

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

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ABSTRACT: *Naiadocystis phykoterion* n. gen., n. sp. (Apicomplexa: Eugregarinida: Hirmocystidae), is described from the Mexican pygmy grasshopper, *Paratettix mexicanus* (Orthoptera: Tetrigidae), collected from sandbars along Harmon Creek, Walker County, Texas, in the western edge of the Texas Big Thicket. *Naiadocystis* n. gen. is distinguished by the form of the epimerite complex, a simple cordoid or toroid epimerite with an interior obconoid structure resembling a funnel that tapers to a distinct axial canal bisecting the protomerite, which is conspicuous in all stages of development, and a satellite protomerite reduced to a linearly crateriform cup or sucker that receives and enfolds posterior end of primate deutomerite. Association is precocious, caudofrontal, and biassociative. Gametocysts are spherical. Sporoducts are present but vestigial and irregular in number. Oocysts are broadly ellipsoid with 4 small spherical polar knobs, 1 each at 30°, 150°, 210°, and 330°, and dehisce en masse. The species described herein are differentiated by their overall size and relative proportion of cellular structures. *Naiadocystis acantholobae* (Hoshide, 1952) n. comb., *Naiadocystis acrydiinarum* (Semans, 1939) n. comb., and *Naiadocystis tetrigis* (Corbel, 1968) n. comb. are recognized as members of *Naiadocystis* previously placed within *Gregarina* (Apicomplexa: Eugregarinida: Gregarinidae).

The Mexican pygmy grasshopper, *Paratettix mexicanus* (Saussure, 1861) Rehn and Grant, 1957 (Orthoptera: Tetrigidae), is a small (ca. 10 mm) grouse locust occurring throughout northern Mexico and from Florida to California in the southern United States (Rehn and Grant, 1961; Capinera et al., 1997; Bastow et al., 2002). *Paratettix mexicanus* is a specialist herbivore associated with riparian habitats grazing on river algae stranded by seasonal changes in water level (Capinera et al., 1997; Bastow et al., 2002). During an ongoing biotic survey of the gregarine parasites of North American insects, a heretofore unknown gregarine species was discovered in populations of *P. mexicanus* collected from the sandbars of Harmon Creek on the western edge of the Texas Big Thicket. The gregarine populations recovered are taxonomically distinct from known gregarine species and represent a new species. The structure of the epimerite and the protomerite of the satellite unites this species with 3 previously described species, *Gregarina acantholobae* Hoshide, 1952, *Gregarina acrydiinarum* Semans, 1939, and *Gregarina tetrigis* Corbel, 1968, and distinguishes the group from all other described species of *Gregarina*. This work uses an extended gregarine morphometric set (Clopton, 1999; Clopton and Nolte, 2002) on mature or invariant stages to describe the new species, establishes a new genus within Hirmocystidae, and accompanies the placement of *G. acantholobae*, *G. acrydiinarum*, and *G. tetrigis* within the new genus with new nomenclatural combinations.

MATERIALS AND METHODS

Paratettix mexicanus adults were collected from exposed sandbars in Harmon Creek on the Sam Houston State University (SHSU) Center for Biological Field Studies, Huntsville, Walker County, Texas (30°44'44.7"N, 95°28'46.2"W), on 30 May 2002. Grasshoppers were transported to the laboratory at SHSU and held in a screened insect cage before processing. Eight individuals were prepared as permanent voucher specimens, and 13 individuals were killed and examined for gregarine parasites within 24 hr of collection. Grasshoppers were evis-

cerated 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 with ethanol, formalin, and acetic acid, stained with either Semichon acetocarmine or Harris hematoxylin and eosin-xytol, and mounted in Damar balsam as described by Clopton (1996, 1999, 2000). Gametocysts were collected from the hindgut and rectum during postmortem examinations, triple rinsed in insect muscle saline, and transferred with a moist 000 paintbrush to individual glass microvials (insect genitalia vials, BioQuip Products, Gardena, California). Distilled water (50 µl) was added to half the vials; the remaining vials were stored dry, retaining only the surface moisture of the gametocyst. Vials were sealed with white silicon stoppers and gametocysts held for maturation and dehiscence. Gametocysts were observed daily, and the appearance, form, distribution, and number of sporoducts were noted. Oocyst structure and dimensions were taken from fresh preparations of oocysts in agar monolayer mounts (Clopton, 1999, 2000).

Observations were made using an Olympus B-Max 50 compound microscope with ×20, ×40, and ×100 universal planapochromatic objectives and either phase-contrast condensers or differential interference contrast prisms. Digital photographs were taken with an 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 digitized images of live and preserved specimens using Image-Pro Express® version 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® 7.0.1 software (Adobe Systems, Inc., San Jose, California).

