Gregarina tropica n. sp. (Apicomplexa: Eugregarinorida: Gregarinicae: Gregarinidae) Parasitizing the Brown-Winged Earwig, *Vostox brunneipennis* (Dermaptera: Labiidae), in the Texas Big Thicket

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ABSTRACT: *Gregarina tropica* n. sp. (Apicomplexa: Eugregarinorida) is described from the brown-winged earwig, *Vostox brunneipennis* (Dermaptera: Labiidae) collected from the Turkey Creek Unit, Big Thicket National Preserve, Tyler County, Texas, U.S.A. We review the morphometric data and nomenclatural status of the 8 previously described species of *Gregarina* infecting earwigs and recognize 7 valid species: *Gregarina ovata, Gregarina nalae, Gregarina megaspora, Gregarina ambigua, Gregarina fallax, Gregarina chelidurellae*, and *Gregarina labidurae*. Although apparently valid taxa, the latter 3 species are very poorly described and thus considered species inquirendae pending new collections and redescription. *Gregarina forficulae* is recognized as a junior synonymy of *G. ovata*.

KEY WORDS: Apicomplexa, Eugregarinorida, Septatorina, Gregarinidae, Gregarine, Gregarina tropica n. sp., Gregarina ovata, Gregarina nalae, Gregarina megaspora, Gregarina ambigua, Gregarina fallax, Gregarina chelidurellae, Gregarina forficulae, Gregarina labidurae, earwig, Dermaptera, Labiidae, Vostox brunneipennis, Texas, U.S.A., Nearctic.

The first gregarine genus recognized, Gregarina Dufour, 1828, was erected for Gregarina ovata (Dufour, 1828) parasitizing the digestive tracts of European Earwigs, Forficula auricularia Linnaeus 1758 (Dermaptera: Forficulidae) in France. As the founding taxon in what has proven to be a very large group, G. ovata is partially described by most major works on gregarines (Dufour, 1837; Siebold, 1837, 1839; Hammerschmidt, 1838; Frantzius, 1848; Lankester, 1863; Schneider, 1873, 1875, 1882; Léger, 1892; Wasielewski, 1896; Labbé, 1899; Wellmer, 1911; Watson, 1916; Foerester, 1938; Grassé, 1953; Lipa, 1967; Geus, 1969), but only Geus (1969) and Lipa (1967) report metric data sufficient to characterize the gamonts of the species. Paehler (1904) describes chromatoid figures during gametocyst development and details nuclear morphology and early trophozoite development. Watson (1916) resolves early nomenclatural issues of synonymy and homonomy for the taxon. In the intervening 180 years since Gregarina was established the taxon has grown to include more than 300 species primarily infecting coleopterous and orthopterous insects but also members of the insect orders Collembola, Dermaptera, Dictyoptera, Diptera, Embioptera, Ephemeroptera, Hymenoptera, Hemiptera, Isoptera, Lepidoptera, Neuroptera, Raphidiopterorida, Thysanura, and Trichopterorida as well as Acari and several orders of Crustacea (Levine, 1988). As is often the case with nominate genera, *Gregarina* has become a miscellaneous agglomeration of taxa that includes a number of unrecognized or cryptic genera (see Kula and Clopton, 1999; Clopton, 2002; Clopton and Nolte, 2002; Hays et al., 2004; Clopton and Hays, 2006; Clopton et al., 2004, 2008).

Gregarina species infecting earwigs are the nominotypical taxic group underpinning the systematic stability of *Gregarina* and thus the Septatorina at large. The taxonomic stability and predictive utility of any gregarine systematic thus depends upon our understanding of the taxonomy and relationships of gregarines infecting earwigs.

As part of an on-going survey of the insect and eugregarine diversity of the Big Thicket region of eastcentral Texas, U.S.A., we collected a heretofore unknown gregarine species from adults and immatures of the native brown-winged earwig, *Vostox brunneipennis* (Serville, 1839) (Dermaptera: Labiidae). The gregarines recovered are referable to *Gregarina* but taxonomically distinct from known species infecting earwigs and represent a new species of *Gregarina*. Herein we review the 7 known species of *Gregarina* infecting earwigs, delineate an extended gregarine morphometric set for *Gregarina* consistent with those established for the family Stylocephalidae and the genera *Amoebogregarina*, *Calyxocephalus*, *Clitellocephalus*, *Geneiorhynchus*, *Leidyana*, *Protomagalhaensia*, *Naiadocystis*,

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Stictospora, *Trichurispora*, and *Xiphocephalus* (see Clopton, 1999, 2004a, 2006; Kula and Clopton, 1999; Clopton and Nolte, 2002; Clopton et al., 2004, 2007, 2008; Hays et al., 2004; Clopton and Hays, 2006); and describe a new species within the genus.

MATERIALS AND METHODS

Collection, preservation, and analysis of specimens

Seventy-four V. brunneipennis adults and immatures were collected from underneath the bark of a downed elm tree beside Turkey Creek in the Turkey Creek Unit, Big Thicket National Preserve, Tyler County, Texas, U.S.A. (30°33'06.2"N; 94°19' 03.6"W) on 19 March 2007, placed in 1-liter plastic jars, and transported to the laboratory at Sam Houston State University, Huntsville, Texas, U.S.A. Three individuals were prepared as permanent voucher specimens. The remaining 71 specimens were placed in glass petri dishes to collect frass and gametocysts and then examined for gregarine infection. Earwigs 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 were fixed by flotation on hot AFA (ethanol, formalin, and acetic acid); stained with either Semichon's acetocarmine or Harris' hematoxylin and eosin-xylol; dehdrated in ethanol series; cleared in xylene series; and mounted in Damar balsam. Subsamples of gregarines from 11 hosts were collected and pooled in groups of 30-100 individuals each. The DNA from each pooled sample was isolated using a protocol similar to that reported by Laird et al. (1991). Isolated DNA samples were resuspended in AE buffer (10 mM TrisCl; 0.5 mM EDTA, pH 9.0) and stored at -20°C for future genetic analysis.

