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Revision of *Geneiorhynchus* Schneider, 1875 (Apicomplexa: Eugregarinida: Actinocephalidae: Acanthosporinae) with Recognition of Four New Species of *Geneiorhynchus* and Description of *Geneiorhynchus manifestus* n. sp. Parasitizing Naiads of the Green Darner, *Anax junius* (Odonata: Aeshnidae) in the Texas Big Thicket

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ABSTRACT: *Geneiorhynchus manifestus* n. sp. (Apicomplexa: Eugregarinida) is described from the naiads of *Anax junius* (Odonata: Aeshnidae) collected from the Big Sandy Creek Unit of the Big Thicket National Preserve, Polk County, Texas, U.S.A. The genus *Geneiorhynchus* is revised and its constituent species reviewed. Descriptions are provided for 2 previously named species, *Geneiorhynchus monnieri* from naiads of *Libellula depressa* (Odonata: Libellulidae) collected from Bayreuth, Germany and Roscoff, France and *Geneiorhynchus aeshnae* from naiads of *Aeshna constricta* and *Aeshna* sp. (Odonata: Aeshnidae) collected from Pennsylvania, U.S.A., and Cheboygan County, Michigan, U.S.A.; and 3 previously reported taxa recognized as new species: *Geneiorhynchus desportesi* n. sp. from naiads of *Aeshna cyanea* (Odonata: Aeshnidae) collected from Montpellier, France, *Geneiorhynchus baudoini* n. sp. from naiads of *Aeschna grandis* (Odonata: Aeshnidae) collected from Vincennes and Besse-et-Saint Anastaise, France, and *Geneiorhynchus shteini* n. sp. from naiads of *Aeshna cyanea* and *Aeshna* sp. (Odonata: Aeshnidae) collected from Lakes Pert and Svyat, Karelian Republic, Russian Federation and both Hersbruck and Bamberg, Germany.

KEY WORDS: Apicomplexa, Actinocephalidae, Actinocephalinae, Gregarine, *Geneiorhynchus monnieri*, *Geneiorhynchus aeshnae*, *Geneiorhynchus desportesi* n. sp., *Geneiorhynchus baudoini* n. sp., *Geneiorhynchus shteini* n. sp., *Geneiorhynchus manifestus* n. sp., dragonfly, Odonata, Aeshnidae, *Anax junius*, *Aeshna*.

Geneiorhynchus was established by Schneider (1875) as a monotypic genus comprising *Geneiorhynchus monnieri* Schneider, 1875 described from the digestive tracts of dragonfly (Odonata) naiads collected from the biological station at Roscoff, France. The original description addresses trophozoite and oocyst life-cycle stages. However, the description provides no metric character, identifies no host beyond the subordinal level, establishes neither host voucher nor parasite type material, and stresses the unique nature of the spined holdfast as justification for both the new genus and its type species. The trophozoites and epimerite are well illustrated, but no oocyst is illustrated. *Geneiorhynchus aeshnae* Crawley, 1907 (=*Geniorhynchus aeshnae* Crawley, 1907, lapsus calami) is the only other described species in the genus and was originally described from naiads of *Aeshna constricta* Say collected in southeastern Pennsylvania, U.S.A. The description includes morphological details of the trophozoite, reportedly 420 μm long, but no other metric characters or descriptions of other life-cycle stages. Crawley states that the Pennsylvania form of *Geneiorhynchus* is "probably distinct from the European form," but makes no supporting morphological case. Although *Geneiorhynchus* appears in the literature numerous times (Schneider, 1875; Léger, 1892; Labbé, 1899; Crawley, 1907; Ellis, 1913; Watson, 1916; Watson-Kamm, 1922; Shtein, 1960; Desportes, 1963; Baudoin, 1967; Geus, 1969; Levine, 1985, 1988; Clopton, 2002), neither redescription nor significant supplementary metric data have been published, leaving the known species of *Geneiorhynchus* so inadequately described that they are difficult to distinguish from one another (Desportes, 1963).

As part of an ongoing survey of the insect and eugregarine diversity of the Big Thicket region of east-central Texas, U.S.A., we collected an heretofore unknown gregarine species from naiads of the green darner, *Anax junius* (Drury) (Odonata: Anisoptera: Aeshnidae). The gregarines recovered are referable to *Geneiorhynchus* but taxonomically distinct from known species and represent a new species of *Geneiorhynchus*. Herein we revise the genus *Geneiorhynchus* Schneider, 1875; delineate an extended

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gregarine morphometric set for *Geneiorhynchus* consistent with those established for the family Stylocephalidae and the genera *Amoebogregarina*, *Calyxocephalus*, *Clitellocephalus*, *Leidyana*, *Protomagalhaensia*, *Naiadocystis*, *Stictospora*, and *Xiphocephalus* (see Clopton, 1999, 2004a, 2006; Kula and Clopton, 1999; Clopton and Nolte, 2002; Clopton et al., 2004; 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

Sixty-eight *A. junius* naiads were collected from Beaver Slide Pond, Big Sandy Creek Unit, Big Thicket National Preserve, Polk County, Texas, U.S.A. (30°38′49.0″N; 96°17′64.6″W) on 22 February 2006 with the use of aquatic dip nets, placed in 1-liter plastic jars with pond water, and stored on ice for transportation to the laboratory at Sam Houston State University, Huntsville, Texas, U.S.A. Two individuals were prepared as a permanent voucher specimens. The remaining 66 naiads were examined for gregarine infection. Dragonflies were eviscerated and their alimentary canals dissected in insect muscle saline (Belton and Grundfest, 1962). Permanent parasite preparations were made with the use of wet smears of gregarines and host gut tissues fixed by flotation on hot AFA (ethanol, formalin, and acetic acid); stained with either Semichon's acetocarmine or Harris hematoxylin and eosin–xylol; dehydrated in an ethanol series; cleared in a xylene series; and mounted in Damar balsam. Subsamples of gregarines from 10 hosts were collected and pooled in groups of 100 individuals each. The DNA from each pooled sample was isolated with the use of a protocol similar to that reported by Laird et al. (1991). Isolated DNA samples were resuspended in AE buffer (10 mM Tris · Cl; 0.5 mM EDTA, pH 9.0) and stored at –20°C for future genetic analysis.

