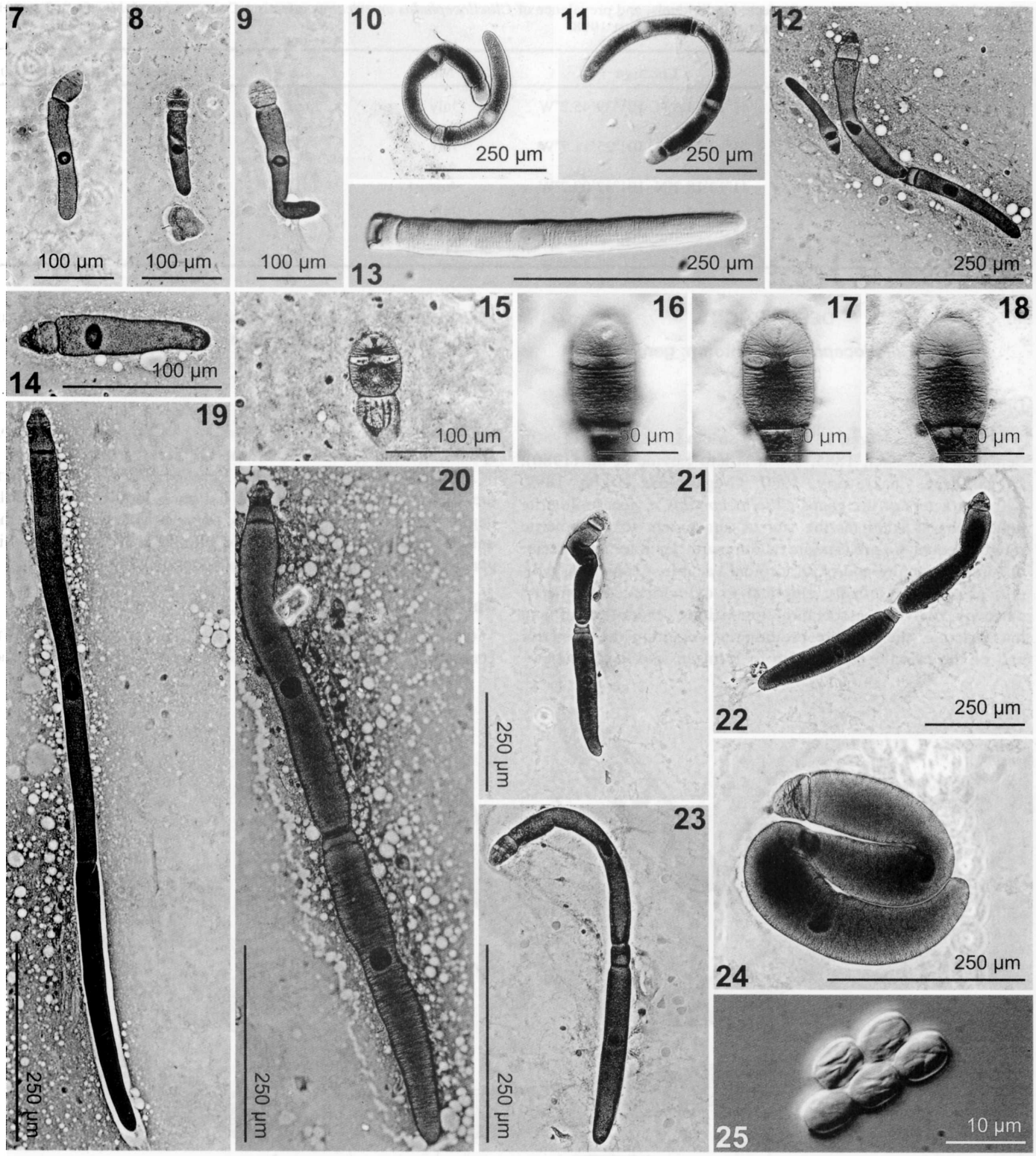
Etymology: The generic name *Clitellocephalus* is taken from the Latin root *clitella* meaning a "pack saddle" or "saddle bag." The name is given to mark the resemblance between the unique epimerite–protomerite complex that characterizes this genus and the "clitellum" of lumbriculid earthworms.