Gametocysts were isolated from collected feces, triplerinsed in insect muscle saline, surface sterilized in 0.1% formalin, triple-rinsed in spring water, placed in individual silicon stoppered 4×12 mm glass microvials (BioQuip Products, Gardena, California, U.S.A.) on filter paper disks and held for maturation and dehiscence. Gametocysts were observed daily and any changes in structure, maturation, or dehiscence noted. Oocyst structure and dimensions were taken from fresh preparations of oocysts in wet mounts and agar monolayer mounts prepared as follows. Molten agar (1.5% solution) was pipetted onto a clean glass slide, allowed to drain, and the slide was quickly chilled on a cold aluminum block to produce a thin, uniform layer of agar. Oocysts were placed in a small (ca. 7 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, providing a uniform object plane for light microscopy.

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 doubler. Digital photographs were taken with an Olympus DP-70 digital camera through the aforementioned microscope. Measurements were taken from the digitized images of preserved specimens using Image-Pro Discovery v 4.0 image analysis software (Media Cybernetics, L.P., Silver Spring, Maryland,

U.S.A.). Photographic plates were processed and assembled using Adobe PhotoShop 7.0.1 software (Adobe Systems Inc., San Jose, California, U.S.A.).

Morphometric characters, abbreviations, and terminology

Extended gregarine morphometric sets (Clopton 1999, 2004a, 2006; Kula and Clopton, 1999; Clopton and Nolte, 2002; Clopton et al., 2004, 2007, 2008; Hays 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 Gregarina is similar to those used for Leiydana (see Clopton and Hays, 2006). These characters are presented in Figures 1 and 2, and individual metrics are abbreviated as follows: width of septum at primite-satellite junction (AscSW); 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); length of nucleus (NL); distance from nucleus to protomerite-deutomerite septum, (NSD); width of nucleus (NW); maximum interior oocyst length (OLI); maximum exterior oocyst length (OLM); maximum exterior oocyst width (OWM); exterior width of oocyst terminus (OWTE); interior width of oocyst terminus (OWTI); 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); primite (Pr); width of protomerite at equatorial axis (PWE); maximum width of protomerite (PWM); width of protomerite at anterior terminus (PWT); and satellite (Sat). 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 generally follows that proposed by Levine (1971). Terminology for shapes of planes and solids follows Clopton (2004b). Additional descriptive terminology is derived from Harris and Harris (1994). Use of "species inquirenda," "incertae sedis," and "lapsus calami" at the species level in gregarine taxonomy and systematics is consistent with the guidelines proposed by Clopton et al. (2007) and Hays et al. (2007).

RESULTS

Gregarina tropica n. sp. R. E. Clopton and T. J. Cook (Figs. 1–14, 18, 25)

Generic diagnosis

With the characters of Order Eugregarinorida Léger, 1892, sensu Clopton (2002); Suborder Septatorina Lankester, 1885, sensu Clopton (2002); Superfamily Gregarinicae Chakaravarty, 1960 sensu Clopton (2002); Family Gregarinidae Labbé, 1899, sensu Clopton (2002); and characters of the genus *Gregarina* Dufour, 1828 sensu Clopton (2002) as follows: association precocious; caudofrontal; epimerite



Figures 1, 2. Morphometric character set for gamonts and oocysts of Gregarina species. 1. Generalized gamont morphometric characters are mapped on a primite and satellite association of *Gregarina tropica* n. sp. 2. Generalized oocyst morphometric characters mapped on an oocyst of *Gregarina tropica* n. sp. (AscSW, width of septum at primite-satellite junction; DL, length of deutomerite; DLAM, distance from protomerite-deutomerite

conical, button-shaped, globular, or cylindrical; oocysts doliform, navicular, or spherical, dehiscing from gametocyst in long chains from multiple spore tubes.

Description

Young trophozoites (Fig. 3): Solitary, extracellular forms attached to epithelium of mesenteron. Epimerite very broadly ovoid, becoming ovoid with development, without ornamentation or diamerite, nonpersistant in gamontic forms. Protomerite shallowly elliptoid with distinct constriction at protomerite–deutomerite septum. Deutomerite obovoid, truncated by constriction of protomerite–deutomerite septum. Nucleus broadly elliptoid to orbicular, with single large elliptoid karyosome.

Association (Figs. 1, 5–8, 18): Gamonts anisomorphic; epimerite absent, replaced by shallow omphalitic scar on the anterior margin of the primite protomerite; association precocious, tandem, caudo-frontal. Indices: PriTL/SatTL 1.04 (0.79–1.24, ± 0.11 , 30), PriPL/SatPL 1.33 (0.9–1.91, ± 0.25 , 30), PriDL/SatDL, 1 (0.75–1.2, ± 0.11 , 30), PriPWM/SatDWM, 0.85 (0.75–0.95, ± 0.06 , 30), PriDWM/SatDWM 0.96 (0.77–1.08, ± 0.08 , 30).