Gametocysts were isolated from collected feces, triple rinsed in insect muscle saline, surface sterilized in 1% formalin, triple rinsed in spring water, and placed in individual silicon-stoppered 4 × 12-mm glass microvials (BioQuip Products, Gardena, California, U.S.A.) with ca. 50 μl spring water 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 were prepared as follows. Molten agar (1.5% solution) was pipetted onto a clean glass slide and allowed to drain, and the slide was quickly chilled on a cold aluminum block to produce a thin, uniform layer of agar. Oocysts were placed in a small (ca. 7 μl) drop of water on a 12-mm round cover glass (No. 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 with the use of 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 with the use of Image-Pro Discovery® version 4.0 image analysis software (Media Cybernetics, L.P., Silver Spring, Maryland, U.S.A.). Photographic plates were processed and assembled with the use of Adobe® PhotoShop® 7.0.1 software (Adobe Systems, Inc., San Jose, California, U.S.A.).

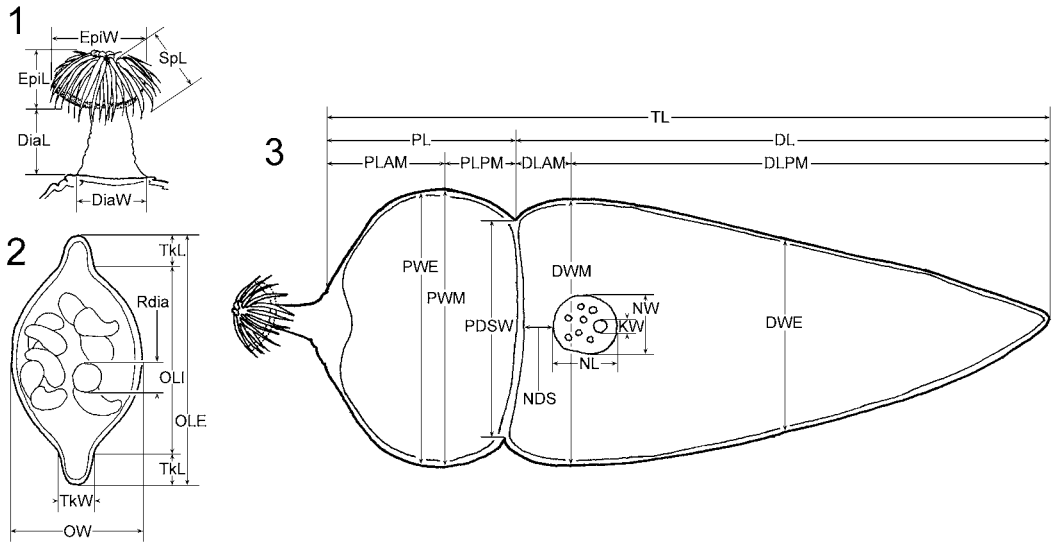
Morphometric characters and abbreviations

Extended gregarine morphometric sets (Clopton, 1999, 2004a, 2006; Kula and Clopton, 1999; Clopton and Nolte, 2002; Clopton et al., 2004; 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 *Geneiorhynchus* is delineated in Figures 1–3 and is consistent with the guidelines for actinocephalid extended character sets described by Clopton (2004a). 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).

The following metric characters and abbreviations are used herein: length of diamerite (DiaL), width of diamerite (DiaW), 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 epimerite (EpiL), width of epimerite (EpiW), karyosome diameter (KW), distance from anterior margin of nucleus to protomerite–deutomerite septum (NDS), length of nucleus (NL), width of nucleus (NW), exterior oocyst length (OLE), interior oocyst length (OLI), oocyst width (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), residuum diameter (Rdia), length of epimerite spine (SpL), length of terminal oocyst knob (TkL), width of terminal oocyst knob (TkW), total length (TL).

Use of lapsus calami, incertae sedis, and species inquirenda

We adopt the following guidelines for the use of species inquirenda, incertae sedis, and lapsus calami at the species level in gregarine taxonomy and systematics. Species inquirendae are gregarine taxa that can be confidently referred to an existing genus but for which existing data sets are insufficient to assess all of the cardinal characters that distinguish species within the genus with confidence. Such taxa require new collections and redescription to establish fully and to stabilize their identity. A gregarine taxon is of incertae sedis if it cannot be confidently referred to an existing genus because of insufficient data, distinguished as an indicator taxon representing a new genus based on the



Figures 1–3. Morphometric character set for gamonts and oocysts of *Geneiorhynchus* species. **1.** Epimerite characters mapped onto epimerite of *Geneiorhynchus manifestus* n. sp. **2.** Oocyst characters mapped onto oocyst of *Geneiorhynchus manifestus* n. sp. **3.** Trophozoite characters mapped onto mature trophozoite of *Geneiorhynchus manifestus* n. sp. (DiaL, length of diamerite; DiaW, width of diamerite; DL, length of deutomerite; DLAM, distance from protomerite–deutomerite 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; EpiL, length of epimerite; EpiW, width of epimerite; KW, karyosome diameter; NDS, distance from nucleus to protomerite–deutomerite septum; NL, length of nucleus; NW, width of nucleus; OLE, exterior oocyst length; OLI, interior oocyst length; OW, oocyst width; PDSW, width of protomerite–deutomerite septum; PL, length of protomerite; PLAM, distance from anterior end of protomerite to protomerite axis of maximum width; PLPM, distance from protomerite–deutomerite septum to protomerite axis of maximum width; PWE, width of protomerite at equatorial axis; PWM, maximum width of protomerite; Rdia, residuum diameter; SpL, length of epimerite spine; TkL, length of terminal knob; TkW, width of terminal knob; TL, total length.).

presence of unique characters, or confidently synonymized with existing stable taxa. These are, in essence, taxa that are unique but so poorly defined that they probably would not be recognized on recollection. We deem lapsus calami all subsequent incorrect spellings unless the author made specific their intent to emend the spelling of a name. Names formed by lapsus calami have no nomenclatural status.