Morphometric measurements taken are largely according to those proposed by Clopton (1999), although additional metrics particular to the genus of study are also presented in this study. 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 is largely according to 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 J. G. Harris and M. W. Harris (1994).

DESCRIPTION

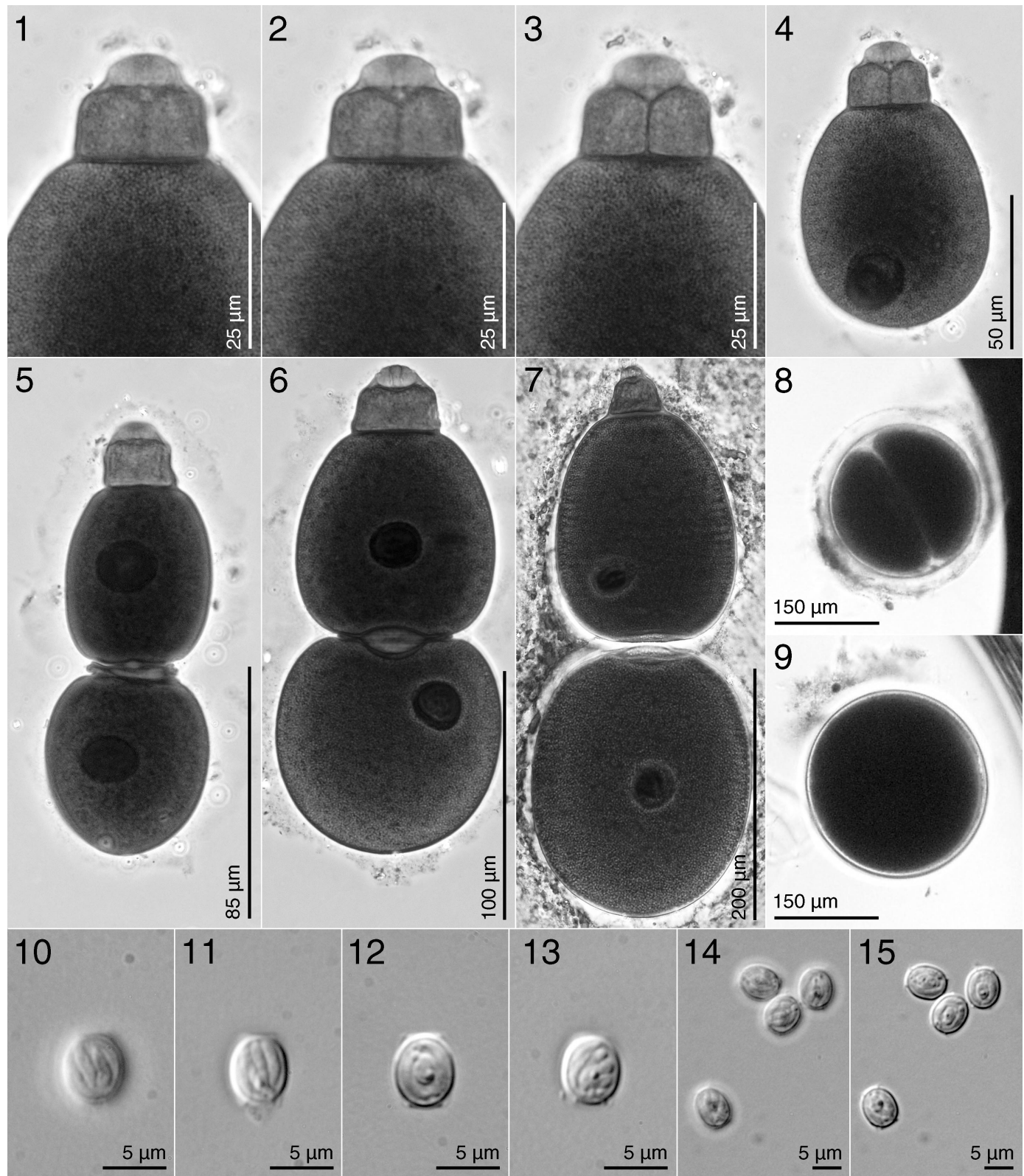
***Naiadocystis* n. gen.**

(Figs. 1–26)