Remarks

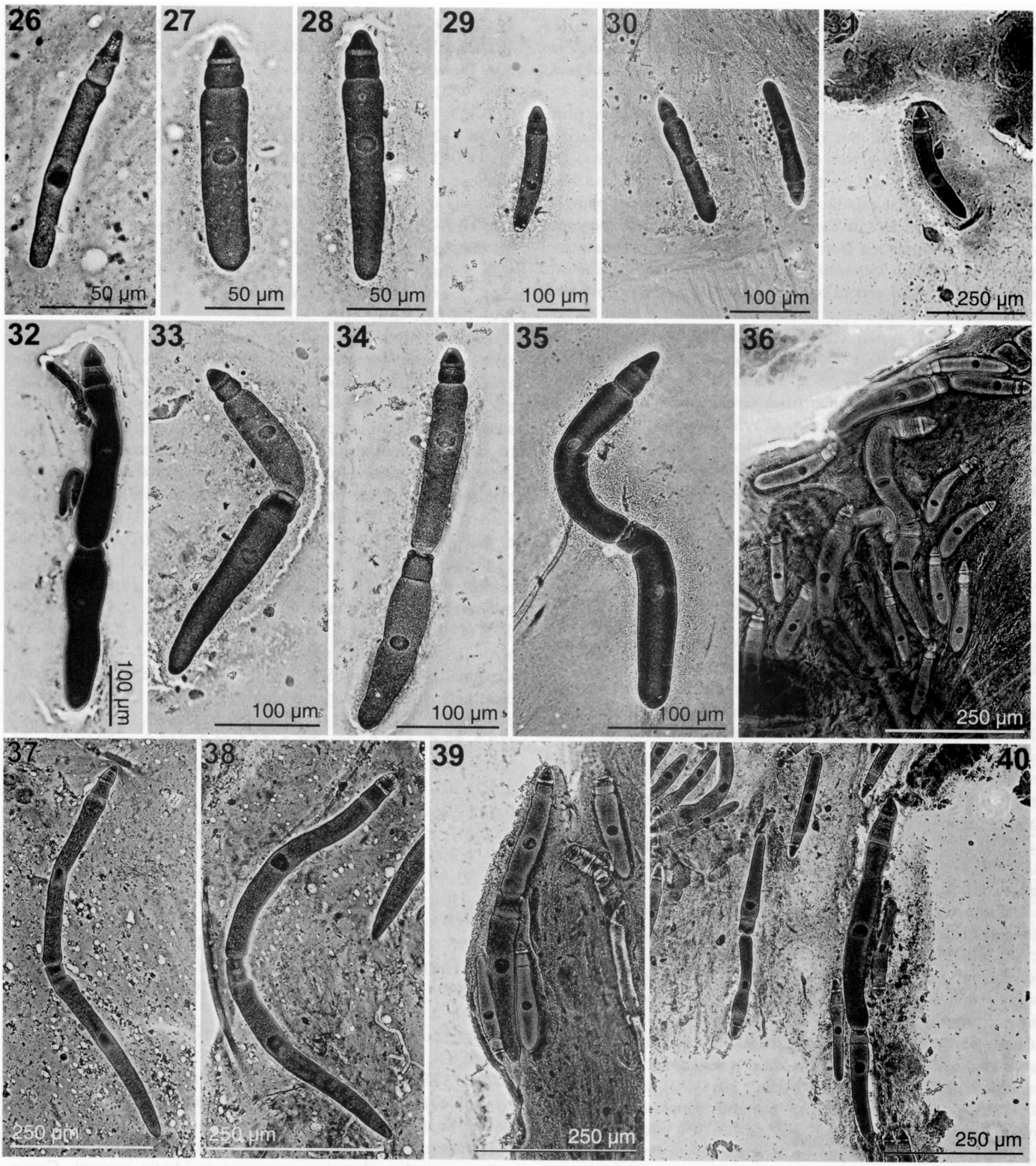
Clitellocephalus bears general resemblance to several known genera in 2 families, including *Gregarina*, *Torogregarina*, and



FIGURES 1–6. *Clitellocephalus ophoni* n. comb. and *C. americanus* n. sp. *Clitellocephalus ophoni*: **1.** Young trophozoite. **2.** Mature association. *Clitellocephalus americanus*: **3.** Young gamont. **4.** Association. Note superficial crenulation in satellite. **5.** Mature association. Note superficial crenulation. **6.** Oocysts.