RESULTS

Geneiorhynchus Schneider, 1875 revised

Revised diagnosis: With the characters of order Eugregarinorida Léger, 1892, sensu Clopton (2002); suborder Septatorina Lankester, 1885, sensu Clopton (2002); superfamily Stenophoricae Levine, 1984, sensu Clopton (2002); family Actinocephalidae Léger, 1892, sensu Clopton (2002); subfamily Actinocephalinae Labbé, 1899, sensu Clopton (2002); and characters of the genus *Geneiorhynchus* Schneider, 1875 revised as follows: trophozoites solitary, epimerite an orbicular, hemispherical or toroidal tumidus bearing many semifalciform or semiuniform spines, borne on an intercalating diamerite; association laterofrontal, late, just prior to syzygy; oocysts hesperidiform, released from gametocysts by simple rupture.

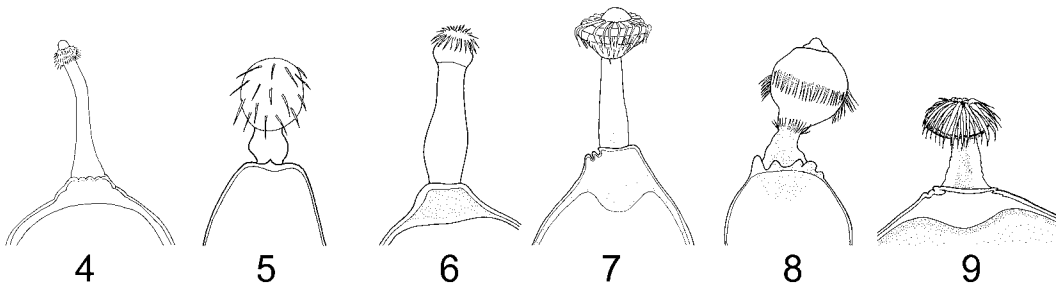
Taxonomic summary

Type species: Geneiorhynchus monnieri Schneider, 1875.

Remarks

Geneiorhynchus has made a particularly tortured nomenclatural journey from its original description to the present day. Although frequently mentioned in the literature, few new data have been added to the original generic and species descriptions of the taxon and no fully adequate species description exists for a member of the genus.

Geneiorhynchus was established by Schneider (1875) as a monotypic genus comprising only *Geneiorhynchus monnieri* Schneider, 1875 described from the digestive tracts of unidentified dragonfly (Odonata) naiads collected from the biological station



Figures 4–9. Comparative epimerite structure of *Geneiorhynchus* spp. **4.** *Geneiorhynchus monnieri* Schneider, 1875 (after Schneider [1875]). **5.** *Geneiorhynchus aeshnae* Crawley, 1907 (after "*Geniorhynchus aeshnae*" lapsus calami of Crawley [1907]). **6.** *Geneiorhynchus desportesi* n. sp. (after "*Geniorhynchus monnieri*" lapsus calami of Desportes [1963]). **7.** *Geneiorhynchus baudoini* n. sp. (after "*Geniorhynchus aeschnae*" lapsus calami of Desportes [1963]). **8.** *Geneiorhynchus shteini* n. sp. (after "*Geneiorhynchus aeschnae*" lapsus calami of Shtein [1960]). **9.** *Geneiorhynchus manifestus* n. sp.

at Roscoff, France. The original description addresses trophozoite and oocyst life-cycle stages. However, the description provides no metric characters, identifies no host beyond the subordinal level, established neither host voucher nor parasite type material, and stressed the unique nature of the spined holdfast (Fig. 4) as justification for both the new genus and its type species. The trophozoites and epimerite are well illustrated, but no oocyst is figured. Léger (1892) included *Geneiorhynchus* in his arrangement of the septate gregarines, placing the genus in Actinocephalidae group II based on oocyst shape. He included a stylized epimerite but no new figure nor datum. In his review of the sporozoans, Labbé (1899) repeated the description of Schneider, 1875, and places the genus in the subfamily Actinocephalinae, but provided no figure or datum. Curiously, Labbé (1899) emended the spelling of the generic name even though Schneider (1875) is monolithic in spelling and usage of *Geneiorhynchus*. The emendation is unjustified and an inappropriate act of the first reviser, creating 2 junior synonyms, *Geniorhynchus* Labbé, 1899 and *Geniorhynchus monnieri* Labbé, 1899, generating general confusion and a proliferation of incorrect subsequent spellings within the group (herein noted lapsus calami).

Geneiorhynchus aeshnae Crawley, 1907 ("*Geniorhynchus aeshnae*" lapsus calami) was originally described from naiads of *Aeshna constricta* Say collected in southeastern Pennsylvania, U.S.A. The description included morphological details of the trophozoite, particularly the epimerite (Fig. 5), but no metric characters or descriptions of other life-cycle stages. Crawley stated that the Pennsylvania form of *Geneiorhynchus* is "probably distinct from the European form," but elaborated no supporting morphological case. As with *G. monnieri*, no type or voucher material of *G. aeshnae* is known, no host voucher specimen is reported, and neither a metric data set nor a photographic plate documenting the species has been published.

In his "List of Gregarines of the New World," Ellis (1913) repeated the original description of *G. aeshnae* but provided no figure and no new datum. Watson (1916) listed both *G. aeshna* ("*Geniorhynchus aeschnae*" lapsus calami) and *G. monnieri* in a host–parasite cross list, but provided no description. Watson-Kamm (1922) repeated the original descriptions of *G. monnieri* ("*Genriorhynchus monnieri*" lapsus calami) and *G. aeshnae* ("*Geneiorhynchus aeschnae*" lapsus calami) and redrew figures for each but provided no new datum or figure.

Shtein (1960) reported new collections of *G. aeshnae* ("*Geneiorhynchus aeschnae*" lapsus calami) from naiads of an unidentified species of *Aeshna* collected from Lake Pert and Lake Svyat in what is now the Karelian Republic of the Russian Federation. Shtein (1960) provided gametocyst maturation and dehiscence data, new figures and observations regarding the oocyst, and a detailed description and figures of the epimerite (Fig. 8). Although this work clearly helps define the genus *Geneiorhynchus*, details of epimerite structure in the taxon described by Shtein (1960) clearly distinguish it from *G. aeshnae*, indicating a new species of *Geneiorhynchus*.