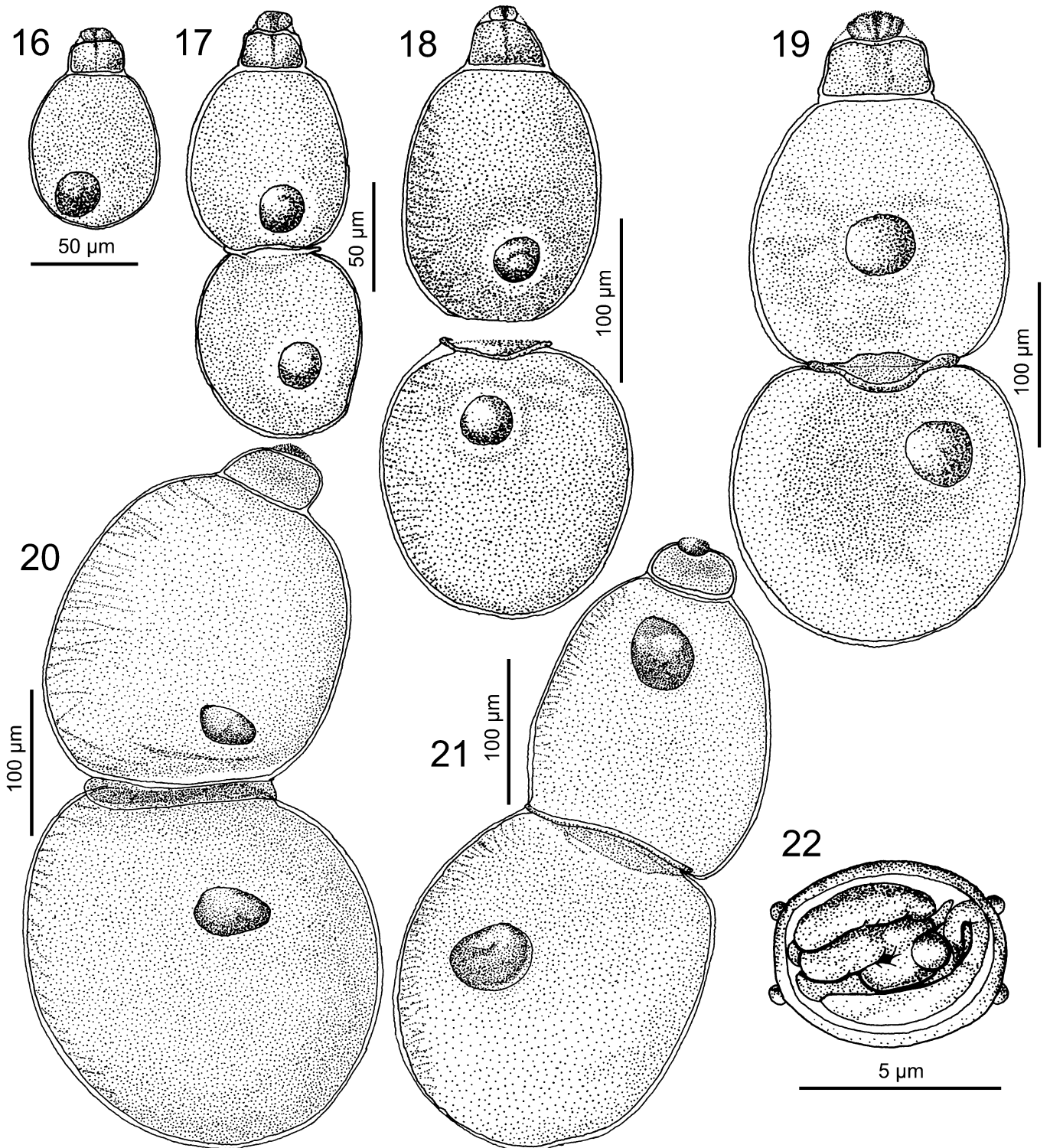
Diagnosis: Eugregarinida Léger, 1892, sensu strictu Levine et al. (1980); Septatina Lankester, 1885, sensu strictu Levine et