Primite: Total length (PrTL) 355.8 (314–402, \pm 26.64, 30). Epimerite absent, replaced by shallow omphalitic scar on the anterior margin of the protomerite. Protomerite shallowly ovoid: PL 53.83 (44–67.5, \pm 6.01, 30), PWT 43.18 (27–61, \pm 8.72, 30), PWE 81.81 (63–116, \pm 15.48, 30), PWM 91.38 (65.9–121, \pm 15.25, 30), PLAM 41.95 (28–56, \pm 6.3, 30), PLPM 11.68 (2–20, \pm 4.2, 30), PDSW 89.89 (68.1–117, \pm 13.75, 30), PL/PWT 1.28 (0.86–1.63, \pm 0.21, 30), PL/PWE 0.67 (0.44–0.84, \pm 0.09, 30), PL/PWM 0.6 (0.43–0.83, \pm 0.09, 30), PL/PDSW

septum to deutomerite axis of maximum width; DLPM, distance from posterior end of deutomerite to deutomerite axis of maximum width; DWE, width of deutomerite at equatorial axis; DWM, maximum width of deutomerite; NL, length of nucleus; NSD, distance from nucleus to protomerite-deutomerite septum; NW, width of nucleus; OLI, maximum interior oocyst length; OLM, maximum exterior oocyst length; OWM, maximum exterior oocyst width; OWTE, exterior width of oocyst terminus; OWTI, interior width of oocyst terminus; PDSW, width of protomeritedeutomerite septum; PL, length of protomerite; PLAM, distance from anterior end of protomerite to protomerite axis of maximum width; PLPM, distance from protomeritedeutomerite septum to protomerite axis of maximum width; Pr, primite; PWE, width of protomerite at equatorial axis; PWM, maximum width of protomerite; PWT, width of protomerite at anterior terminus; Sat, satellite.).



Figures 3–14. Trophozoites, gamontic associations, and oocysts of *Gregarina tropica n.* sp. 3. Young trophozoite, differential interference microscopy (DIC). 4–7. Gamontic associations, DIC. 8. Mature gamontic association, phase contrast microscopy (PC). 9, 10. Oocysts photographed under DIC and PC microscopy, respectively, to demonstrate observable differences in interior oocyst detail. 11, 12. Oocyst chains, DIC in dorsal and mixed dorsal and lateral views, respectively. 13, 14. Oocysts chain, DIC.

0.61 (0.47-0.84, ±0.09, 30), PLAM/PL 0.78 (0.6-0.88, ±0.06, 30), PLAM/PLPM 4.28 (1.47-16.5, ±2.65, 30), PWE/PWT 1.92 (1.38–2.37, ±0.24, 30), PWM/PWT 2.15 (1.69-2.93, ±0.3, 30), PWM/PWE 1.12 (1.01–1.24, ± 0.07 , 30). Deutomerite very deltoid, constricted deeply at protomeritedeutomerite septum: DL 303.8 (263-346, ±24.24, 30), DWE 134.83 (101-171, ±17.86, 30), DWM 140.8 (116-172, ±15.25, 30), DLAM 240.37 (155-299, ±36.11, 30), DLPM 64.23 (34.7-137, ±23.64, 30), DL/DWE 2.29 (1.72-2.79, ±0.35, 30), DL/ DWM 2.18 (1.68-2.59, ±0.3, 30), DLAM/DL 0.79 (0.53-0.88, ±0.08, 30), DLAM/DLPM 4.22 (1.13-6.81, ±1.51, 30), DWM/DWE 1.05 (0.99-1.23, ± 0.06 , 30). Nucleus roughly orbicular to broadly elliptoid with a variable number of karyosomes: NL 45.77 (36-59, ±5.32, 30), NW 38.45 (27.7-52.5, ±6.3, 30), NDS 53.09 (10.9-180, ±51.69, 30), NL/ NW 1.20 (1.00-1.36, ±0.11, 30), NDS/NL 1.13 (0.26-3.98, ±1.09, 30), DL/NDS 10.07 (1.5-27.8, ±6.49, 30). Indices: TL/PL 6.66 (5.73-8.07, ±0.6, 30), DL/PL 5.68 (4.84-6.84, ±0.54, 30), TL/DL 1.17 (1.15-1.20, ±0.01, 30), DWM/PWM 1.56 (1.31- $1.82, \pm 0.15, 30$).

Satellite: Total length (SatTL) 344.6 (282-438, $\pm 39.07, 30$). Protomerite depressed ovoid, broadly joined to primite at association junction, association interface linear, unbiased: AscSW 59.84 (46.2-85, ±9.51, 30), PL 41.53 (28.9-54.6, ±6.94, 30), PWE 95.42 (70.4-138, ±18.11, 30), PWM 108.24 (78.5-144, ±18.19, 30), PLAM 26.66 (1.28-36.3, ±7.14, 30), PLPM 12.51 (3-22, ±4.07, 30), PDSW 108.78 (78.2-142, ±17.65, 30), PL/AscSW 0.71 (0.39-1.06, ±0.17, 30), PL/PWE 0.45 (0.28–0.7, ±0.12, 30), PL/ PWM 0.4 (0.24-0.63, ±0.1, 30), PL/PDSW 0.39 (0.24-0.64, ±0.1, 30), PLAM/PL 0.65 (0.03-0.83, ±0.13, 30), PLAM/PLPM 2.35 (0.08-5.67, ±0.94, 30), PWE/AscSW 1.59 (1.34-1.97, ±0.16, 30), PWM/AscSW 1.81 (1.49-2.16, ±0.17, 30), PWM/ PWE 1.14 (1.04-1.35, ±0.07, 30). Deutomerite elliptoid, with shallow constriction at protomeritedeutomerite septum: DL 306.9 (251-402, ±39.24, 30), DWE 143.33 (108-169, ±19.31, 30), DWM 148.23 (111-176, ±20.07, 30), DLAM 108.95 (35-193, ±36.98, 30), DLPM 198.4 (150-282, ±35.98, 30), DL/DWE 2.17 (1.8-2.78, ±0.3, 30), DL/DWM 2.09 (1.73-2.68, ±0.3, 30), DLAM/DL 0.35 (0.11-0.53, ±0.1, 30), DLAM/DLPM 0.58 (0.13-1.07, ±0.24, 30), DWM/DWE 1.03 (0.99-1.06, ±0.02, 30). Nucleus roughly orbicular with a single, eccentrically placed orbicular karyosome: NL 46.23 (33-73, ±8.97, 30), NW 40.54 (27-52, ±5.42, 30), NDS 60.74 (3–198, ±59.08, 30), NL/NW 1.14 (0.94–1.5, ±0.15, 30), NDS/NL 1.39 (0.07–4.85, ±1.41, 30), DL/NDS 14.12 (1.53–102.67, ±19.92, 30). Indices: TL/PL 8.49 (6.36–13.77, ±1.54, 30), DL/PL 7.57 (5.34–12.87, ±1.54, 30), DWM/PWM 1.38 (1.2–1.53, ±0.11, 30), TL/DL 1.12 (1.07–1.19, ±0.03, 30).

