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Neoasterophora megasilvestrensis n. gen., n. sp. (Apicomplexa: Eugregarinida: Actinocephalidae: Pileocephalinae) Parasitizing *Cheumatopsyche analis* (Trichoptera: Hydropsychidae) in the Texas Big Thicket

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ABSTRACT: *Neoasterophora megasilvestrensis* n. gen., n. sp. (Apicomplexa: Eugregarinida: Actinocephalidae: Pileocephalinae) is described from the larvae of the little sister sedge caddisfly, *Cheumatopsyche analis* (Trichoptera: Hydropsychidae) collected from Harmon Creek, Sam Houston State University Center for Biological Field Studies, Walker County, Texas, U.S.A.

Neoasterophora is distinguished from known genera of Pileocephalinae by distinct fusiform oocysts lacking polar plugs, an epimerite in the form of an apical ovoidal tumidus, and a diamerite with a milled toroidal disk. This is the first description or report of a septate gregarine infecting larval Trichoptera from the New World.

KEY WORDS: Actinocephalidae, Apicomplexa, *Cheumatopsyche analis*, Eugregarinida, Hydropsychidae, *Neoasterophora megasilvestrensis* n. gen., n. sp., Trichoptera, Texas Big Thicket, U.S.A.

As part of an ongoing survey of the insect and eugregarine diversity of the Primitive Big Thicket region of east-central Texas, U.S.A., we collected an heretofore unknown gregarine species from larvae of the little sister sedge caddisfly, *Cheumatopsyche analis* (Trichoptera: Hydropsychidae). The gregarines recovered are referable to the family Actinocephalidae but are taxonomically distinct from all existing genera within the family. Herein we recognize and describe *Neoasterophora* gen. n. within Actinocephalidae, delineate an extended gregarine morphometric set for *Neoasterophora*, and describe the new taxon as the type species.

MATERIALS AND METHODS

Cheumatopsyche analis larvae were collected with kick screens along a rocky-bottomed riffle of Harmon Creek at the Sam Houston State University Center for Biological Field Studies, Walker County, Texas U.S.A. (30°44′44.7″N; 95°28′46.2″W) in September 2006 ($n = 13$), October 2006 ($n = 27$), and November 2007 ($n = 27$). Larvae were placed in 500-ml plastic containers with creek water for transportation to the laboratory at Sam Houston State University, Huntsville, Texas, U.S.A.

Larvae were eviscerated and their alimentary canals dissected in insect muscle saline (Belton and Grundfest, 1962). Gametocysts collected from the rectum were freed from fecal material, triple rinsed in insect muscle saline (Belton and Grundfest, 1962), triple rinsed in deionized water, and transferred with ca. 50 µl deionized water to individual 4 × 12-mm glass microvials (BioQuip Products, Gardena, California, U.S.A.). Vials were sealed with white silicon stoppers and gametocysts held for maturation and dehiscence. Gametocysts were observed daily to determine time of dehiscence. Fresh preparations of oocysts were examined as wet mounts or as agar monolayer mounts (Clopton, 2004a; Clopton et al., 2008). Oocyst observations were made using an Olympus B-Max 50 compound microscope with ×10, ×20, ×40, and ×60 universal planapochromatic objectives with either phase contrast condensers or differential interference contrast prisms and an infinity-optics turret image-doubler. Digital photographs were taken with an Olympus DP-70 digital camera through the aforementioned microscope. Permanent parasite preparations were made following the techniques described by Clopton (2004a). Observations of trophozoites and gamonts were made using an Olympus B-Max 41 compound microscope with ×10, ×40, and ×100 universal planapochromatic objectives with either bright field or phase contrast condensers. Digital photographs were taken using an Olympus DP-12 digital camera through the aforementioned microscope.

Morphometrics of all life cycle stages were taken from the digitized images using Image Pro Express v4.5 image analysis software (Media Cybernetics, L.P., Silver Spring, Maryland, U.S.A.). Images of preserved specimens used in the photographic plates were taken using the Olympus DP-70 digital camera attached to the Olympus B-Max 50 compound microscope described above. Photographic plates were processed and assembled using Adobe® PhotoShop® 7.0.1 software (Adobe Systems Inc., San Jose, California, U.S.A.).

Terminology for gregarine ontogenetic stages and anatomy follows that proposed by Levine (1971). Terminology for shapes of planes and solids follows Clopton (2004b). Morphometric terminology follows Clopton (1999), Kula and Clopton (1999), and Clopton and Nolte (2002).