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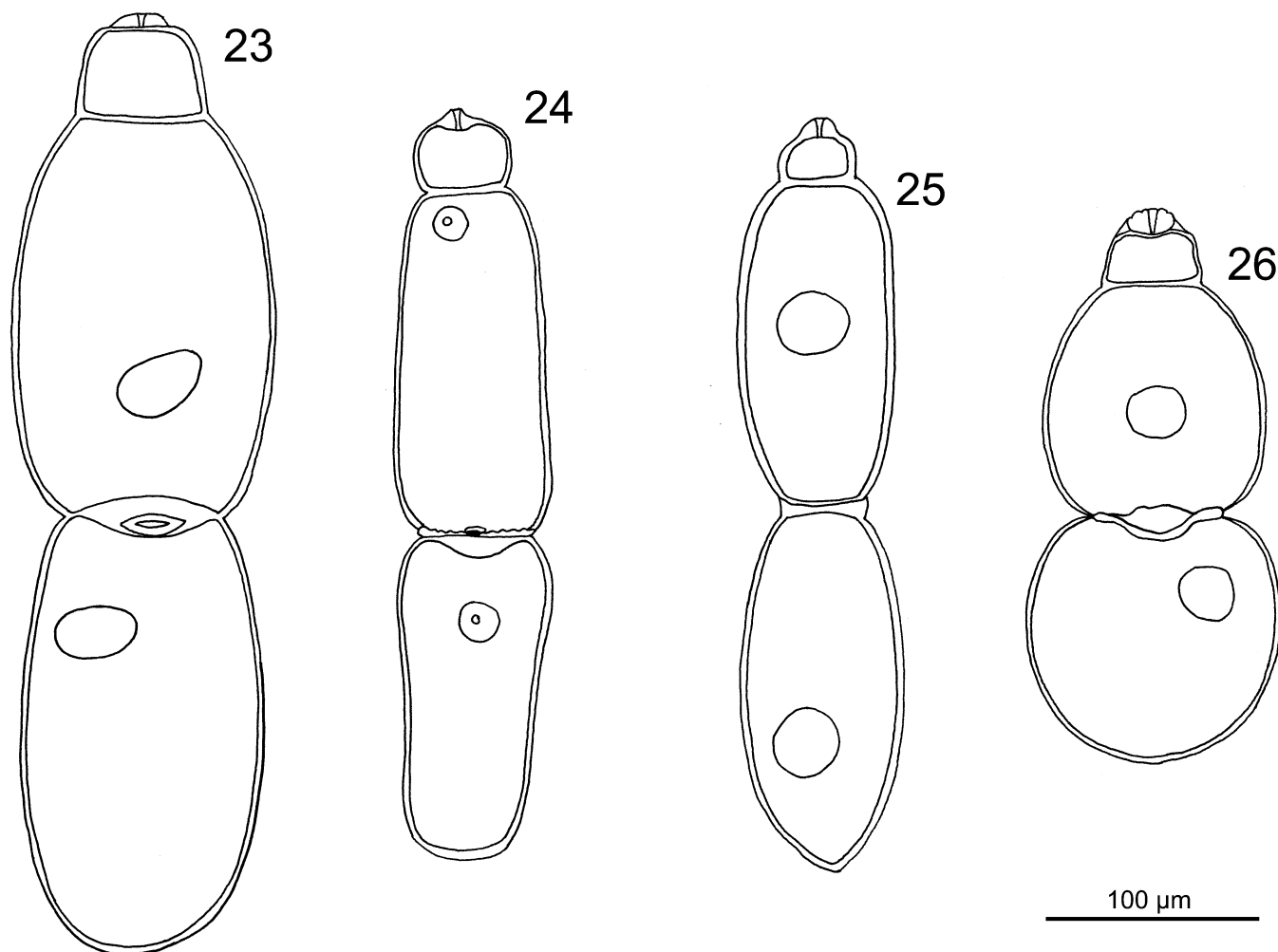
FIGURES 1–15. *Naiadocystis phykoterion*, n. gen, n. sp. 1–3. Optical sections through a young trophozoite detailing the epimeritic funnel with associated axial canal through protomerite. 4. Young trophozoite. 5. Immature association. 6–7. Mature associations. 8. Fresh gametocyst containing unfused gamonts. 9. Gametocyst with fused gamonts. 10–15. Oocysts.



FIGURES 16–22. *Naiadocystis phykoterion*, n. gen., n. sp. 16. Young solitary trophozoite. 17. Trophozoites in precocious association. 18. Trophozoites in precocious association separated to detail the nature of the satellite's protomeritic cupule. 19–21. Mature associations. 22. Oocyst.

al. (1980); Gregarinicae Chakaravarty, 1960; and Hirmocystidae Grassé, 1953, sensu Clopton, 2002, in Perkins et al. (2002); with characters of *Naiadocystis* n. gen.: epimerite a simple cordoid or toroid epimerite with an interior obconoid structure resembling a funnel that tapers to a distinct axial canal bisecting

the protomerite, enveloped by an accessory form-fitting membrane, conspicuous in all stages of development but reduced in satellites in association; satellite protomerite reduced to a linearly crateriform cup or sucker that receives and enfolds posterior end of primate deutomerite; association precocious, cau-