FIGURES 7–25. *Clitellocephalus americanus* n. sp. **7–9.** Young solitary trophozoites. **10–12.** Trophozoites in precocious association. **13.** Trophozoitic satellite dislodged from precocious association to demonstrate the bowl-shaped nature of primite–satellite interlock. **14.** Young solitary trophozoite with clear basal toroidal vacuole. **15.** Young gamontic primite with distinct anterior obconoid structure and toroidal basal epimeritic vacuole. (Semichon's acetocarmine, phase contrast.) **16–18.** Young gamontic primite optically sectioned to demonstrate anterior obconoid structure and toroidal nature of basal epimeritic vacuole. (Semichon's acetocarmine, differential interference contrast.) **19–23.** Gamonts in association. **24.** Gamonts in early syzygy. **25.** Chains of oocysts. (Agar oocyst monolayer, differential interference contrast.)



FIGURES 26–40. *Clitellocephalus ophoni* n. comb. **26–31.** Solitary trophozoites. **32–35.** Trophozoites in precocious association. **36.** Trophozoites and associations in host gut epithelial tissue. **37–38.** Gamonts in association. **39–40.** Trophozoites and associations.

Bolivia in the Gregarinidae and *Protomagalhaenisa*, *Hyalospora*, and *Euspora* in the Hirmocystidae. Hirmocystidae is diagnosed primarily by gametocysts, which dehisce by simple rupture. Gametocyst dehiscence through sporoducts clearly places this genus among the Gregarinidae.

Individually, *Clitellocephalus* is distinguished from similar

hirmocystid genera by structural epimerite and oocyst differences among taxa. The epimerite–protomerite complex of *Protomagalhaenisa* is most similar to that described here but lacks the unique epimeritic conoid and toroidal structures (Figs. 15–18) of *Clitellocephalus*. Both genera share the distinctive primite–satellite interlock, but the oocysts of *Protomagalhaenisa* possess corner spines not observed in *Clitellocephalus*. *Hyalospora* is clearly differentiated by an epimerite in the form of a simple globular papilla. Although the cardinal trophozoite and gamont characters of *Euspora* are poorly defined, the genus is clearly distinguished from *Clitellocephalus* by prismatic oocysts. Thus, *Clitellocephalus* bears superficial resemblance to several hirmocystid genera but is clearly diagnosed at both family and generic levels.

The epimeritic structures of *Clitellocephalus* (Figs. 15, 16), consisting of an anterior obconoid structure and a basal toroidal vacuole, are observed in no other known gregarine taxon and clearly distinguish the genus from *Gregarina*, *Torogregarina*, and *Bolivia* in the Gregarinidae. *Clitellocephalus* is also distinguished by its primite–satellite interlock, although the general arrangement of the primite–satellite association is similar to that observed in *Gregarina*, *Torogregarina*, and *Bolivia*.

***Clitellocephalus americanus* Clopton n. sp.**
(Figs. 3–25)

Trophozoite: (Figs. 3, 7–14) Developing trophozoites solitary or in precocious association, attached to host ventricular epithelium. Solitary individuals similar in structure to gamontic primites but with a relatively shorter deutomerite.

Association: (Figs. 19–23) Caudofrontal, biassociative, and precocious; slightly isogamontic (protomerite–epimerite complex differences); associated pairs folding to fuse in normal syzygial motion (Fig. 24); associations, syzygial pairs, and gametocysts located between host ventricular peritrophic membrane and posterior ventricular epithelium. Data reported for mature gamonts in associations only. Association 782.6 (514.4–1,115.9, ±132.4, 30), width of primite–satellite junction (JW) 31.9 (16.4–47.6, ±7.3, 30) Primite total length–satellite total length 1.1 (0.8–1.7, ±0.2, 30).