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Extended gregarine morphometric sets (e.g., Clopton, 2004a, 2006; Clopton et al., 2004; Clopton and Hays, 2006) include both standard mensural data and ratios common to all gregarine species and additional metrics particular to the genus of study. The extended character set used herein for *Neoasterophora* gen. n. includes the following metric characters and abbreviations: diamerite length (DiaL), diamerite width (DiaW), epimerite length (EpiL), epimerite width (EpiW), length of epimerite plus diamerite (TEL), length of epimerite toroidal disk (ToL), width of epimerite toroidal disk (ToW). Standard metric characters and abbreviations used herein include 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), width of deutomerite at equatorial axis (DWE), maximum width of deutomerite (DWM), distance from nucleus to protomerite–deutomerite septum (NDS), length of nucleus (NL), width of nucleus (NW), length of oocyst (OL), length of oocyst residuum (OrL), width of oocyst residuum (OrW), width of oocyst at equator (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), width of protomerite at equatorial axis (PWE), maximum width of protomerite (PWM), total length (TL). Relative trophozoite morphometrics used herein are consistent with those proposed by Clopton (2006). Measurements are presented in micrometers as mean values followed parenthetically by range values, standard deviations, and sample sizes.

DESCRIPTION

Neoasterophora gen. n.
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Diagnosis

Eugregarinorida Léger, 1892, sensu Clopton (2002); Septatorina Lankester, 1885, sensu Clopton (2002); Stylocephaloidea Clopton, 2009, Actinocephalidae Léger, 1892, sensu Clopton (2002, 2009); Pileocephalinae Léger, 1899, sensu Baudoin (1967); with the characters of *Neoasterophora* gen. n. as follows: association late, caudofrontal; epimerite in the form of an apical ovoidal tumidus; diamerite present, with milled toroidal disk; oocysts fusiform in outline, without polar plugs; oocyst residua present as a central cluster; released from gametocysts by simple rupture.

Taxonomic summary

Type species: Neoasterophora megasilvestrensis n. sp.

Etymology: The name *Neoasterophora* reflects its similarity to the type species of the genus *Asterophora*.

Remarks

Pileocephalinae (sensu Baudoin, 1967) are characterized by a globular epimerite and smooth, biconical oocysts and include the genera *Pileocephalus* Schneider, 1875, *Discorhynchus* Labbé, 1899 (= *Discocephalus* Léger, 1892), *Asterophora* Léger, 1892, *Gemmicephalus*, Baudoin, 1967, and *Globulocephalus* Baudoin, 1967. *Pileocephalus* is characterized by broadly hesperidiform oocysts with polar plugs and lacks a diamerite. *Asterophora* has narrowly hesperidiform oocyst with polar plugs, and possesses a diamerite. The type species, *Asterophora mucronata* Léger, 1892, has a thick horizontal disk, with a milled border, surrounding the diamerite, but many species described since lack such a structure. Thus, differentiation of diamerite and a reduction in oocyst diameter in *Asterophora* permit its distinction from *Pileocephalus*. The epimerite/diamerite complex of *Neoasteropha* gen. n. most closely resembles that originally described for *Asterophora* (Léger, 1892). However, it can be distinguished from *Asterophora* by its fusiform oocysts lacking polar plugs. *Neoasterophora* can be distinguished from *Globulocephalus* and *Gemmicephalus*, which also lack oocyst polar plugs, by the presence of a diamerite. *Neoasterophora* can be distinguished from *Discorhynchus*, which also lacks oocyst polar plugs, by oocyst morphology and epimerite/diamerite structure. The oocysts of *Neoasterophora* are fusiform, while those of *Discorhynchus* are biconical with ventricose swelling. The epimerite of *Neoasterophora* is in the form of an ovoidal tumidus while that of *Discorhynchus* is a flattened elliptoid tumidus.