Gametocysts: Opaque white with thin enclosing hyaline layer, orbicular, maturing to dehiscence of spore chains through spore tubes within 48–96 hr.

Oocysts (Figs. 2, 9–14, 25): Dolioform in outline, comprising an internal dolioform oocyst with terminal lateral condyles and an enclosing oocyst sheath; sporozoites visible; no apparent residuum; released in chains through spore tubes: OLM 17.4 (17–18, ± 0.29 , 30), OLI 16 (15.5–16.5, ± 0.28 , 30), OWM 8.6 (7.5–9.9, ± 0.51 , 30), TWE 4.5 (3.8–5.1, ± 0.35 , 30), TWI 3 (2.5–3.5, ± 0.24 , 30), OLM/OLI 1.1 (1–1.1, ± 0.02 , 30), OLM/OWM 2 (1.7–2.3, ± 0.12 , 30), OLI/OWM 1.9 (1.6–2.2, ± 0.11 , 30), OLM/TWE 3.9 (3.4–4.6, ± 0.33 , 30), OLI/TWI 5.4 (4.6–6.4, ± 0.46 , 30), OWM/TWE 1.9 (1.6–2.3, ± 0.17 , 30), TWE/TWI 1.5 (1.2–1.7, ± 0.12 , 30).

Taxonomic summary

Type host: Vostox brunneipennis (Serville, 1839) (Dermaptera: Labiidae), immatures and adults.

Type locality: Turkey Creek in the Turkey Creek Unit, Big Thicket National Preserve, Tyler County, Texas, U.S.A. (30°33'06.2"N; 94°19'03.6"W).

Symbiotype: Three symbiotype specimens stored in 85% EtOH (authors' specimens REC070061, REC070090, REC070091) are deposited in the Sam Houston State University Insect Collection (SHSUIC), Department of Biological Sciences, 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. Gamonts enrobed in peritrophic membrane by posterior end. Gametocysts were collected from the lower ileum, hindgut, rectum, and feces.

Prevalence: Sixty-six of 71 individuals examined, 92%; 42/45 females, 93%; 23/26 males, 88%.

Specimens deposited: The type series is deposited in the Harold W. Manter Laboratory for Parasitology (HWML), Division of Parasitology, University of Nebraska State Museum, Lincoln, Nebraska, U.S.A.

The holotype and allotype are an association marked by an etched circle and is contained on hapantotype slide HWML48797 (authors' slide REC07125). The paratype series comprises 54 slides containing trophozoites, gamonts, and associations deposited in 1 lot: HWML48798 (REC07063, REC07064, REC07067, REC07068, REC07069, REC07070, REC07072, REC07073, REC07078, REC07079, REC07085, REC 07086A-B, REC07087, REC07089A-C, REC07093, REC07102, REC07103, REC07104, REC07105, REC07109, REC07111, REC07112, REC07113, REC 07115, REC07116, REC07117A-B, REC07118, REC07120A-B, REC07121, REC07122, REC07123, REC07126, REC07076A-B, REC07082A-D, REC 07071, REC07075, REC07077, REC07080, REC 07081, REC07083, REC07092, REC07100, REC 07101, REC07106, REC07108, REC07110, REC 07114, REC07119, REC07124, REC07127A-F). No specimen from the type series is retained by the authors.

Etymology: The specific epithet marks the discovery of this taxon in the Big Thicket of southern Texas, U.S.A.

Remarks

Species of *Gregarina* infecting earwigs can be differentiated based on differences in oocyst size and shape, gamontic nucleus size, and gamont size and shape. Of the known species of *Gregarina* infecting earwigs, *G. tropica* is readily differentiated from *Gregarina fallax*, *Gregarina nalae*, and *Gregarina megaspora* by gross differences in oocyst size. Oocysts of *G. tropica* are roughly twice as long as those of *G. fallax* and *G. nalae* (17.4 vs. 8 and 7.8, respectively) but only about three fifths as long as the oocysts of *G. megaspora* (17.4 vs. 26).

Gregarina tropica is differentiated from *G. ovata* and *Gregarina labidurae* by lesser differences in oocyst size but significant disparity in oocyst shape. Oocysts of *G. tropica* are wider than those *G. labidurae* (8.6 vs. 7.0, respectively) and longer than those of *G. ovata* (17.4 vs. 16.0, respectively). These metric differences are readily perceived as distinct differences in oocyst shape among *G. tropica*, *G. ovata*, and *G. labidurae* (dolioform vs. dolioformoblong vs. oblong, respectively). These species also differ in the average size of their gamontic nuclei: those of *G. tropica* and *G. ovata* are roughly 2.5 times larger than those of *G. labidurae* (46.2 and 46.0 vs. 20.0, respectively).