FIGURES 23–26. Comparative morphology of 4 species of *Naiadocystis*. **23.** *Naiadocystis tetrigris*, n. comb. (after Corbel, 1968). **24.** *Naiadocystis acantholobae*, n. comb. (after Hoshide, 1952). **25.** *Naiadocystis acrydiinarum*, n. comb. (after Semans, 1939). **26.** *Naiadocystis phykoterion* n. sp.

dofrontal, biassociative; gametocysts spherical, hyaline coat present; sporoducts present but reduced, irregular in number; oocysts axially symmetric, broadly elliptoid with 4 small spherical polar knobs, 1 each at 30°, 150°, 210°, and 330°, relative to the longitudinal axis of the oocyst, extruded en masse through rupture of sporoducts or by simple rupture in loose chains that immediately dissipate as individual oocysts in water.

Taxonomic summary

Type species: *Naiadocystis phykoterion* n. sp.

Other described species: *Naiadocystis acantholobae* n. comb., syn. *G. acantholobae* Hoshide, 1952; *Naiadocystis acrydiinarum* n. comb., syn. *G. acrydiinarum* Semans, 1939; and *Naiadocystis tetrigris* n. comb., syn. *G. tetrigris* Corbel, 1968.

Etymology: The generic name *Naiadocystis* is taken from the Latin root *Naias*, meaning a water nymph. The name is given to mark the association of the genus with hosts restricted to riparian habitats.

Remarks

Naiadocystis bears general resemblance to only 2 known gregarine genera: *Gregarina* (Gregarinidae) and *Didymophyes*

(Didymophyidae). Reduction of the satellite protomerite is common to both *Naiadocystis* and *Didymophyes*; however, the protomerite is reduced to a linearly transverse cupule in *Naiadocystis*, whereas it is lost in *Didymophyes*. *Naiadocystis* and *Gregarina* are generally similar in form, but *Naiadocystis* is characterized by the reduced, linearly transverse cupule form of the satellite protomerite and the distinct, internally complex form of the epimerite. Whereas the epimerite among *Gregarina* is a simple sphere or button, the epimerite of *Naiadocystis* is cordoid with an interior obconoid funnel tapering to a distinct axial canal that bisects the protomerite. The 3 genera are also distinguished by oocyst structure and gametocyst dehiscence. Oocysts are dolioform or elliptic and unornamented in *Gregarina* and ovoid and unornamented in *Didymophyes* but broadly elliptoid with 4 small spherical polar knobs, 1 each at 30°, 150°, 210°, and 330°, relative to the longitudinal axis of the oocyst in *Naiadocystis*. Among *Gregarina*, gametocysts dehiscence in chains through multiple sporoducts, and among *Didymophyes*, they dehiscence by simple rupture. In contrast, the gametocysts of *Naiadocystis* dehiscence through rupture of vestigial sporoducts in loose chains that immediately dissipate into a spore mass.

Gametocyst dehiscence in *Naiadocystis* most closely resembles the simple rupture observed among Hirmocystidae. Although vestigial sporoducts are present in the maturing gametocyst, they do not fully develop or oocysts do not issue from these sporoducts in the adherent chains characteristic of *Gregarina*. No known species of *Gregarina* possesses an oocyst ornamented with polar knobs, but such oocysts are not unknown among Hirmocystidae. The oocysts of *Protomagalhaensia* (Hirmocystidae) possess corner spines or knobs but their trophozoites and gamonts are markedly different from those of *Naiadocystis*. Thus, *Naiadocystis* shares the cardinal characters of Hirmocystidae but is clearly distinct from known hirmocystid genera.

***Naiadocystis phykoterion* n. sp.**

(Figs. 1–22)

Trophozoites (Figs. 1–5, 16–18): Developing trophozoites solitary or in precocious association, attached to host cecal or intercecal epithelium. Solitary individuals similar in structure to gamontic primites but with a relatively smaller and more elongate deutomerite. Young associations similar to gamontic associations but with relatively smaller and more ovoid deutomerites.

Gamontic association (Figs. 6, 7, 19–21): Caudofrontal, biasociative, precocious; isogamontic because of differences in the protomerite. Data reported for mature gamonts in associations only. Association length (AsL) 260.9 (148.3–440.4, 67.2, 60), width of primate–satellite junction (JW) 58.3 (26.8–105.3, 16.9, 60), primate total length (PTL) 139.4 (84.6–222.0, 31.9, 60), satellite total length (STL) 122.4 (63.7–218.7, 35.5, 60), PTL/STL 1.2 (1.0–1.5, 0.1, 60), AsL/JW 4.6 (2.6–6.5, 0.8, 60), AsL/PTL 1.9 (1.6–2.0, 0.1, 60), AsL/STL 2.2 (2.0–2.5, 0.1, 60).