Neoasterophora megasilvestrensis n. sp.
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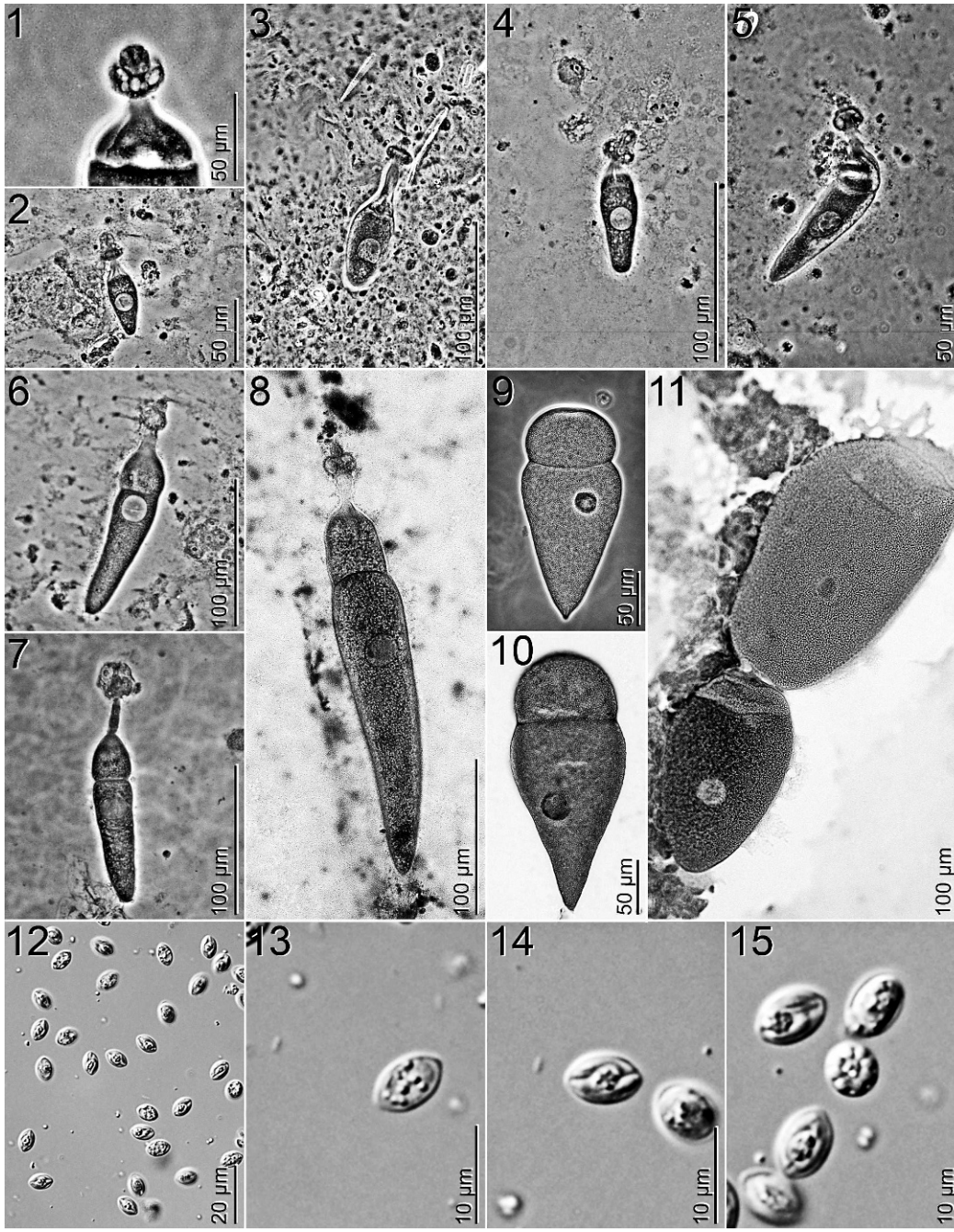
(Figs. 1–15)

Description

Trophozoites (Figs. 1–8): Solitary, attached to host ventricular epithelium, with epimerite complex. Epimerite narrowly ovoid to deltoid, surrounded by diaphanous, milled, toroidal disk at juncture with diamerite; TEL 63.0 (25.6–122.2, ±29.2, 11); EpiL 20.3 (11.9–28.7, ±5.4, 11); EpiW 7.7 (5.4–9.4, ±1.4); DiaL 41.5 (11.9–92.2, ±25.8, 11); DiaW 8.0 (6.0–12.4, ±2.3, 11); ToL 9.9 (1.5–18.5, ±4.4, 11); ToW 23.9 (16.4–31.5, ±4.5, 11). Indices: EpiL/EpiW 2.6 (1.9–3.7, ±0.6, 11); DiaL/DiaW 5.5 (2.0–13.7, ±3.7, 11); DiaL/EpiL 2.1 (0.9–3.8, ±1.1, 11);



Figures 1–15. Ontogenetic stages of *Neoasterophora megasilvestrensis* n. gen., n. sp. **1.** Epimerite/diamerite complex. **2–8.** Trophozoites of increasing age and development. **9–10.** Gamonts. **11.** Mature gamonts in association. **12–15.** Oocysts, differential interference contrast microscopy.