Primite: Epimerite and protomerite form a larger protomerite–epimerite complex (PEC), length (PECL) 46.2 (31.7–57.4, ±7.4, 30) (Figs. 4, 5, 19–23), conspicuous in all stages of development. Epimerite narrowly deltoid in young gamonts to broadly deltoid in older gamonts, forming a dome or cap over the protomerite, length (EL) 22.1 (12.6–39.0, ±6.0, 30), width at base (EW) 37.1 (20.7–57.4, ±10.9, 30), with an internal anterior obconoid structure and a basal toroidal vacuole, toroidal vacuole length (EtorL) 6.3 (3.5–10.0, ±1.8, 30), width (EtorW) 37.1 (20.7–57.4, ±10.9, 30); protomerite depressed to broadly ovate, length (PL) 24.6 (16.1–36.2, ±4.3, 30), width (PW) 38.4 (22.3–51.4, ±9.6, 30), anterior distance to widest point (PLA) 15.6 (9.9–28.2, ±4.3, 30). Protomerite–deutomerite septum clearly marked, uniform with marginal constriction, width (SW) 35.8 (21.1–54.8, ±9.1, 30). Deutomerite narrowly to linearly cylindrical, tapering slightly to round posteriorly at junction with satellite, length (DL) 366.0 (229.7–573.2, ±81.7, 30), maximum width (DW) 50.4 (24.1–95.8, ±18.7, 30), anterior distance to widest point (DLA) 90.3 (11.3–249.9, ±66.2, 30). Total length (TL) 410.3 (261.3–594.5, ±85.7, 30). Indices: EL/PECL 0.5 (0.3–0.7, ±0.1, 30), PL/PECL 0.5 (0.4–0.7, ±0.1, 30), EL/EW 0.6 (0.3–1.2, ±0.3, 30), PL/PW 0.7 (0.4–1.2, ±0.2, 30), PLA/PW 0.4 (0.2–1.0, ±0.2, 30), PW/SW 1.1 (0.9–1.4, ±0.1, 32), DL/DW 8.6 (3.0–19.5, ±4.7, 30), DLA/DW 2.1 (0.2–8.3, ±2.0, 30), DL/PL 15.1 (8.8–23.7, ±3.5, 30), DW/PW 1.3 (0.9–2.0, ±0.3, 30), TL/EL 19.5 (9.7–34.8, ±5.4, 30), TL/PL 17.0 (8.6–23.7, ±3.6, 30), TL/DL 1.1 (1.0–1.3, ±0.1, 30). Nucleus narrowly elliptical to elliptical, axial, length (NL) 27.6 (19.1–41.4, ±5.2, 30), width (NW) 25.8 (8.4–157.3, ±25.6, 30), NL/NW 1.4 (0.2–3.4, ±0.6, 30), distance from protomerite–deutomerite septum (NDS) 161.9 (15.0–283.3, ±64.3, 30), with a single large, central endosome, length (KL) 14.3 (8.1–25.1, ±4.0, 30), width (KW) 11.6 (5.2–42.3, ±6.9, 30), KL/KW 1.4 (0.4–2.8, ±0.5, 30).

Satellite: Epimerite and protomerite form a larger protomerite–epimerite complex, PECL 26.4 (13.9–46.0, ±6.2, 30), the epimerite proper forming an interlock cup or mortise into which the primite deutomerite is inserted to form the interlocking association junction (Figs. 4, 5, 19–23). Epimerite very broadly to shallowly cylindrical, flaring slightly anteriad, and with a deep anterior cup or mortise pocket, the entire epimerite structure forming a dome or cap over the protomerite, EL 11.5 (5.6–16.0, ±3.0, 30), EW 24.8 (13.9–37.3, ±6.3, 30), width of pocket wall or lip (EWW) 7.3 (5.1–10.1, ±1.2, 30), anterior width of pocket (EPAW) 27.2 (14.2–41.7, ±7.2, 30), basal width of pocket (EPBW) 17.5 (8.8–31.4, ±6.1, 30). Protomerite depressed to broadly ovate, PL 15.1 (8.7–33.7, ±4.8, 30), PW 36.8 (18.4–55.3, ±8.6, 30), PLA 9.4 (2.6–17.0, ±3.0, 30). Protomerite–deutomerite septum clearly marked, uniform with marginal constriction, SW 35.8 (16.7–54.5, ±8.7, 30). Deutomerite narrowly to linearly cylindrical, tapering slightly to round posteriorly, DL 337.1 (235.4–489.5, ±64.9, 30), DW 48.6 (17.7–86.6, ±16.9, 30), DLA 56.6 (6.0–115.6, ±33.9, 30). TL 380.9 (258.4–560.6, ±73.0, 30). Indices: EL/EW 0.5 (0.2–1.1, ±0.2, 30), PL/PW 0.4 (0.2–0.9, ±0.2, 30), PLA/PW 0.3 (0.1–0.5, ±0.1, 30), DL/DW 7.7 (4.1–15.4, ±2.8, 30), DLA/DW 1.2 (0.1–3.1, ±0.8, 30), DL/PL 24.0 (10.8–38.2, ±7.4, 30), DW/PW 1.3 (1.0–1.7, ±0.2, 30), TL/EL 35.1 (19.3–58.6, ±10.0, 30), TL/PL 26.7 (12.1–38.0, ±6.9, 30), TL/DL 1.2 (1.0–2.2, ±0.3, 30). Nucleus narrowly elliptical to elliptical, axial, NL 28.3 (20.2–34.6, ±3.8, 30), NW 20.0 (12.2–37.2, ±5.7, 30), NL/NW 1.5 (0.7–2.3, ±0.4, 30), NDS 130.9 (85.5–211.0, ±31.2, 30), with a single large, central endosome, KL 13.9 (9.6–20.9, ±2.8, 30), KW 10.4 (6.0–19.6, ±2.9, 30), KL/KW 1.4 (0.8–2.1, ±0.3, 30).