The remaining gregarines species known to infect earwigs, *Gregarina chelidurellae* and *Gregarina ambigua*, are differentiated from *G. tropica* by differences in gamont size and shape. Primites and satellites of *G. tropica* are roughly twice as long as those of *G. chelidurellae* and *G. ambigua* (355.8 and 344.6 vs. 186.8 and 186 vs. 101 and 150, respectively by gamont type and taxon). Gamonts of these 3 species also differ in overall gamont shape. The primite protomerites of *G. tropica* and *G. chelidurellae* are both shallowly ovoid but those of *G. ambigua* are shallowly trullate. Primite deutomerites for these species are very deeply deltoid, oblong, and dolioform, respectively. Satellites of these 3 species exhibit unique protomerite/deutomerite shape profiles by taxon. Those of *G. tropica* are depressed ovoid/elliptoid; those of *G. chelidurellae* are very shallowly ovoid/obdeltoid; and, those of *G. ambigua* are very shallowly oblong/spatulate.

Gregarina chelidurellae Geus, 1969 Species Inquirenda (Fig. 15)

Description

Primite: Total length 186.8 (162–198). Protomerite shallowly ovoid, PL 28.3 (26–30), PWM 48.3 (46–51), PL/PWM 0.6 (0.5–0.7). Deutomerite oblong, DL 158.5 (132–168), DWM 74.5 (61–84), DL/ DWM 2.1 (1.9–2.3). Nucleus, NL 25.3 (24–28), NW 25.3 (24–28), NL/NW 1.0 (1.0–1.0). Indices: TL/PL 6.6 (5.4–7.2), TL/DL 1.2 (1.2–1.2), DL/PL 5.6 (4.4–6.2), DWM/PWM 1.5 (1.3–1.7).

Satellite: Total length 186 (157–200). Protomerite very shallowly ovoid, PL 21.7 (19–27), PWM 47.8 (45–53), PL/PWM 0.5 (0.4–0.5). Deutomerite obdeltoid, DL 164.3 (136–181), DWM 75 (63–81), DL/ DWM 2.2 (2.1–2.4). Nucleus, NL 25.3 (24–28), NW 25.3 (24–28), NL/NW 1.0 (1.0–1.0). Indices: TL/PL 8.7 (7–10.5), TL/DL 1.1 (1.1–1.2), DL/PL 7.7 (6–9.5), DWM/PWM 1.6 (1.4–1.8).

Association: Gamonts anisomorphic; epimerite absent; association precocious, tandem, caudofrontal. Indices: PriTL/SatTL 1.0 (0.9–1.1), PriPL/SatPL 1.3 (1.1–1.4), PriDL/SatDL 1.0 (0.9–1.0), PriPWM/ SatPWM 1.0 (0.9–1.1), PriDWM/SatDWM 1.0 (0.9–1.1).

Oocyst: unknown.

Taxonomic summary

Type host: Chelidurella acanthopygia, (Geus, 1969).

Type locality: Germany (Geus, 1969).

References: Geus, 1969; Thèodoridés et al., 1982.



Figures 15–28. Associations and oocysts of *Gregarina* sp. reported from Dermaptera. 15. *Gregarina chelidurellae*, association (after Geus, 1969). 16. *Gregarina nalae*, association (after Datta and Haldar, 1984). 17. *Gregarina ovata*, association (after Lipa, 1967). 18. *Gregarina tropica* n. sp., association. 19. *Gregarina ambigua*, association (after Amoji and Rodgi, 1976). 20. *Gregarina labidurae*, association (after Thèodoridés et al., 1982). 21. *Gregarina megaspora*, association (after Ormières, 1975). 24. *Gregarina ovata*, oocyst (after Ormières, 1975; Thèodoridés et al., 1982). 25. *Gregarina fallax*, oocyst (after Ormières, 1975). 24. *Gregarina ovata*, oocyst (after Amoji and Rodgi, 1976). 25. *Gregarina digua*, oocyst (after Thies, 1975). 27. *Gregarina labidurae*, oocyst (after Thies, 1975). 24. *Gregarina megaspora*, oocyst (after Theodoridés et al., 1982). 25. *Gregarina tropica* n. sp., oocyst. 26. *Gregarina ambigua*, oocyst (after Amoji and Rodgi, 1976). 27. *Gregarina labidurae*, oocyst (after Theodoridés et al., 1982). 28. *Gregarina megaspora*, oocyst (after Amoji and Rodgi, 1976).

Remarks

Gregarina chelidurellae has not been reported since its original description. Geus (1969) provides the only available morphometric data and descripton for associations and gamonts but no report or description of an oocyst. Placement of the taxon is tentative and based on host association and general features of life-cycle timing and morphology. As gametocyst dehiscence and oocyst morphology are cardinal characters differentiating species within the genus, *G. chelidurellae* should be considered species inquirenda until new collections, neotype designation, and redescription fully establish and stabilize the taxonomic identity of the species.

Gregarina ovata Dufour, 1828 (Figs. 17, 24)

(=Clepsidrina conoidea, Hammerschmidt, 1838)
 (=Clepsidrina ovata, Schneider, 1873)
 (=Gregarina forficulae Lipa, 1967)

Description

Primite: Total length 444.7 (312–593). Protomerite shallowly dolioform, PL 66.6 (33–91), PWM 103.9 (54–146), PL/PWM 0.65 (0.31–0.89). Deutomerite obovoid–elliptoid, DL 376.9 (272–514), DWM 222.1 (108–328), DL/DWM 1.79 (1.44–2.59). Nucleus roughly orbicular, NL 46 (34–58), NW 48 (36–60), NL/NW 0.96 (0.94–0.97). Indices: TL/PL 6.93 (5–10.18), TL/DL 1.18 (1.11–1.25), DL/PL 5.92 (4–9.18), DWM/PWM 2.16 (1.6–3.5).