DiaW/EpiW 1.0 (0.8–1.4, ±0.2, 11); ToL/ToW 0.4 (0.05–0.6, ±0.2, 11); DiaL/ToL 8.7 (1.4–61.0, ±17.4, 11); EpiL/ToL 3.4 (1.2–17.9, ±4.8, 11); EpiW/ToW 0.3 (0.2–0.5, ±0.1, 11); Protomerite ovoid to broadly ovoid, truncated by distinct constriction at protomerite deutomerite septum, about as wide as deutomerite. Length of protomerite 69.6 (45.1–106.9, ±13.7, 32); PWE 48.2 (28.5–69.8, ±10.9, 32); PWM 53.9 (35.9–75.4, ±11.6, 32); PLAM 51.9 (22.5–84.5, ±12.6, 32); PLPM 18.1 (5.1–36.7, ±7.7, 32); PDSW 46.8 (29.2–68.2, ±10.2, 32). Indices: PL/PWE 1.5 (0.9–2.4, ±0.4, 32); PL/PWM 1.3 (0.7–1.9, ±0.3, 32); PL/PDSW 1.6 (0.7–2.4, ±0.4, 32); PLAM/PL 0.7 (0.4–1.0, ±0.1, 32); PLAM/PLPM 3.6 (0.7–10.5, ±2.1, 32); PWM/PWE 1.1 (1.0–1.3, ±0.1, 32); PWM/PDSW 1.2 (1.0–1.4, ±0.1, 32). Deutomerite narrowly obovoid to spatulate, truncated by distinct constriction. Length of deutomerite 201.8 (138.5–305.4, ±38.5, 32); DWE 53.2 (36.0–97.7, ±13.5, 32); DWM 60.1 (37.3–100.0, ±14.4, 32); DLAM 43.2 (11.1–107.3, ±29.0, 32); DLPM 159.9 (96.0–237.7, ±36.5, 32). Indices: DL/DWE 3.9 (2.1–5.9, ±0.9, 32); DL/DWM 3.5 (2.1–5.0, ±0.8, 32); DL/PDSW 4.4 (2.6–6.5, ±0.9, 32); DLAM/DL 0.2 (0.04–0.5, ±0.1, 32); DLAM/DLPM 0.3 (0.05–0.9, ±0.2, 32); DWM/DWE 1.1 (1.0–1.5, ±0.1, 32); DWM/PDSW 1.3 (1.1–1.6, ±0.1, 32). Total length 271.5 (198.4–366.4, ±42.9, 32); TL/PL 4.0 (3.0–6.1, ±0.8, 32); PL/DL 0.4 (0.2–0.5, ±0.1, 32); DWM/PWM 1.1 (0.9–1.4, ±0.2, 32); TL/DL 1.4 (1.2–1.5, 0.1, 32). Nucleus orbicular to elliptoid, placement variable; NL 26.1 (15.7–47.7, ±6.3, 32); NW 18.9 (8.9–26.7, ±4.7, 32); NDS 77.9 (24.0–176.6, ±34.9, 32); NL/NW 1.5 (0.8–3.2, ±0.5, 32); NDS/NL 3.2 (0.9–9.0, ±1.7, 32); DL/NDS 3.1 (1.4–7.5, ±1.5, 32).