Gametocysts: White to opalescent in color; roughly spherical; length (GL) 224.0 (211.8–246.9, ±10.5, 30), width (GW) 215.8 (203.6–232.4, ±7.5, 30), GL/GW 1.0 (1.0–1.1, ±0.0, 30); no hyaline coat apparent. Gametocysts stored dry matured within 48–72 hr and dehisced through small or vestigial spore ducts perforating the gametocyst wall; oocysts extruded in chains; epispore packet absent, gametocyst residuum present. Gametocysts stored in water failed to develop, whereas gametocysts stored in potassium dichromate developed oocysts but failed to dehisce.

Oocysts: (Figs. 6, 25) Axially symmetric, dolioform, very uniform in size and shape; length (OL) 6.8 (6.6–7.0, ±0.1, 30), width (OW) 5.1 (4.8–5.4, ±0.2, 30), OL/OW 1.3 (1.3–1.4, ±0.0, 30), width at terminus 2.7 (2.3–2.9, ±0.2, 30), wall thick-

ness 0.4 (0.2–0.4, ±0.1, 30); oocyst residuum absent; octozooic, extruded in chains.

Taxonomic summary

Host: Cratacanthus dubius (Beauvois, 1811) Dejean, 1829 (Coleoptera: Carabidae: Harpalinae: Harpalini).

Symbiotype: Five symbiotype specimens (author's specimens REC981198–REC981202) are deposited with the Division of Entomology, University of Nebraska State Museum (UNSM), Lincoln, Nebraska. They are identified with 3 labels: a collection label, "NE: Keith Co.; Cedar Point Biol Stn, N41°12′25.8″W101°36′56.8″, July, 26 1998: R. E. Clopton"; an NSF deposition label, "Clopton: NSF DEB-9705179, NSF PROJECT VOUCHER, REC-981XXX"; and a blue UNSM voucher label "RESEARCH PROJECT Voucher Specimen." Additional voucher specimens (MCN980094, MCN980095, MCN980118–MCN980122, REC981203–REC981258, and REC990381–REC990397) are retained in the collections of the Department of Natural Science, Peru State College, Peru, Nebraska.

Host records: Cratacanthus dubius; adults.

Localities: Cedar Point Biological Station (41°12′44.6″N, 101°39′45.2″W), Nevens Ranch (41°12′25.8″N, 101°25′11.7″W) (type locality), White-Tail Creek (41°13′18.2″N, 101°37′09.7″W), Keith County, Nebraska.