Satellite: Total length 435.8 (317–582). Protomerite depressed dolioform, PL 40.9 (28–55), PWM 125.3 (76–171), PL/PWM 0.33 (0.25–0.42). Deutomerite elliptoid, DL 395 (285–528), DWM 235.7 (114–346), DL/DWM 1.77 (1.16–2.5). Nucleus roughly orbicular, NL 44 (34–54), NW 48 (36–60), NL/NW 0.92 (0.9–0.94). Indices: TL/PL 10.84 (8.27–12.72), TL/DL 1.1 (1.09–1.14), DL/PL 9.85 (7.27–11.72), DWM/PWM 1.87 (1.33–2.49).

Association: Gamonts anisomorphic; epimerite absent; association precocious, tandem, caudofrontal. Indices: PriTL/SatTL 1.02 (0.87–1.19), PriPL/SatPL 1.63 (1–2.24), PriDL/SatDL 0.95 (0.86–1.13), PriPWM/SatPWM 0.83 (0.6–1.08), PriDWM/ SatDWM 0.95 (0.68–1.31).

Oocyst: oblong, OL 16, OW 7.75, OL/OW 2.

Taxonomic summary

Host reports: Forficula auricularia (Dufour, 1828, 1837; Paehler, 1904; Tuzet and Ormières, 1956; Thèodoridés, 1963; Baudoin, 1967; Lipa, 1967; Geus, 1969; Ormières, 1975; Thèodoridés et al., 1982; Datta and Haldar, 1984; Ball et al., 1986); Euborrelia moesta (Thèodoridés, 1963); Euborrelia annulipes (Hoshide, 1958; Théodoridès and Jolivet, 1991); Anisolabis maritima (Hoshide, 1958).

Locality reports: France (Dufour, 1828, 1837; Schneider, 1873, 1885; Ormières, 1975), Germany (Wellmer, 1911; Foerster, 1938; Geus, 1969), Poland (Wellmer, 1911; Foerster, 1938; Lipa, 1967), England (Ball et al., 1986), Cabo Verde Islands (Théodoridès and Jolivet, 1991), Japan (Hoshide, 1958).

References: Dufour, 1828, 1837; Hammerschmidt, 1838; Frantzius, 1848; Schneider, 1873, 1885; Paehler, 1904; Wellmer, 1911; Watson, 1916; Watson-Kamm, 1922; Foerster, 1938; Tuzet and Ormières, 1956; Hoshide, 1958; Thèodoridés, 1963; Baudoin, 1967; Lipa, 1967; Geus, 1969; Ormières, 1975; Thèodoridés et al., 1982; Théodoridès and Jolivet, 1991; Datta and Haldar, 1984; Ball et al., 1986.

Remarks

This taxon has been problematic since its original description. Dufour (1828, 1837) originally described G. ovata from both an earwig, F. auricularia, and a cricket, Gryllus campestris. He provided figures for gregarines from each host taxon but they clearly represent 2 distinct gregarine taxa. He also reported disparate oocysts of 2 distinct sizes for G. ovata from F. auricularia (15.8 \times 7.9 and 8.3 \times 3.7), again indicating the presence of 2 gregarine taxa. Thus in retrospect, the original description erroneously confounds 3 gregarine taxa: 1 from G. campestris and 2 from F. auricularia. Recognizing the host error, Frantzius (1848) provided an unambigous figure for G. ovata and named F. auricularia the type host. Schneider (1873, 1885) studied gametocyst and oocyst formation in G. ovata, confirming oocysts of 2 distinct sizes ("macrospores" and "microspores") but failing to make the underlying species distinction. Paehler (1904) provides detailed studies of nuclear and cytoplasmic changes during development as well as extensive studies of oocyst development, and although his figures represent G. ovata, not metric is reported. Tuzet and Ormières (1956) provide empirical evidence that gametocyst diameter and sporoduct number are highly variable in the taxon and do not correlate with oocyst size. They concluded that the

"macrospore" and "microspore" oocysts of previous authors were definitive evidence of 2 distinct species but committed no nomenclatural act in response. Ormières (1975) reported extensive infection and life-cycle experiments with G. ovata, demonstrating that the taxon included 2 distinct gregarine species differing in both life-cycle span and oocyst size but not in gamont metrics. He recognized the species associated with macrospores as G. ovata and established a new taxon, Gregarina fallax Ormières, 1975, for the species associated with microspores (see Gregarina fallax, below). Although Ormières (1975) asserts that these species are indistinguishable as gamonts, no metric data are provided for either taxon. Ball et al. (1986) provide polypeptide profile data and limited morphometric demographics for G. ovata. Watson (1916) provides a lucid discussion of the nomenclatural vagaries surrounding G. ovata.

Lipa (1967) described Gregarina forficulae from F. auricularia in Poland, basing his diagnosis on smaller gamont size and cytoplasmic transparency and a single, undersized gametocyst that did not mature. He reported no oocyst. His photographic plates plates show a clear difference in size, but those associations representing G. forficulae are clearly immature specimens, commensurate with both smaller overall size and greater cytoplasmic transparency. Ball et al. (1986) found no convincing difference in polypeptide profiles to distinguish G. forficulae from G. ovata, and their photographic plates and descriptions also suggest that G. forficulae is based on immature forms typical of precocious association rather than true gamonts. The gametocyst reported by Lipa (1967) falls well within the extended range of gametocyst diameters experimentally confirmed for G. ovata by Tuzet and Ormières (1956). Thus there is no evidence to support the unique taxonomic status of G. forficulae, and we hereby declare it a subjective junior synonym of G. ovata.