Primate (Figs. 6, 7, 19–21): Holdfast a simple cordoid or toroid epimerite with inconspicuous longitudinal surface sulci and an interior obconoid structure resembling a funnel that tapers to a distinct axial canal bisecting the protomerite, conspicuous in all stages of development, enveloped by an accessory form-fitting membrane, epimerite very broadly elliptoid, becoming transversely elliptoid in larger gamonts, length (EpiL) 9.1 (5.0–14.0, 1.8, 60), width (EpiW), 15.4 (9.6–21.7, 2.6, 60), width at septal junction with protomerite (EpiSW) 22.6 (15.9–31.2, 3.7, 60). Protomerite obturbinoid to narrowly transverse obturbinoid with retuse anterior margin at septal junction with epimerite, length (PL) 21.1 (12.8–31.7, 4.2, 60), width (PW) 32.7 (20.7–45.2, 5.3, 60). Protomerite–deutomerite septum clearly marked, retuse, without conspicuous marginal constriction, width at septum (SW) 39.4 (25.0–53.8, 6.5, 60). Deutomerite elliptoid to very broadly elliptoid with truncate anterior margin at junction with protomerite, length (DL) 109.6 (62.6–185.0, 28.5, 60), maximum width (DWM) 96.2 (49.9–160.0, 23.1, 60), distance from protomerite–deutomerite septum to DWM (DLA) 64.7 (30.1–124.1, 20.0, 60), distance from DWM to primate–satellite junction (DLP) 44.9 (27.4–83.4, 11.2, 60). Total length (TL) 139.4 (84.6–222.0, 31.9, 60). Indices: EpiL/EpiW 0.6 (0.4–1.1, 0.1, 60), PL/PW 0.7 (0.4–1.0, 0.1, 60), PL/SW 0.5 (0.4–0.9, 0.1, 60), PW/SW 0.8 (0.6–1.0, 0.1, 60), DL/DWM 1.1 (0.8–1.5, 0.1, 60), DLA/DWM 0.7 (0.4–1.0, 0.1, 60), DLP/DWM 0.5 (0.4–0.7, 0.1, 60), DLA/DL 0.6 (0.4–0.7, 0.1, 60), DWM/SW 2.4 (1.9–3.4, 0.3, 60), TL/PL 6.6 (5.2–9.2, 0.9,

60), DL/PL 5.2 (3.8–7.7, 0.9, 60), DWM/PW 2.9 (2.0–4.9, 0.6, 60), TL/DL 1.3 (1.2–1.4, 0.0, 60). Nucleus roughly spherical but ranging from elliptoid to transversely elliptoid in larger gamonts, axial to abaxial, equatorial to postequatorial, length (NL) 23.5 (14.7–33.7, 4.3, 60), width (NW) 25.0 (13.8–35.6, 5.2, 60), distance from protomerite–deutomerite septum to nucleus (NDS) 56.1 (10.8–138.3, 25.9, 60), NL/NW 1.0 (0.6–1.6, 0.2, 60).

Satellite (Figs. 6, 7, 19–21): Holdfast absent. Protomerite reduced to a linearly crateriform cup or sucker that receives and enfolds posterior end of primate deutomerite (Figs. 6, 7, 18). Protomerite–deutomerite septum clearly marked, retuse to convex to match the posterior margin of primate deutomerite, usually with pronounced marginal constriction. Deutomerite spheroid to broadly elliptoid, with retuse to obcordate anterior margin at junction with protomerite, becoming reniform in larger gamonts, DL 122.4 (63.7–218.7, 35.5, 60), DWM 114.7 (55.7–194.9, 30.8, 60), DLA 54.7 (30.9–108.1, 18.0, 60), DLP 67.6 (33.2–113.4, 19.6, 60). Total length 122.4 (63.7–218.7, 35.5, 60). Indices: TL/DL 1.0 (1.0–1.0, 0.0, 60), DL/DWM 1.1 (0.8–1.4, 0.1, 60), DLA/DWM 0.5 (0.3–0.7, 0.1, 60), DLP/DWM 0.6 (0.4–0.9, 0.1, 60), DLA/DL 0.4 (0.3–0.6, 0.1, 60), DWM/SW 2.0 (1.3–2.7, 0.3, 60). Nucleus roughly spherical but ranging from elliptoid to transversely elliptoid in larger gamonts, generally abaxial and pre-equatorial, NL 24.1 (12.2–38.1, 5.8, 60), NW 26.4 (16.7–37.5, 4.9, 60), NDS 43.4 (7.2–113.4, 24.5, 60), NL/NW 0.9 (0.4–1.4, 0.2, 60).