Gamont (Figs. 9–11): Solitary prior to syzygy. Similar in size and morphology to mature trophozoites, protomerite becomes slightly wider than deutomerite; PL 51.3 (34.6–70.6, ±10.8, 33); PWE 65.2 (24.9–116.1, ±22.3, 33); PWM 70.9 (25.3–123.3, ±23.5, 33); PLAM 39.2 (2.4–64.0, ±12.1, 33); PLPM 12.3 (2.8–27.0, ±7.4, 33); PDSW 63.6 (23.3–123.9, ±23.9, 33); PL/PWE 0.9 (0.4–1.6, ±0.3, 33); PL/PWM 0.8 (0.4–1.6, ±0.3, 33); PL/PDSW 0.9 (0.4–1.7, ±0.3, 33); PLAM/PL 0.8 (0.04–1.2, ±0.2, 33); PLAM/PLPM 5.2 (0.2–20.8, ±4.5, 33); PWM/PWE 1.1 (1.0–1.4, ±0.1, 33); PWM/PDSW 1.1 (1.0–1.4, ±0.1, 33); DL 160.8 (77.7–253.2, ±41.4, 33); DWE 64.9 (20.3–128.6, ±27.4, 33); DWM 77.8 (25.7–146.7, ±29.1, 33); DLAM 17.9 (4.5–38.9, ±8.8, 33); DLPM 141.6 (68.0–233.2, ±37.7, 33); DL/DWE 2.8 (1.2–5.1, ±1.1, 33); DL/DWM 2.2 (1.1–3.9, ±0.7, 33); DL/PDSW 2.7 (1.4–4.6, ±0.8, 33); DLAM/DL 0.1 (0.04–0.3, ±0.1, 33); DLAM/DLPM 0.1 (0.04–0.5, ±0.1, 33); DWM/DWE 1.2 (1.0–1.7, ±0.2, 33); DWM/PDSW 1.2 (1.0–1.6, ±0.1, 33); TL 213.0 (121.8–339.4, ±50.2, 33); TL/PL 4.2 (2.7–6.0, ±0.8, 33); PL/DL 0.3 (0.2–0.6, ±0.1, 33); DWM/PWM 1.1 (0.9–1.3, ±0.1, 33); TL/DL 1.3 (1.2–1.6, ±0.1, 33); NL 26.0 (11.9–40.4, ±6.7, 33); NW 21.1 (8.3–36.9, ±6.1, 33); NDS 55.6 (10.6–121.3, ±29.3, 33); NL/NW 1.3 (0.6–3.9, ±0.6, 33); NDS/NL 2.3 (0.5–7.8, ±1.5, 33); DL/NDS 3.7 (1.5–11.8, ±2.1, 33).

Gametocysts: White in color, orbicular with hyaline coat. Gametocysts stored in water dehisce by simple rupture in 3–5 d.

Oocysts (Figs. 12–15): Fusiform in outline, with central cluster of 8 sporocyst residua, OL 8.3 (8.1–8.9, ±0.2, 39); OW 5.5 (5.2–6.0, ±0.2, 39); OrL 3.1 (2.3–1.3, ±0.3, 39); OrW 2.3 (1.3–1.7, ±0.1, 39); OL/OW 1.5 (1.4–1.7, ±0.1, 39); OrL/OrW 1.4 (1.0–2.2, ±0.2, 39).

Taxonomic summary

Type host: Cheumatopsyche analis (Banks, 1903) (Trichoptera: Hydropsychidae), larvae.

Type locality: Harmon Creek, Sam Houston State University Center for Biological Field Studies, Walker County, Texas, U.S.A., (30°44′44.7″N; 95°28′46.2″W).

Symbiotype: Two symbiotype specimens (authors' specimens SDX060285 and RJC060238) are deposited in the Sam Houston State University Insect Collection (SHSUIC), Department of Biology, Sam Houston State University, Huntsville, Texas, U.S.A. Individual accession numbers are not assigned by SHSUIC.

Site of infection: Trophozoites and gamonts were collected from the length of the mesenteron. Gametocysts were collected from the host hindgut and rectum.

Prevalence: Eleven of 13 (85%) specimens of *C. analis* were infected in September 2006; 17 of 25 (68%) specimens of *C. analis* were infected in October 2007; 11 of 27 (41%) specimens of *C. analis* were infected in November 2007.

Specimens deposited: The holotype slide is deposited in the Harold W. Manter Laboratory for Parasitology (HWML), Division of Parasitology, University of

Table 1. Species and host range of Pileocephalinae (Apicomplexa: Eugregarinida: Actinocephalidae).