Desportes (1963) examined a single specimen, disposition unknown, of *G. monnieri* ("*Geniorhynchus monnieri*" lapsus calami) collected from *Aeshna cyanea* Müller in Montpellier, France. She provided an illustration of the epimerite (Fig. 6) and noted that the holdfast of *G. monnieri* was appreciably narrower and shorter than that of *G. aeshnae*, but no other

morphological detail and no metric datum were provided. In the same work, Desportes (1963) reported *G. aeshnae* ("*Geniorhynchus aeschnae*" lapsus calami) from naiads of *Aeschna grandis* Linnaeus collected near Vincennes, France. She provided new figures of the trophozoite and epimerite (Fig. 7) as well as a size range for observed specimens, but deposited no permanent specimens. Details of epimerite morphology (Fig. 4 vs. Fig. 5 vs. Fig. 6 and Fig. 7) clearly distinguish the gregarines reported by Desportes (1963) from *G. monnieri* sensu stricto Schneider (1875) and *G. aeshnae* sensu stricto Crawley (1907), indicating that both taxa reported by Desportes (1963) represent previously unrecognized species of *Geneiorhynchus*.

Baudoin (1967) reported new specimens of *G. aeshnae* ("*Geniorhynchus aeschnae*" lapsus calami) from naiads of *A. grandis* collected in Lake Bourdouze, south of Besse-et-Saint Anastaise, France. He provided metric data for oocysts (12 × 5.5 μm), a detailed description of the epimerite, and the first published photographs of the epimerite and oocyst of a *Geneiorhynchus* species. The taxon reported is not consistent with *G. aeshnae* sensu stricto Crawley (1907), but conforms to the taxon reported as *G. aeshnae* by Desportes (1963). No permanent specimen is known from this work.

Geus (1969) collected *G. monnieri* ("*Geneiorhynchus monieri*" lapsus calami) from naiads of *Libellula depressa* Linnaeus collected near Bayreuth, Germany. Geus (1969) reproduced the original epimerite figure of Schenider (1875) and provided metric data for gamonts but no details of epimerite, trophozoite, or oocyst morphology. He also reported new collections of *G. aeshnae* ("*Geneiorhynchus aeschnae*" lapsus calami) from naiads of *A. cyanea* collected near Hersbruck and Bamburg, Germany. He provided metric data for gamonts but also provided a complete description of the epimerite and clearly described the distinct circular and lateral bands illustrated by Shtein (1960). The disposition of no permanent specimen is known from this work. Based on his description and figure of the epimerite, the taxon reported by Geus (1969) is not *G. aeshnae* sensu stricto Crawley (1907) but rather confers to the taxon originally reported by Shtein (1960).

Thus our knowledge of *Geneiorhynchus* is not supported by a type specimen, or any permanent specimen base for that matter; is largely without metric data; and includes a confusion of poorly known taxa haphazardly grouped to form 2 indistinct species. Regardless of these problems, the genus itself is stable and easily diagnosed, given the revision herein. Although the subfamily includes several genera characterized by hesperidiform oocysts, *Geneiorhynchus* is distinguished from other members of Actinocephalinae by the generalized structure and spine-bearing nature of the epimerite.

Geneiorhynchus monnieri Schneider, 1875 (Fig. 4)

(=*Geniorhynchus monnieri* Labbé, 1899 [unjustified emendation].)

Description

Trophozoite: Solitary. Epimerite comprising a toroid to very shallowly dolioform base supporting a spineless hemielliptoid terminal tumidus, epimerite base tufted by retroarcate bristles or spines, short, sharp; epimerite borne on a long, slender diamerite; length at least 10 times length of epimerite; epimerite base width approximately equal to basal width of diamerite; protomerite broadly rounded to obvate; acuminate anteriad; protomerite deutomerite septum sharply constricted; deutomerite elongate ellipsoidal to cardioid, broadly tapering from the protomerite deutomerite septum to a sharp point posteriad; nucleus spherical, with several karyosomes.

Gamont: Solitary. Protomerite deeply deltoid to deeply cardioid, truncated posteriad by sharp constriction at protomerite–deutomerite septum, PL 74.7 (66–85, ±6.36, 11); PWM 49.8 (42–60, ±6.21, 11); PL/PWM 1.5 (1.4–1.6, ±0.09, 11). Deutomerite narrowly obdeltoid, DL 232.8 (208–257, ±17.89, 11); DWM 71.5 (60–82, ±7.8, 11); DL/DWM 3.3 (3.1–3.5, ±0.14, 11). Total length TL 307.5 (276–342, ±24.11, 11); TL/PL 4.1 (4–4.2, ±0.06, 11); DL/PL 3.1 (3–3.2, ±0.06, 11); DWM/PWM 1.4 (1.3–1.6, ±0.07, 11); TL/DL 1.3 (1.3–1.3, ±0.01, 11). Nucleus orbicular to narrowly elliptoid NL 19.3 (18–20, ±1.15, 3); NW 16.3 (15–18, ±1.53, 3); NL/NW 1.2 (1.1–1.3, ±0.07, 3) with several karyosomes.

Oocyst: Hesperidiform; liberated from the gametocyst by simple rupture.

Taxonomic summary

Type host: Dragonfly naiads.

Type locality: Roscoff, France.

Symbiotype: None.

Site of infection: Intestine.

Other records: Libellula depressa, naiads, Bayreuth, Germany.

Disposition of type specimens: No specimen from the original type series is known.

Disposition of other specimens: No permanent specimen is known.

References: Schneider (1875), Geus (1969), Clopton (2002).

Remarks

The description given here is a composite incorporating data and observations from Schneider (1875) and Geus (1969). Although sufficient data exist to diagnose the taxon, *G. monnieri* is poorly described and no permanent specimen representing the taxon exists. This species needs redescription based on new collections. *Geneiorhynchus monnieri* is the type species of *Geneiorhynchus* by monotypy based on Schneider (1875); thus new collections should lead to redescription and the disposition of neotype and voucher material to anchor both taxa.