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

Prevalence: Seasonal prevalence by sample site is presented in Table I. Overall study prevalence is 22.5% (22 of the 98 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 slide HWML 16660 (author's slide REC99138) is a hapantotype, containing multiple trophozoites, gamonts, and associations. The following information appears on the hapantotype slide: left label, "*Clitellocephalus americanus*; ex. *Cratacanthus dubius*; July 8, 1999; NE: Keith Co.; (N41.12.13W101.37.15); *HAPANTOTYPE*"; right label, "*NSF Project Voucher; DEB-9705179;* REC99138; R. E. Clopton, coll." Trophozoites, gamonts, and associations on 6 slides comprising HWML 16661 (author's slides REC980427, REC980428, REC980430, REC980432, REC980435, and REC980437) are paratypes. The following information appears on these slides: left label, "*Clitellocephalus americanus*; ex. *Cratacanthus dubius*; August 1, 1998; NE: Keith Co.; (N41.12.25W101.36.56); *PARATYPE*"; right label, "*NSF Project Voucher; DEB-9705179;* REC9XXXX; R. E. Clopton, coll." Trophozoites, gamonts, and associations on 2 slides comprising HWML 16662 (author's slides REC980444 and REC980445) are paratypes. The following information appears on these slides: left label, "*Clitellocephalus americanus*; ex. *Cratacanthus dubius*; August 2, 1998; NE: Keith Co.; (N41.12.25W101.36.56); *PARATYPE*"; right label, "*NSF Project Voucher; DEB-9705179;* REC9XXXX; R. E. Clopton, coll." Trophozoites, gamonts, and associations on 2 slides comprising HWML 16663 (author's slides REC980453 and REC980454) are paratypes. The following information appears on these slides: left label, "*Clitellocephalus americanus*; ex. *Cratacanthus dubius*; August 2, 1998; NE: Keith Co.; (N41.12.26W101.25.04.); *PARATYPE*"; right label, "*NSF Project Voucher; DEB-9705179;* REC9XXXX; R. E. Clopton, coll." Trophozoites, gamonts, and associations on 10 slides comprising HWML 16664 (author's slides REC99133A–REC99133F, REC99134, REC99135, REC99137, and REC99141) are paratypes. The following information appears on these slides: left label, "*Clitellocephalus americanus*; ex. *Cratacanthus dubius*; July, 8 1999; NE: Keith Co.; (N41.12.13.W101.37.15.); *PARATYPE*"; right label, "*NSF Project Voucher; DEB-9705179;* REC9XXXX; R. E. Clopton, coll." No paratype is retained by the authors.

Etymology: The specific epithet *americanus* is given to mark the New World distribution of this species.

Clitellocephalus ophoni (Tuzet and Ormières, 1956) Clopton n. comb.

Gregarina ophoni Tuzet and Ormières, 1956 (Tuzet and Ormières, 1956)

Gregarina ophoni Tuzet and Ormières, 1956 (Geus, 1969) (Figs. 1, 2, 26–40)

Trophozoite: (Figs. 1, 26–31, 36, 40) Developing trophozoites solitary or in precocious association. Solitary individuals similar in structure to all but the most mature gamontic primites, which have a relatively longer deutomerites.

Association: (Figs. 2, 32–40) Caudofrontal, biassociative, and precocious; slightly isogamontic (protomerite–epimerite complex differences). Data reported for mature gamonts in associations only. Association length 511.9 (289.9–732.0, ±145.5, 30), JW 27.6 (17.1–43.0, ±6.8, 30) Primite TL–satellite TL 1.1 (0.8–1.4, ±0.2, 30).

Primite: Epimerite and protomerite form a larger protomerite–epimerite complex, PECL 50.2 (26.9–69.4, ±13.4, 30), conspicuous in all stages of development. Epimerite narrowly deltoid in young gamonts to broadly deltoid in older gamonts, forming a dome or cap over the protomerite, EL 27.1 (12.1–36.1, ±7.1, 30), EW 25.4 (16.1–40.4, ±5.9, 30), with an internal anterior obconoid structure and a basal toroidal vacuole, EtorL 5.9 (3.1–9.0, ±1.7, 30), EtorW 25.4 (16.1–40.4, ±5.9, 30); protomerite depressed to broadly elliptic, PL 23.6 (14.0–36.2, ±6.5, 30), PW 28.6 (18.8–47.5, ±7.1, 30), PLA 15.5 (7.9–27.2, ±5.3, 30). Protomerite–deutomerite septum clearly marked, uniform with marginal constriction, SW 26.2 (17.3–40.7, ±6.5, 30). Deutomerite narrowly to linearly cylindrical, tapering sharply to round posteriorly at junction with satellite, DL 224.1 (117.2–329.2, ±68.9, 30), DW 34.4 (24.5–51.5, ±6.8, 30), DLA 29.2 (6.1–142.8, ±30.1, 30). TL 273.2 (118.7–391.0, ±86.1, 30). Indices: EL/PECL 0.5 (0.4–0.6, ±0.0, 30), PL/PECL 0.5 (0.4–0.6, ±0.0, 30), EL/EW 1.1 (0.7–1.4, ±0.2, 30), PL/PW 0.8 (0.6–1.2, ±0.2, 30), PLA/PW 0.5 (0.3–0.9, ±0.2, 30), PW/SW 1.1 (0.9–1.4, ±0.1, 32), DL/DW 6.6 (4.0–10.1, ±1.8, 30), DLA/DW 0.9 (0.2–4.0, ±0.8, 30), DL/PL 9.5 (6.8–12.9, ±1.5, 30), DW/PW 1.2 (1.0–1.4, ±0.1, 30), TL/EL