Gregarine species	Host species*	Host order
Asterophora mucronata Léger, 1892	*Rhyacophila* sp.	Trichoptera
	Rhyacophila septentrionis†	
	Rhyacophila dorsalis‡	
	Rhyacophila foliacea‡	
	Rhyacophila italica‡	
	Rhyacophila rougemonti‡	
Asterophora capitata Baudoin, 1966	*Rhyacophila praemorsa*	Trichoptera
	Rhyacophila obliterata†	
Asterophora pachydera Baudoin, 1966	*Rhyacophila evoluta*	Trichoptera
Asterophora calciformis Baudoin, 1967	*Agrypnia obsolete*	Trichoptera
Asterophora cordiformis Baudoin, 1967	*Mystacides longicornis*§	Trichoptera
	Triaenodes bicolor§	
	Oecetis furva§	
Asterophora cupressiformis Baudoin, 1967	*Oligoplectrum maculatum*	Trichoptera
Asterophora tiaroides Baudoin, 1967	*Trichostegia minor*	Trichoptera
	Ecnomus tenellus‡	
Asterophora heeri (Kölliker, 1845)	*Sericostoma* sp.	Trichoptera
	Phryganea grandis†	
	Agrypnia pagetana†	
	Athripsodes aterrimus†	
	Ecnomus tenellus‡	
Asterophora caloglyphi Geus, 1969	*Caloglyphus moniezi*	Acari
Asterophora hemicerae K. Hoshide, 1979	*Hemicera zigzaga*	Coleoptera
Asterophora orientalis H. Hoshide, 1959	*Holostrophus orientalis*	Coleoptera
Asterophora pygmaea H. Hoshide, 1959	*Mycetophagus* (larva/adult)	Coleoptera
Asterophora philica (Leidy, 1889)	*Nyctobates pennsylvanicus*	Coleoptera
Asterophora cratoparis Crawley, 1903	*Cratoparis lunatus*	Coleoptera
Asterophora hydropsyches (Hoshide, 1953)	*Phryganea varia*	Trichoptera
	Hydropsyches pellucidula‡	
	Hydropsyches sattleri‡	
Globulocephalus hydropsyches Baudoin, 1965	*Hydropsyche* sp.	Trichoptera
	Hydropsyche dissimulata‡	
	Hydropsyche instabilis‡	
	Hydropsyche pellucidula‡	
	Hydropsyche sattleri‡	
Gemmicephalus mutabilis Baudoin, 1967	*Athripsodes cinereus*	Trichoptera
Gemmicephalus japonicus K. Hoshide, 1972	*Acrophylax* sp.	Trichoptera
Discorhynchus truncatus (Léger, 1892)	*Sericostoma* sp.	Trichoptera
	Plectrocnemia conspersa†	
Pileocephalus glyphotaelii Stein, 1960	*Limnophilus stigma*†	Trichoptera
	Limnophilus falvicornis†	
	Potamophylax nigricornis†	
	Grammotaulius nigropunctatus‡	
Pileocephalus sinensis Schneider, 1875	*Chaetopteryx villosa*	Trichoptera
	Anabolia nervosa†	
	Mesophylax aspersus‡	
	Protoneura sp.‖	Plecoptera
Pileocephalus lanceatus Baudoin, 1967	*Drusus discolor*	Trichoptera
	Drusus improvisus‡	
	Allogammus antennatus‡	
	Allogammus hilaris‡	
	Odontocerum albicorne‡	
Pileocephalus scyphoides Baudoin, 1967	*Potamophylax nigricornis*	Trichoptera
	Potomophylax cingulatus‡	
Pileocephalus agilis Geus, 1969	*Limnophilus aricula*	Trichoptera
	Potamophylax cingulatus‡	
	Micropterna wagerneri‡	
Pileocephalus striatus Léger and Dubosq, 1909	*Ptychoptera contaminata*	Diptera
Pileocephalus benli Geus, 1969	Lepismatidae¶	Thysanura
Pileocephalus astaurovi Lipa, 1967	*Baicalina spinosa*	Trichoptera

Table 1. Continued.

Gregarine species	Host species*	Host order
Pileocephalus dinarthrodes K. Hoshide, 1972	*Dinarthrodes japonica*	Trichoptera
Pileocephalus rhyntinotus Amogi and Rodgi, 1975	*Rhytinota impolita*	Coleoptera
Pileocephalus sapporoensis K. Hoshide, 1982	*Limnophilinae* sp.	Trichoptera
Neoasterophora megasilvestrensis gen. et n. sp.	*Cheumatopsyche analis*	Trichoptera

* First host species listed is the type host unless otherwise noted; other reported hosts follow.
† Data from Baudoin (1967).
‡ Data from Moretti and Sorcetti (1981).
§ Baudoin (1967) did not designate a type host for *A. cordiformis* but reported from these 3 species in the family Leptoceridae.
‖ *Pileocephalus sinensis* from *Protoneura* sp. was originally described as *Pileocephalus nemurae* Foerster, 1938. However, Désportes (1963) synonymized this species with *P. sinensis*.
¶ Geus (1969) did not designate a type host species, but indicated that the host was in the family Lepismatidae (Thysanura).