Geneiorhynchus aeshnae **Crawley, 1907 (Fig. 5)**

(=*Geniorhynchus aeshnae* in Crawley, 1907, lapsus calami; *Actinocephalus brachydactylus* [Ellis, 1913] Shtein, 1960.)

Description

Trophozoite: Solitary. Epimerite broadly elliptoid with multiple longitudinal rows of stout retroarcate bristles or spines, terminal spineless tumidus absent; diamerite short, length about equal to length of epimerite; protomerite finely to deeply deltoid with anterior truncation, basal width greater than deutomerite; protomerite deutomerite septum sharply constricted; deutomerite narrowly ellipsoid to dolioform with anterior truncation at protomerite–deutomerite septum; nucleus spherical, with several karyosomes.

Gamont: Solitary. Protomerite orbicular, truncated posteriad by sharp constriction at protomerite–deutomerite septum, PL 80; PWM 80; PL/PWM 1.0; deutomerite narrowly elliptoid, gently rounded posteriad, truncated anteriad by sharp constriction at protomerite–deutomerite septum, DL 240; DWM 75; DL/DWM 3.2. Total length TL 320; TL/PL 4.0; DL/PL 3.0; DWM/PWM 0.94; TL/DL 1.3. Nucleus unknown.

Gametocysts: Unknown.

Oocyst: Unknown.

Taxonomic summary

Type host: Aeshna constricta Say, naiads.

Type locality: Southeastern Pennsylvania, U.S.A.

Symbiotype: None.

Site of infection: Intestine.

Other records: Aeshna sp., naiads, University of Michigan Biological Station, Douglas Lake, Cheboygan County, Michigan, U.S.A.

Disposition of type specimens: No specimen from the original type series is known.

Disposition of other specimens: No permanent specimen is known.

References: Crawley (1907), Ellis (1913), Shtein (1960), Geus (1969), Clopton (2002).

Remarks

The description given here is a composite description incorporating data and observations from Crawley (1907) and Ellis (1913). Shtein (1960) noted the original synonymy with *G. aeshnae* but the European taxon observed by Shtein (1960) is not consistent with *G. aeshnae* sensu stricto Crawley (1907), particularly in the shape of the epimerite and the arrangement of epimeritic spines. As the taxa described by Ellis (1913) and Crawley (1907) are both Nearctic, we have retained the original synonymy of Shtein (1960). Although sufficient data exists to diagnose the taxon, *G. aeshnae* is poorly described and no permanent specimen representing the taxon exists. This species needs redescription based on new collections. Collections of hesperidiform oocysts will confirm the placement of this taxon in *Geneiorhynchus*. New collections of trophozoite and gamont material, particularly comparative collections from Pennsylvania, U.S.A. and Douglas Lake, Michigan, U.S.A., will test the synonymy adopted here, stabilize the taxon, and lead to redescription and the disposition of neotype and voucher material.

Geneiorhynchus desportesi **n. sp. R. E. Clopton and T. J. Cook (Fig. 6)**

(=*Geneiorhynchus monnieri* Schneider, 1875 in part sensu "*Geniorhynchus monnieri*" lapsus calami Desportes [1963].)

Description

Trophozoite: Epimerite very broadly dolioform with an anterior tuft of retroarcate bristles or spines, with

small terminal spineless papilla; diamerite narrowly dolioform, length about 3 times length of epimerite. Protomerite, deutomerite, and nucleus unknown.

Gamont: Unknown.

Gametocysts: Unknown.

Oocyst: Unknown.

Taxonomic summary

Type host: Aeshna cyanea Müller, naiads.

Type locality: Montpellier, France.

Symbiotype: None.

Site of infection: Intestine.

Other records: None.

Disposition of type specimens: No specimen from the original type series is known.

Disposition of other specimens: No permanent specimen is known.

Etymology: The specific epithet is an honorific marking the author of the original report of this taxon, Isabella Desportes.

References: Schneider (1875), Desportes (1963).

Remarks

The description given here reflects the short descriptive report of Desportes (1963) for *G. monnieri*. Although only epimerite and host data are available, the taxon reported by Desportes (1963) is referable to *Geneiorhynchus*, but lacking both the terminal epimeritic papilla and multiple rows of epimeritic spines observed in *G. monnieri* sensu stricto Schneider (1875), differs considerably from the type (compare Fig. 4 vs. Fig. 6). Although the species is referable to *Geneiorhynchus* and is readily distinguished from existing species solely on the basis of epimerite structure, no permanent specimen is known and no description beyond the epimerite exists. We deem *G. desportesi* species inquirenda pending new collections and redescription. Collections of hesperidiform oocysts will confirm the placement of this taxon in *Geneiorhynchus*. New collections of trophozoite and gamont material will stabilize the taxon and lead to redescription and the disposition of neotype and voucher material.

Geneiorhynchus baudoini n. sp.
R. E. Clopton and T. J. Cook
(Fig. 7)

(=*Geneiorhynchus aeshnae* Crawley, 1907 in part sensu "*Geniorhynchus aeschnae*" lapsus calami Desportes [1963].)

Description

Trophozoite: Epimerite conical, very shallowly to depressed obtrullate with at least 3 circular rows of retroarcate, deeply semicrescentic spines decreasing in length posteriad by row; small terminal spineless papilla transitory; diamerite oblong, length about 2 times length of epimerite, distinctly differentiated by collar at point of insertion with protomerite. Protomerite dolioform, constricted at protomerite–deutomerite septum; endocyte densely pigmented and differentiated from sarcocyte. Deutomerite obovoid, truncated anteriad by protomerite–deutomerite septum. Total length 300–570. Nucleus elliptoid with 7–8 karyosomes.

Gamont: Unknown.

Gametocysts: Spherical, diameter 430.

Oocyst: Hesperidiform, OLE 12; OW 5.5; OLE/OW 2.2.

Taxonomic summary

Type host: Aeschna grandis Linnaeus, naiads.

Type locality: Vincennes, France.

Symbiotype: None.

Site of infection: Intestine.