10.0 (7.3–13.0, ±1.2, 30), TL/PL 11.5 (8.0–15.3, ±1.7, 30), TL/DL 1.2 (0.9–1.5, ±0.1, 30). Nucleus narrowly elliptical, often convex posteriad, creating the impression of a broad horse shoe, axial, NL 18.1 (10.3–30.2, ±4.7, 30), NW 18.3 (9.8–28.9, ±4.7, 30), NL/NW 1.0 (0.6–1.8, ±0.3, 30), NDS 87.8 (27.1–175.2, ±45.5, 30), with a single large, central endosome, KL 9.1 (5.2–13.6, ±2.2, 30), KW 8.8 (5.0–20.1, ±2.9, 30), KL/KW 1.1 (0.6–1.8, ±0.2, 30).

Satellite: Epimerite and protomerite form a larger protomerite–epimerite complex, PECL 28.1 (16.4–37.9, ±6.3, 30), the epimerite proper forming an interlock cup or mortise into which the primite deutomerite is inserted to form the interlocking association junction. Epimerite very broadly to shallowly cylindrical, flaring slightly anteriad, and with a deep anterior cup or mortise pocket, the entire epimerite structure forming a dome or cap over the protomerite, EL 9.5 (5.5–13.3, ±1.8, 30), EW 18.2 (10.1–32.2, ±5.5, 30), EWW 6.9 (3.8–11.3, ±1.9, 30), EPAW 20.2 (13.0–38.9, ±6.5, 30), EPBW 11.3 (6.0–24.2, ±4.1, 30). Protomerite depressed to broadly elliptic, PL 18.8 (9.3–26.9, ±5.2, 30), PW 30.5 (19.9–52.4, ±7.4, 30), PLA 11.0 (6.1–19.2, ±3.7, 30). Protomerite–deutomerite septum clearly marked, uniform with marginal constriction, SW 30.0 (20.4–50.5, ±7.0, 30). Deutomerite narrowly to linearly cylindrical, rounded posteriorly, DL 215.7 (123.2–322.6, ±63.2, 30), DW 38.8 (28.1–70.6, ±9.0, 30), DLA 17.4 (6.6–53.6, ±9.4, 30). TL 243.8 (142.8–355.9, ±69.0, 30). Indices: EL/EW 0.6 (0.3–1.1, ±0.2, 30), PL/PW 0.6 (0.3–1.2, ±0.2, 30), PLA/PW 0.4 (0.1–0.6, ±0.1, 30), DL/DW 5.7 (3.6–8.4, ±1.6, 30), DLA/DW 0.5 (0.2–1.6, ±0.3, 30), DL/PL 11.8 (6.7–17.3, ±2.8, 30), DW/PW 1.3 (1.1–1.7, ±0.1, 30), TL/EL 26.0 (13.1–36.6, ±6.7, 30), TL/PL 13.3 (7.9–19.3, ±2.9, 30), TL/DL 1.1 (1.1–1.2, ±0.0, 30). Nucleus narrowly elliptical, often convex posteriad, creating the impression of a broad horse shoe, axial, NL 18.7 (11.1–27.8, ±4.7, 30), NW 18.6 (11.6–25.4, ±4.1, 30), NL/NW 1.0 (0.7–1.7, ±0.3, 30), NDS 64.0 (17.1–117.6, ±29.7, 30), with a single large, central endosome, KL 9.7 (5.3–14.4, ±2.5, 30), KW 9.7 (5.9–15.1, ±2.8, 30), KL/KW 1.0 (0.7–1.5, ±0.2, 30).