Nebraska State Museum, Lincoln, Nebraska, U.S.A. The holotype slide HWML100033 (author's slide number TJC060260) is a hapantotype containing multiple trophozoites, gamonts, and associations. It is 1 of a series of 97 hapantotype slides comprising the type series (HWML 100033–100041), which includes 96 paratype slides accessioned as HWML100034 (11 slides, author's slide numbers JJH060570, JJH060573–JJH060575, JJH060576a–b, JJH060577, JJH060579, JJH060580, JJH060582, JJH060583); HWML100035 (7 slides, SXD060288a, SXD060289, SXD060290, SXD060293a–b, SXD060295, SXD060298); HWML-100036 (8 slides, SXD060309, SXD060310, SXD-060311a–b, SXD060313, SXD060314, SXD060316, SXD060317); HWML100037 (24 slides, TJC060239a–b, TJC060243–TJC060257, TJC060258a–b, TJC060259, TJC060261, TJC060262, TJC060264, TJC060265); HWML100038 (18 slides, TJC060292–TJC060297, TJC060299–TJC060304, TJC060306a–b, TJC060307a–b, TJC060308, TJC060313); HWML100039 (11 slides, TJC060636, TJC060637a–b, TJC060638, TJC060640, TJC060641a–b, TJC060642–TJC060644, TJC060646); HWML100040 (6 slides, TJC07159, TJC07162, TJC-07166, TJC07167a–b, TJC07171); HWML100041 (13 slides, TJC07183b, TJC07184a–b, TJC07193a–b, TJC-07194, TJC07195, TJC07196a–c, TJC07199, TJC-07205a–b). No specimen from the type series is retained by the authors.

Etymology: The specific epithet *megasilvestrensis* is derived from Latin meaning "big woods" and is given to mark the type locality in the primitive Big Thicket region of East Texas, U.S.A.

Remarks

Neoasterophora megasilvestrensis n. sp. is the type species of the genus. This is the first description or report of a septate gregarine infecting larval Trichoptera in the New World. With the exception of *Gemmicephalus japonicus, Pileocephalus dinarthrodes,* and *Pileocephalus sapporoensis* reported from Japan, all previous reports of gregarines infecting Trichoptera larvae are from Europe.

DISCUSSION

The subfamily Pileocephalinae sensu Baudoin (1967) is comprised of 6 genera: *Pileocephalus* Schneider, 1875, *Asterophora* Léger, 1892, *Discorhynchus* Labbé, 1899 (= *Discocephalus* Léger, 1892), *Gemmicephalus*, Baudoin, 1967, *Globulocephalus* Baudoin, 1967, and *Neoasterophora* gen. n. Table 1 summarizes the putative species of Pileocephalinae and their known host ranges. Ten of the 15 species of *Asterophora* are reported from Trichoptera larvae. The original descriptions for 4 of the 5 species of *Asterophora* not from Trichoptera, *Asterophora caloglyphi*, *Asterophora hemicerae, Asterophora pygmaea, Asterophora philica,* and *Asterophora cratoparis* (see Table 1) contain little detailed information and provide no information regarding oocysts, nor have these species been reported since their original description. Based on the limited information provided, these species are probably not referable to *Asterophora*, and we deem them to be species inquirenda. Eight of the 11 species of *Pileocephalus* are reported from Trichoptera larvae. The original descriptions for 2 of the 3 species not from Trichoptera contain little detailed information and provide no information regarding oocysts. Based on the limited information provided, these species are probably not referable to *Pileocephalus*, and we deem them to be species inquirenda. Both species of *Gemmicephalus* as well as the monotypic *Discorhynchus*, *Globulocephalus*, and *Neoasterophora* gen. n. are known only from Trichoptera larvae. Thus, Pileocephalinae appears to be a lineage that radiated within Trichoptera larvae.

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LITERATURE CITED

Baudoin, J. 1967. Contribution a l'étude morphologique, biologique et écologique des Grégarines d'insectes a larves aquatiques. Annales de la Station Biologique de Besse-en-Chandesse 2:13–160.