Other records: A. grandis, naiads, Lake Bourdouze, Besse-et-Saint Anastaise, France.

Disposition of type specimens: No specimen from the original type series is known.

Disposition of other specimens: No permanent specimen is known.

Etymology: The specific epithet is an honorific marking the author to first publish oocyst micrographs of this taxon, J. Baudoin.

References: Desportes (1963), Baudoin (1967).

Remarks

The description given here is a composite description incorporating data and observations for *G. aeshnae* (as "*Geniorhynchus aeschnae*" lapsus

calami) given by Desportes (1963) and Baudoin (1967). Existing descriptions and figures of the epimerite provided by Desportes (1963) and Baudoin (1967), combined with the oocyst data and micrographs of Baudoin (1967) and known host associations, are sufficient to confirm placement of this species within *Geneiorhynchus*. The taxon reported by Desportes (1963) and Baudoin (1967) is consistent among these authors but is not consistent with *G. aeshnae* sensu stricto Crawley (1907), particularly in the shape of the epimerite and the arrangement of epimeritic spines. The shape of the epimerite and the arrangement of epimeritic spines are unique and sufficient to distinguish *G. baudoini* from existing species of *Geneiorhynchus*. Although sufficient data exist to diagnose the taxon, *G. baudoini* is poorly known and no permanent specimen representing the taxon exists. The species needs redescription based on new collections. New collections of trophozoite and gamont material will stabilize the taxon and lead to redescription and the disposition of neotype and voucher material.

Geneiorhynchus shteini n. sp.
R. E. Clopton and T. J. Cook
(Fig. 8)

(=*Geneiorhynchus aeshnae* Crawley, 1907 in part sensu "*Geneiorhynchus aeschnae*" lapsus calami Shtein [1960], =*Geneiorhynchus aeshnae* Crawley, 1907 in part sensu "*Geneiorhynchus aeschnae*" lapsus calami Geus [1969].)

Description

Trophozoite: Solitary. Epimerite broadly elliptoid with more than 100 bristles or spines arranged in 4 bands: 2 lateral, 1 equatorial, and 1 basal, spines of lateral and equatorial bands retroarcate, spines of basal band arcate; terminal spineless tumidus trullate; diamerite very short, fragile, length less than length of epimerite; protomerite shallowly deltoid, constricted at protomerite–deutomerite septum; deutomerite very deeply obdeltoid with anterior truncation at protomerite–deutomerite septum; nucleus spherical, with several karyosomes.

Gamont: Solitary. Protomerite shallowly deltoid, truncated posteriad by constriction at protomerite–deutomerite septum, PL 117.8 (103–126, ±7.38, 10); PWM 124.4 (111–132, ±7.28, 10); PL/PWM 0.9 (0.9–1, ±0.01, 10); deutomerite very deeply obdeltoid with anterior truncation at protomerite–deutomerite septum, DL 356.5 (315–395, ±29.12, 10); DWM 135.4 (123–146, ±7.12, 10); DL/DWM 2.6 (2.3–2.9, ±0.17, 10). Total length TL 474.3 (420–521, ±34.64, 10); TL/PL 4 (3.6–4.2, ±0.17, 10); DL/PL 3 (2.6–3.2, ±0.17, 10); DWM/PWM 1.1 (1.1–1.1, ±0.03, 10); TL/DL 1.3 (1.3–1.4, ±0.02, 10). Nucleus spherical, NL 45 (45–45, ±0, 1); NW 35 (35–35, ±0, 1); NL/NW 1.3 (1.3–1.3, ±0, 1); with several karyosomes.

Gametocysts: Orbicular, 500–700.

Oocyst: Hesperidiform, octozoic, released from gametocyst by simple rupture in water.

Taxonomic summary

Type host: Aeshna sp., naiads.

Type locality: Lakes Pert and Svyat, Karelian Republic, Russian Federation.

Symbiotype: None.

Site of infection: Intestine.

Other records: Aeshna cyanea, naiads, Hersbruck, Germany; *A. cyanea*, naiads, Bamberg, Germany.

Disposition of type specimens: No specimen from the original type series is known.

Disposition of other specimens: No permanent specimen is known.

Etymology: The specific epithet is an honorific marking the author of the original report of this taxon, Г. А. Штеин (G. A. Shtein).

References: Shtein (1960), Geus (1969).

Remarks

The description given here is a composite description incorporating data and observations for *G. aeshnae* (as "*Geneiorhynchus aeschnae*" lapsus calami) given by Shtein (1960) and Geus (1969). Existing descriptions and figures of the epimerite and oocyst provided by Shtein (1960) combined with the epimerite and gamont descriptions and morphometric data of Geus (1969) and known host associations are sufficient to confirm placement of this species within *Geneiorhynchus*. The taxon reported by Shtein (1960) and Geus (1969) is consistent among these authors but is not consistent with *G. aeshnae* sensu stricto Crawley (1907), particularly in the shape of the epimerite and the arrangement of epimeritic spines. The shape of the epimerite and the arrangement and orientation of epimeritic spinal bands are

unique and sufficient to distinguish *G. shteini* from existing species of *Geneiorhynchus*. Although sufficient data exist to diagnose the taxon, *G. shteini* is poorly known and no permanent specimen representing the taxon exists. The species needs redescription based on new collections. New collections of trophozoite and gamont material will stabilize the taxon and lead to redescription and the disposition of neotype and voucher material.

Geneiorhynchus manifestus n. sp. (Figs. 9–23)

Young trophozoites (Figs. 10–13): Solitary, extracellular forms attached to epithelium of mesenteron. Epimerite broadly elliptoid, becoming ovoid with development, armed with an equatorial row of retroarcate spines about half the length of epimerite, with development becoming a terminal circlet of spines extending beyond margin of epimerite; diamerite gladiate. Protomerite broadly ovoid, becoming broader than deutomerite with development, distinct constriction at protomerite–deutomerite septum. Deutomerite narrowly to very deeply obdeltoid, truncated by constriction of protomerite–deutomerite septum. Nucleus broadly elliptoid, with 7–10 distinct karyosomes.