Gametocysts and oocysts: Tuzet and Ormières (1956) reported finding neither gametocyst nor oocyst in their original study. However, Ormières' personal working notes and field notes confirm that both gametocysts and oocysts were recovered in later field seasons. Although his drawings and notes contain no indication of size, they do confirm that gametocysts are roughly spherical with a very thin hyaline coat. They dehisce through 5 spore ducts leaving a distinct gametocyst residuum. Oocysts are dolioform and extruded in chains (Ormières, laboratory and field notes.)

Taxonomic summary

Host: Ophonus pubescens (Müller, 1776) (Coleoptera: Carabidae: Harpalinae: Harpalini).

Symbiotype: No symbiotype is known.

Host records: Ophonus pubescens; adults.

Locality: Sète, France.

Infection site: Mesenteron.

Prevalence: Low. Tuzet and Ormières (1956) reported that infections were rare in more than 20 individual beetles examined in their original study. Only 1 slide was made before 1956, and thus prevalence was less than 5%.

Specimens deposited: Tuzet and Ormières prepared a single slide before their description of the taxon: this is the holotype by monotypy. The holotype slide (HWML 16665) is deposited in HWML, Division of Parasitology, University of Nebraska State Museum, Lincoln, Nebraska. The slide contains multiple trophozoites, gamonts, and associations, constituting a single hapantotype slide. We have affixed a single label to the hapantotype slide as follows: left label, "*Clitellocephalus ophoni*; ex. *Ophonus pubescens*; 1955; Sète, FRANCE; Rene Ormières, leg.; *HAPANTOTYPE*." Trophozoites, gamonts, and associations on 4 slides comprising HWML 16666 are homotypes used in the redescription. We have affixed a single label to each homotype slide as follows: left label, "*Clitellocephalus ophoni*; ex. *Ophonus pubescens*; 15 September 1967; Sète, FRANCE; Rene Ormières, leg.; *HOMOTYPE*." Trophozoites, gamonts, and associations on 3 slides comprising HWML 16667 are homotypes used in the redescription. We have affixed a single label to each homotype slide as follows: left label, "*Clitellocephalus ophoni*; ex. *Ophonus pubescens*; 18 September 1967; Sète, FRANCE; Rene Ormières, leg.; *HOMOTYPE*." Trophozoites, gamonts, and associations on 2 slides comprising HWML 16668 are homotypes used in the redescription. We have affixed a single label to each homotype slide as follows: left label, "*Clitellocephalus ophoni*; ex. *Ophonus pubescens*; 28 September 1967; Sète, FRANCE; Rene Ormières, leg.; *HOMOTYPE*." Trophozoites, gamonts, and associations on 1 slide comprising HWML 16669 are homotypes used in the redescription. We have affixed a single label to each homotype slide as follows: left label, "*Clitellocephalus ophoni*; ex. *Ophonus pubescens*; 7 June 1973; Sète, FRANCE; Rene Ormières, leg.; *HOMOTYPE*." No specimen is retained by the authors.

Remarks

This work describes the 2 known species comprising *Clitellocephalus*. *Clitellocephalus americanus* n. sp. is distinguished from *C. ophoni* n. comb. primarily by differences in overall size and relative proportion of cell compartments. Associations of *C. americanus* range from 422.0 to 1,115.9 with an average length of 763.7, well beyond the maximum length of *C. ophoni*, which ranges from 289.9 to 732.0 with an average length of 511.9. Primites and satellites of *C. ophoni* have an average length of only 2/3 that of *C. americanus* (273.2 vs. 403.1 and 243.8 vs. 369.4, respectively). *Clitellocephalus americanus* is proportionally a longer, thinner protozoan than is *C. ophoni*. Primites and satellites of *C. americanus* have DL/DWM ratios 8.4 (3.0–19.5) and 7.6 (4.1–15.4), respectively. They are proportionally 20% longer than the primites and satellites of *G. ophoni* (DL/DWM = 6.6 [4.0–10.1] and 5.7 [3.6–8.4], respectively). In mature association *C. americanus* is diagnosed by a broad protomerite–epimerite complex that lacks a distinct constriction at the base of the toroidal vacuole and a broad, bowl-shaped primite–satellite interlock. In contrast, *C. ophoni* is diagnosed by a tapering protomerite–epimerite complex with a distinct constriction at the base of the toroidal vacuole and a narrow, panduriform primite–satellite interlock. These differences distinguish *C. americanus* from *C. ophoni* and justify their description as separate taxa.

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