Belton, P., and H. Grundfest. 1962. Potassium activation and K spikes in muscle fibers of mealworm larva (*Tenbrio molitor*). American Journal of Physiology 203:588–594.

Clopton, R. E. 1999. 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. Journal of Parasitology 85:84–89.

Clopton, R. E. 2002. Phylum Apicomplexa Levine, 1970: order Eugregarinorida Léger, 1900. Pages 205–288 *in* J. J. Lee, G. Leedale, D. Patterson, and P. C. Bradbury, eds. Illustrated Guide to the Protozoa, 2nd ed. Society of Protozoologists, Lawrence, Kansas.

Clopton, R. E. 2004a. *Calyxocephalus karyopera* g. nov., sp. nov. (Eugregarinorida: Actinocephalidae: Actinocephalinae) from the ebony jewelwing damselfly *Calopteryx maculata* (Zygoptera: Calopterygidae) in southeast Nebraska: implications for mechanical prey–vector stabilization of exogenous gregarine development. Comparative Parasitology 71:141–153.

Clopton, R. E. 2004b. Standard nomenclature and metrics of plane shapes for use in gregarine taxonomy. Comparative Parasitology 71:130–140.

Clopton, R. E. 2006. Two new species of *Xiphocephaus* in *Eleodes tricostata* and *Eleodes fusiformis* (Coleoptera: Tenebrionidae: Eleodini) from the sandhills of western Nebraska. Journal of Parasitology 92:569–577.

Clopton, R. E. 2009. Phylogenetic relationships, evolution, and systematic revision of the septate gregarines (Apicomplexa: Eugregarinorida: Septatorina). Comparative Parasitology 76:167–190.

Clopton, R. E., T. J. Cook, and J. L. Cook. 2004. *Naiadocystis phykoterion* n. gen., n. sp. (Apicomplexa: Eugregarinida: Hirmocystidae) from the Mexican Pygmy Grasshopper *Paratettix mexicanus* (Orthoptera: Tetrigidae) in the Texas Big Thicket with recognition of three previously described species of *Naiadocystis*. Journal of Parasitology 90:301–307.

Clopton, R. E., T. J. Cook, and J. L. Cook. 2008. *Trichurispora wellgundis* n. g., n. sp. (Apicomplexa: Eugregarinida: Hirmocystidae) parasitizing adult water scavenger beetles, *Tropisternus collaris* (Coleoptera: Hydrophilidae) in the Texas Big Thicket. Comparative Parasitology 75:82–91.

Clopton, R. E., and J. J. Hays. 2006. Revision of the genus *Protomagalhaensia* and description of *Protomagalhaensia wolfi* n. comb. (Apicomplexa: Eugregarinida: Hirmocystidae) and *Leidyana haasi* n. comb. (Apicomplexa: Eugregarinida: Leidyanidae) parasitizing the lobster cockroach, *Nauphoeta cinerea* (Dictyoptera: Blaberidae). Comparative Parasitology 73:137–156.

Clopton, R. E., and C. M. Nolte. 2002. *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 *Ophonuspubescens* (Coleoptera: Carabidae: Harpalinae) in Sète, France. Journal of Parasitology 88:750–757.

Desportes, I. 1963. Quelques gregarines parsites d'insectes aquatiques de France. Annales de Parasitologie Humaine et Comparée 38:341–377.

Geus, A. 1969. Sporentierchen. Sporozoa. Die Gregarinida der land- und süßwasserbewohnenden Arthropoden Mitteleuropas. Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise 57:1–608.

Kula, R. R., and R. E. Clopton. 1999. *Amoebogregarina nigra* n. gen., n. comb. (Apicomplexa: Gregarinidae) from adult *Melanoplus differentialis* (Orthoptera: Acrididae) in southeastern Nebraska. Journal of Parasitology 85:321–325.

Levine, N. D. 1971. Uniform terminology for the protozoan subphylum Apicomplexa. Journal of Protozoology 18: 352–355.

Moretti, G. P., and C. C. Sorcetti. 1981. Gregarines in Trichoptera larvae. Pages 213–217 *in* G. P. Moretti ed. Proceedings of the 3rd International Symposium on Trichoptera, Series Entomologica, Vol. 20. Dr. W. Junk Publishers, The Hague.