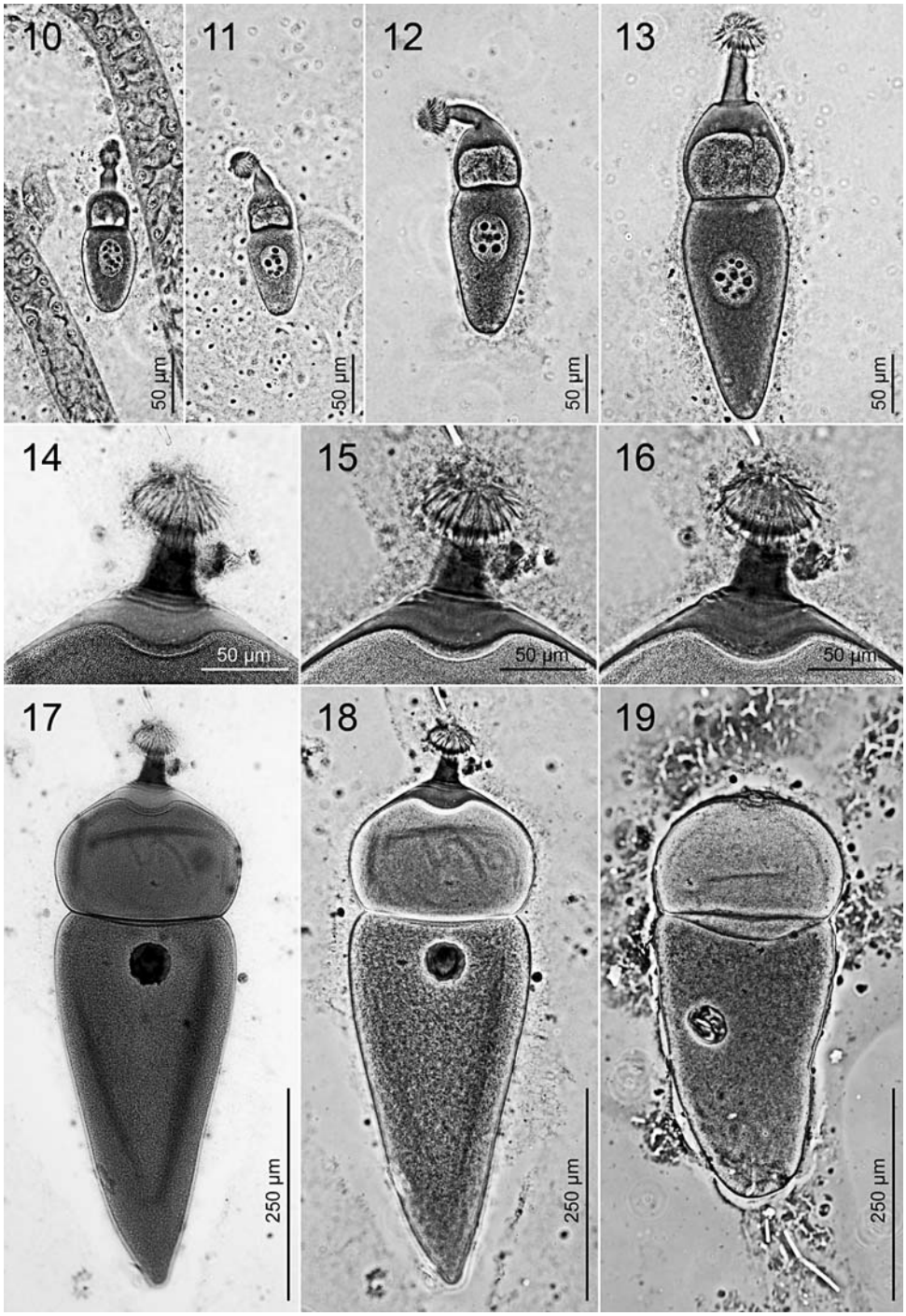
Mature trophozoites (Figs. 9, 14–18): Solitary, extracellular forms attached to epithelium of mesenteron. Epimerite very shallowly ovoid, armed with a terminal circlet of stout retroarcate spines that extend beyond the posterior margin of the epimerite proper; terminal spineless tumidus absent; EpiL 31.1 (17.4–43.5, ±5.45, 35); EpiW 43.5 (30.2–60.9, ±7.06, 35); SpL 20.6 (14.4–28.3, ±3.43, 35); EpiL/EpiW 0.7 (0.5–1.1, ±0.13, 35); EpiL/SpL 1.5 (0.9–2.8, ±0.34, 35). Diamerite short, oblong, DiaL 53.9 (14.1–150, ±22.71, 35); DiaW 25.4 (14–65.8, ±9.74, 35); DiaL/DiaW 2.4 (0.2–10.7, ±1.61, 35); DiaL/EpiL 1.8 (0.7–4.8, ±0.8, 35); EpiW/DiaW 1.9 (0.5–2.9, ±0.53, 35). Protomerite orbicular to dolioform, broader than deutomerite, truncated by distinct constriction at protomerite–deutomerite septum, PL 103.3 (75.7–137, ±17.13, 35); PWE 113.8 (72.1–169, ±19.57, 35); PWM 121.7 (82.2–182, ±21.21, 35); PLAM 67.6 (41.3–93.1, ±13.06, 35); PLPM 35.6 (22.4–49.8, ±6.06, 35); PDSW 98.8 (66.9–156, ±18.1, 35); PL/EpiL 3.4 (2.3–5.7, ±0.65, 35); PWM/EpiW 2.8 (1.9–4.3, ±0.53, 35); PL/DiaL 2.2 (0.8–5.6, ±1.01, 35); PWM/DiaW 5.3 (1.3–10, ±1.55, 35); PL/PWE 0.9 (0.7–1.2, ±0.12, 35); PL/PWM 0.9 (0.6–1.1, ±0.1, 35); PL/PDSW 1.1 (0.8–1.3, ±0.12, 35); PLAM/PL 0.7 (0.5–0.8, ±0.04, 35); PLAM/PLPM 1.9 (1.1–2.9, ±0.33, 35); PWM/PWE 1.1 (1–1.2, ±0.03, 35); PWM/PDSW 1.2 (1.1–1.4, ±0.06, 35); endocyte finely granulated, distinctly separated from sarcocyte. Deutomerite very deeply obdeltoid, truncated by constriction of protomerite–deutomerite septum, DL 258.1 (171–364, ±42.5, 35); DWE 91.2 (71.7–132, ±13.26, 35); DWM 118.3 (90.3–190, ±21.14, 35); DLAM 47.3 (33.3–73.3, ±9.27, 35); DLPM 209.7 (130–294, ±39.22, 35); DL/DWE 2.8 (2–4.3, ±0.41, 35); DL/DWM 2.2 (1.7–3, ±0.28, 35); DL/PDSW 2.6 (2–3.3, ±0.29, 35); DLAM/DL 0.2 (0.1–0.3, ±0.03, 35); DLAM/DLPM 0.2 (0.1–0.4, ±0.05, 35); DWM/DWE 1.3 (1.1–1.4, ±0.07, 35); DWM/PDSW 1.2 (1.1–1.4, ±0.06, 35), endocyte coarsely granulated. Total length TL 360.7 (244–494, ±58.71, 35); EpiL/PL 0.3 (0.2–0.4, ±0.05, 35); TL/PL 3.5 (3.1–4.3, ±0.21, 35); DL/PL 2.5 (2.2–3.3, ±0.21, 35); DWM/PWM 1 (0.9–1.2, ±0.06, 35); TL/DL 1.4 (1.3–1.5, ±0.03, 35). Nucleus orbicular to broadly elliptoid, NL 54 (46.9–65.3, ±5, 35); NW 42.7 (31.5–59.8, ±7.61, 35); NDS 73.3 (20.8–214, ±36.45, 35); NL/NW 1.3 (0.9–1.8, ±0.2, 35); NDS/NL 1.3 (0.4–3.5, ±0.62, 35); DL/NDS 4.3 (1.6–11.3, ±2.09, 35); with 9.7 (9–13, ±1.29, 35) distinct karyosomes, KW 7.7 (5.3–10.5, ±1.19, 35); NL/KW 7.1 (5–9.3, ±0.99, 35).