Although the taxon has been known for almost 2 centuries and has been the subject of numerous studies and reports, *G. ovata* remains poorly described. The description given here is a composite incorporating data and observations from most of the available sources (Dufour, 1828, 1837; Hammerschmidt, 1838; Frantzius, 1848; Schneider, 1873, 1885; Paehler, 1904; Wellmer, 1911; Watson, 1916, Foerster, 1938; Tuzet and Ormières, 1956; Hoshide, 1958; Thèodoridés, 1963; Baudoin, 1967; Lipa, 1967; Geus, 1969; Ormières, 1975; Thèodoridés et al., 1982; Théodoridès and Jolivet, 1991; Datta and Haldar, 1984; Ball et al., 1986), and yet it remains incomplete. The existing assertion that the

species is indistinguishable from *G. fallax* based solely on trophozoite and gamontic characters remains untested: no complete metric data set exists for either species. No type or paratype specimen of *G. ovata* is known. New collections of *G. ovata* trophozoites, gamonts, and oocysts are required to fully redescribe this taxon, establish a neotype specimen, and test the utility of trophozoite and gamontic characters within the species flock.

Gregarina labidurae Thèodoridés, Ormières, and Jolivet, 1982 Species Inquirenda (Figs. 20, 27)

Description

Primite: Total length 450 (400–500). Protomerite orbicular, no metric known. Deutomerite narrowly ovoid, DWM 150 (100–200). Nucleus, unknown. Indices: unknown.

Satellite: Total length 455 (430–480). Protomerite shallowly dolioform, no metric known. Deutomerite narrowly ovoid, no metric known. Nucleus, un-known. Indices: unknown.

Association: Gamonts anisomorphic; epimerite absent; association precocious, tandem, caudofrontal. Indices: PriTL/SatTL 1.0.

Oocyst: oblong, OL 17.5, OW 7, OL/OW 2.5.

Taxonomic summary

Type host: Labidura riparia, (Thèodoridés et al., 1982, 1984).

Locality reports: France, Senegal (Thèodoridés et al., 1982), Vietnam (Thèodoridés et al., 1984).

References: Thèodoridés et al., 1982, 1984.

Remarks

Gregarina labidurae has been reported once since its original description (Thèodoridés et al., 1982) but Thèodoridés et al. (1984) provide no additional descriptive or morphometric datum. This taxon is documented largely by oocyst data, gamont size, and a general gamont morphology that is much slimmer than other known gregarines infecting earwigs. Because no complete gamontic morphometric description exists to document other cardinal characters differentiating species within the genus, *G. labidurae* should be considered species inquirenda until new collections, neotype designation, and redescription fully establish and stabilize the taxonomic identity of the species.

Gregarina fallax Ormières, 1975 Species Inquirenda (Fig. 23)

Description

Primite: Total length unknown. Protomerite shallowly ovoid, no metric known. Deutomerite broadly orbicular, no metric known. Nucleus, unknown. Indices: unknown.

Satellite: Total length unknown. Protomerite very depressed oblong, no metric known. Deutomerite elliptoid, no metric known. Nucleus, unknown. Indices: unknown.

Association: Gamonts anisomorphic; epimerite absent; association precocious, tandem, caudofrontal. Indices: unknown.

Oocyst: Oblong, OL 7.75 (7–8.5), OW 3.5, OL/OW 2.3 (2.2–2.4).

Taxonomic summary

Type host: Forficula auricularia, (Ormières, 1975; Thèodoridés et al., 1982).

Other known hosts: Forficula decipiens (Ormières, 1975; Thèodoridés et al., 1982); *Anechura bipunctata* (Ormières, 1975; Thèodoridés et al., 1982); *Euborellia moesta* (Ormières, 1975; Thèodoridés et al., 1982).

Locality reports: France (Ormières, 1975; Thèodoridés et al., 1982).

References: Ormières, 1975; Thèodoridés et al., 1982.

Remarks

Ormières (1975) established G. fallax to encompass the taxon originally reported as the "microspore" variant of G. ovata (see "Remarks" under Gregarina ovata, above). Although he asserted that G. ovata and G. fallax are indistinguishable based on trophozoite and gamontic morphometrics, he provided morphometric data for neither taxon but simply reported that both species confer to previously reported metrics for G. ovata. Although differences in oocyst size clearly distinguish the taxa, Ormières' assertion remains open to test as no complete morphometric data set exists for the trophozoites or gamonts of either taxon. Although the Thèodoridés et al. (1982) report discusses G. fallax, they provide no additional morphometric datum or descriptive detail. Thus this taxon is documented only by oocyst

data. As no morphometric datum exists to document other cardinal characters differentiating species within the genus, *G. fallax* should be considered species inquirenda until new collections, neotype designation, and redescription fully establish and stabilize the taxonomic identity of the species.

Gregarina nalae Datta and Haldar, 1984 (Figs. 15, 22)

Description

Primite: Total length 219.9. Protomerite shallowly elliptoid, no metric known. Deutomerite oblong, DWM 110.1. Nucleus elliptoid, NL 29.8, NW 17, NL/NW 1.7. Indices: TL/PL 4.3, DWM/PWM 2.1.

Satellite: Total length 219.9. Protomerite hemispherical to very shallowly ovoid, no metric known. Deutomerite oblong, DWM 110.1. Nucleus elliptoid, NL 29.8, NW 17, NL/NW 1.7. Indices: TL/PL 4.3, DWM/PWM 2.1.