Gametocysts (Figs. 8, 9): White to pale yellow in color; roughly spherical, length (GL) 243.8 (195.5–321.2, 34.2, 50), width (GW) 239.1 (192.0–320.1, 34.1, 50), GL/GW 1.0 (1.0–1.0, 0.0, 50); hyaline coat apparent, thickness (HC) 12.1 (6.1–22.4, 6.1, 50), HC/GL 24.3 (11.2–40.0, 9.1, 50). Gametocysts stored in distilled water mature within 72 hr and dehiscence through roughly 3 small or vestigial spore ducts perforating the gametocyst wall; extruded en masse through ruptured sporoducts or by simple rupture in loose chains that immediately dissipate as individual oocysts in water; epispore packet absent, no gametocyst residuum observed. Gametocysts stored dry fail to develop, shriveling to approximately one-third of their original size.

Oocysts (Figs. 10–15, 22): Axially symmetric, very uniform in size and shape, broadly elliptoid, length (OL) 5.6 (5.4–5.8, 0.1, 30), width (OW) 4.7 (4.4–5.0, 0.1, 30), OL/OW 1.2 (1.1–1.3, 0.0, 30); with 4 small spherical polar knobs, 1 each at 30°, 150°, 210°, and 330°, relative to the longitudinal axis of the oocyst; with a single oocyst wall, thickness (WT) 0.4 (0.3–0.5, 0.1, 30), OL/WT 13.1 (10.6–19.2, 2.2, 30); oocyst residuum present, diameter (RD) 0.7 (0.5–1.0, 0.1, 30), residuum eccentricity or distance between residuum and nearest pole (RE) 2.4 (1.8–2.7, 0.2, 30), OL/RD 7.8 (5.9–12.0, 1.1, 30), OL/RE 2.4 (2.1–3.2, 0.2, 30); octozooic; extruded en masse or in loose chains that dissipate as individual oocysts in water.

Taxonomic summary

Host: *Paratettix mexicanus* (Saussure, 1861) Rehn and Grant, 1957 (Orthoptera: Tettigidae).

Symbiotype: Three symbiotype specimens (author's specimens JLC02002, JLC02047, and JLC02048) are deposited in the Texas A&M University Insect Collection (TAMUIC), De-

partment of Entomology, Texas A&M University, College Station, Texas. Five symbiotype specimens (author's specimens JLC02042–JLC02046) are deposited in the Sam Houston State University Insect Collection (SHSUC), Department of Biology, SHSU, Huntsville, Texas. All symbiotype specimens bear a 5-line collection pin-label as follows: "Texas: Walker Co.; SHSU Field Station; Harmon Cr. near Dam; 30-V-2002; Cook, Cook, & Clopton." All specimens bear a secondary pin-label bearing the authors' specimen number. Neither TAMUIC nor SHSUC assigns individual accession numbers.

Host records: *Paratettix mexicanus*; adults.

Localities: Harmon Creek, Sam Houston State University Center for Biological Field Studies, Huntsville, Walker County, Texas (30°44'44.7"N, 95°28'46.2"W) (type locality).

Infection site: Trophozoites and gamonts were collected from the pyloric ceca and intercecal region of the ventriculus. Associations primarily located in the intercecal region and sporadically the ileum. Gametocysts were collected from the host hindgut and rectum.

Prevalence: Overall sample prevalence 92.3% (12 of 13 grasshoppers examined after death).

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 45354 (author's slide REC02021B) is a hapantotype containing multiple trophozoites, gamonts, and associations. The paratype series includes 38 slides containing trophozoites, gamonts, and associations: HWML 45355–45391 (REC02006a–d, REC02007a, REC02007b, REC02008a, REC02008b, REC02020a–c, REC02021a, REC02021c–j, REC02023a–d, REC02024a–d, REC02025a, REC02026a–d, REC02028a–c, and REC02029a). No paratype specimen is retained by the authors.

Etymology: The specific epithet *phykoterion* is derived from Greek, meaning "found in or inhabiting the algae" and is given to mark the association of this parasite with the stranded algal niche of its host, *P. mexicanus*.