Association: Gamonts isomorphic; epimerite absent; association precocious, tandem, caudofrontal. Indices: PriTL/SatTL 1.0.

Oocyst: Dolioform, OL 7. 8, OW 4.4, OL/OW 1.8.

Taxonomic summary

Type host: Nala lividipes, (Datta and Haldar, 1984).

Type locality: India (Datta and Haldar, 1984).

References: Datta and Haldar, 1984.

Remarks

Gregarina nalae has not been reported since its original description in which Datta and Haldar (1984) provide only minimal data for associations, gamonts, and oocysts. This taxon is based largely on oocyst data, gamont size, and relative gamont morphology. Gamontic morphometrics are incompletely known but sufficient to evaluate most of the cardinal characters differentiating species within the genus. The taxonomic identity and stability of *G. nalae* would be considerably strengthened by new collections and full redescription of all life-cycle stages.

Gregarina ambigua Amoji and Rodgi, 1976 (Figs. 19, 26)

Description

Primite: Total length 105 (90-120). Protomerite shallowly trullate, no metric known. Deutomerite

dolioform, DWM 60 (20–100). Nucleus elliptoid, NL 40, NW 18, NL/NW 2.2. Indices: DWM/PWM 1.5.

Satellite: Total length 150 (120–180). Protomerite very shallowly oblong, no metric known. Deutomerite Spatulate, DL , DWM 60 (20–100), DL/DWM. Nucleus elliptoid, NL 40, NW 18, NL/NW 2.2. Indices: DWM/PWM 2.

Association: Gamonts anisomorphic; epimerite absent; association precocious, tandem, caudofrontal. Indices: PriTL/SatTL 0.7.

Oocyst: Oblong, OL 17, OW 9.5, OL/OW 1.8.

Taxonomic summary

Type host: Forficula ambigua, (Amoji and Rodgi, 1976).

Type locality: India (Amoji and Rodgi, 1976).

References: Amoji and Rodgi, 1976; Thèodoridés et al., 1982; Datta and Haldar, 1984.

Remarks

Gregarina ambigua has not been reported since its original description in which Amoji and Rodgi (1976) provide only minimal data and descriptions of associations, gamonts, and oocysts. This taxon is based largely on oocyst data, gamont size, and relative gamont morphology, especially the morphology of the primite protomerite. Gamontic morphometrics are incompletely known but sufficient to evaluate most of the cardinal characters differentiating species within the genus. The taxonomic identity and stability of *G. ambigua* would be considerably strengthened by new collections and full redescription of all life-cycle stages.

Gregarina megaspora Amoji and Rodgi, 1976 (Figs. 21, 28)

Description

Primite: Total length 357 (208–560). Protomerite very shallowly ovoid, no metric known. Deutomerite ovoid, DWM 102 (70–135). Nucleus orbicular, NL 37.5 (35–40), NW 37.5 (35–40), NL/NW 1.0. Indices: TL/PL 5 (4–6), DWM/PWM 1.75 (1.5–2).

Satellite: Total length 357 (208–560). Protomerite depressed oblong to depressed ovoid, no metric known. Deutomerite obovoid, DWM 102 (70–135). Nucleus orbicular, NL 37.5 (35–40), NW 37.5 (35–

40), NL/NW 1.0. Indices: TL/PL 8 (7–9), DWM/ PWM 1.75 (1.5–2).

Association: Gamonts anisomorphic; epimerite absent; association precocious, tandem, caudofrontal. Indices: PriTL/SatTL 1.0.

Oocyst: Dolioform, OL 26, OW 13, OL/OW 2.

Taxonomic summary

Type host: Forficula ambigua, (Amoji and Rodgi, 1976).

Type locality: India (Amoji and Rodgi, 1976).

References: Amoji and Rodgi, 1976; Thèodoridés et al., 1982; Datta and Haldar, 1984

Remarks

Gregarina megaspora has not been reported since its original description in which Amoji and Rodgi (1976) provide only minimal data for associations, gamonts, and oocysts. This taxon is based largely on oocyst and gamont size, both stages being generally much more massive than related taxa. Gamontic morphometrics are incompletely known but sufficient to evaluate most of the cardinal characters differentiating species within the genus. The taxonomic identity and stability of *G. megaspora* would be considerably strengthened by new collections and full redescription of all life-cycle stages.

DISCUSSION

Careful reconsideration of available data and observations of the 9 members of the genus Gregarina reported from dermapteran hosts reveals 1 new synonymy and 3 species inquirendae, leaving 5 species with stable taxonomic identities from earwigs: G. tropica, G. ovata, G. nalae, G. ambigua, and G. megaspora. Gregarina chelidurellae, G. labidurae, and G. fallax are unique taxa but require additional collections and redescription to confirm and stabilize their taxonomic identities. As suggested by Clopton et al. (2007), this review of the dermapteran gregarine guild in the light of the complete data set for G. tropica makes it possible to assess the stability of described species in the guild and set future collection and redescription priorities for gregarines parasitizing earwigs.

ACKNOWLEDGMENTS

Michael A. Barger was the acting editor for this manuscript, arranging reviews and assuming full

editorial discretion in addition to his continued service on the Editorial Board of *Comparative Parasitology*. The manuscript was markedly improved as a result of his editorial suggestions. As Editor and Associate Editor, T.J.C. and R.E.C. thank Dr. Barger for assuming editorial responsibilities so that we can contribute to the Helminthological Society of Washington through continued publication in *Comparative Parasitology*.

This material is based upon work supported by the National Science Foundation through grant NSF DEB 0340774 to R.E.C. and NSF DEB 0340782 to T.J.C. Any opinions, findings, and conclusions, or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

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