Remarks

This work establishes *Naiadocystis* within the Hirmocystidae with the description of *N. phykoterion* and recognizes 3 additional members of the genus previously assigned to *Gregarina*: *N. acantholobae* n. comb., syn. *G. acantholobae* Hoshide, 1952; *N. acrydiinarum* n. comb., syn. *G. acrydiinarum* Semans, 1939; and *N. tetrigris* n. comb., syn. *G. tetrigris* Corbel, 1968. Although the gametocysts and oocysts are unknown for *N. acantholobae*, *N. acrydiinarum*, and *N. tetrigris*, all 3 species share the cardinal gamontic characters of *Naiadocystis*: a reduced, linearly transverse cupule forming the satellite protomerite and the distinct epimeritic complex combining a cordoid epimerite with an interior obconoid funnel tapering to a distinct axial canal that bisects the protomerite.

All 4 species of *Naiadocystis* are differentiated by the morphology of gamontic forms in association (Figs. 23–26). All morphometric data and observations for *N. acrydiinarum*, *N. acantholobae*, and *N. tetrigris* are derived from Semans (1939), Hoshide (1952), and Corbel (1968), respectively. Associations of *N. phykoterion* (Fig. 26) are smaller on average (AsL = 260.9) than those of *N. acantholobae* (Fig. 24), *N. acrydiinarum*

(Fig. 25), and *N. tetrigris* (Fig. 23) (AsL = 334.0, 347.0, and 450, respectively). Primites of *N. phykoterion* possess a protomerite that is relatively shorter (PL/TL = 0.15) and broader (DL/DWM = 1.10) than those of *N. acantholobae*, *N. acrydiinarum*, and *N. tetrigris* (PL/TL = 0.23, 0.20, and 0.20; DL/DWM = 1.50, 1.43, and 1.50, respectively). Satellites of *N. phykoterion* possess a deutomerite that is broad and spherical (DL/DWM = 1.10) rather than ellipsoid (*N. tetrigris* and *N. acrydiinarum*, DL/DWM = 1.84, 1.81, respectively) or cylindroid (*N. acantholobae*, DL/DWM = 1.66) and much wider than the protomeritic cupule (JW/DWM = 0.51). *Naiadocystis acantholobae*, *N. acrydiinarum*, and *N. tetrigris* have average JW/DWM ratios of 0.64, 0.48, and 0.60, respectively. In addition, *N. acantholobae* and *N. tetrigris* possess an epicytic lens or ring at the primate–satellite junction that does not occur in *N. phykoterion* or *N. acrydiinarum*. Ultrastructural studies of the epicytic lens in *N. acantholobae* demonstrate that this is a reliable structural character and not an artifact of fixation (Hoshide, 1975). *Naiadocystis acantholobae* is characterized by a nucleus with a single, distinct karyosome, but no karyosome is reported for any other member of the genus.

All 4 species of *Naiadocystis* are described from tetrigid grasshoppers. *Naiadocystis phykoterion* is described from *P. mexicanus* in Texas; *N. acantholobae* from *Criotettix japonicus* (de Haan, 1842) Günther, 1938 (= *Acantholobus japonicus* (de Haan, 1842) Hancock, 1906; = *Acridium japonicus* de Haan, 1842) in Yamaguti Prefecture, Japan; *N. acrydiinarum* from *Tetrix arenosa* Burmeister, 1838 (= *Acrydium arenosum* Hancock, 1902), and *Paratettix cucullatus cucullatus* (Burmeister, 1838) Rehn and Grant, 1961, in Delaware and Franklin Counties, Ohio; and *N. tetrigris* from *Tetrix tenuicornis* Sahlberg, 1891, in La Celle-sur-Loire, Nièvre, France. All tetrigids are riparian in distribution, and the detailed niche and dietary habits documented for *P. mexicanus* by Bastow et al. (2002) serve to characterize the group in general. *Paratettix mexicanus* is tightly associated with the near-stream riparian, usually within 1 m of the water's edge (Bastow et al., 2002). The pygmy grasshoppers feed almost exclusively on alga stranded on sandbars and cobble by variation in stream flow (Capinera et al., 1997; Bastow et al., 2002), deriving more than 80% of their carbon from this single source. Such habitat fidelity is well suited to gregarine infection. The habitat provides the moisture essential for gametocyst survival and development, and concentrated host populations living and defecating on their food source (stranded algae) probably increase the rate of transmission. In combination, these factors may explain the high prevalence rate of *N. phykoterion* in *P. mexicanus* (92.3%). Strict host habitat fidelity may also contribute to isolation of gregarine populations, producing higher parasite diversity than might otherwise be expected.

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