Gamonts (Fig. 19): Solitary prior to association, rare as epimerite is retained until just prior to association, protomerite and deutomerite similar in size and morphology to those observed in mature trophozoites.

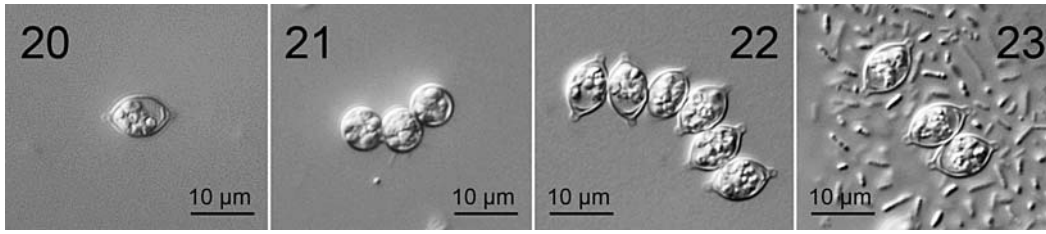
Association: Gamonts isomorphic; lateral, late, associations forming just prior to syzygy, association interface sinuate.

Gametocysts: Opaque white with enclosing hyaline layer, orbicular, maturing to dehiscence by simple rupture in water within 48–96 hr.

Oocysts (Figs. 20 and 21): Hesperidiform, OLI 8.3 (7.9–8.6, ±0.19, 32); OLE 11.4 (11–11.8, ±0.23, 32); OW 6.6 (6.2–6.8, ±0.17, 32); OLI/OW 1.3 (1.2–1.4, ±0.05, 32); OLE/OW 1.7 (1.7–1.9, ±0.05, 32); OLE/OLI 1.4 (1.3–1.5, ±0.04, 32); with terminal knobs, TkL 1.3 (1.1–1.7, ±0.15, 32); TkW 1.4 (1.1–1.7, ±0.19, 32); OLI/TkL 6.7 (4.8–8, ±0.73, 32); OLE/TkL 9.2 (6.7–10.6, ±0.92, 32); OW/TkW 4.9 (3.7–6.4, ±0.72, 32); TkL/TkW 0.9 (0.6–1.2, ±0.13, 32); octozoic with a single, smooth, orbicular residuum, Rdia 1.6 (1.3–2, ±0.17, 32); OLI/Rdia 5.4 (3.9–6.3, ±0.59, 32); OLE/Rdia 7.4 (5.6–9, ±0.78, 32); OW/Rdia 4.2 (3.3–5.2, ±0.45, 32).



Figures 10–19. Trophozoites and gamont of *Geneiorhynchus manifestus* n. sp. **10–13.** Trophozoites of increasing age and development, phase contrast microscopy. **14.** Epimerite of mature trophozoite under bright-field microscopy (Holotype). **15**, **16.** Epimerite of mature trophozoite showing details of spine structure as observed in different optical sections under phase contrast microscopy (Holotype). **17**, **18.** Mature trophozoite, bright-field and phase contrast microscopy, respectively (Holotype). **19.** Gamont, phase contrast microscopy.



Figures 20–23. Oocysts of *Geneiorhynchus manifestus* n. sp., differential interference contrast microscopy. **20.** Oocyst containing sporozoites and single residuum, lateral view. **21.** Three oocysts containing sporozoites and single residuum, optical cross section through equator. **22.** Oocysts in lateral view; note variability in sporozoite arrangement and residuum placement. **23.** Oocysts in lateral view, bacteria in field of view provide visual cue of scale.

Taxonomic summary

Type host: Anax junius (Drury) (Odonata: Anisoptera: Aeshnidae), naiads.

Type locality: Beaver Slide Pond, Big Sandy Creek Unit, Big Thicket National Preserve, Polk County, Texas, U.S.A. (30°38′49.0″N, 96°17′64.6″W).

Symbiotype: Two symbiotype specimens stored in 85% EtOH (authors' specimens REC060001 and REC060080) 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: Forty-six of 66 individuals examined, 69.69%.

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 is marked by an etched circle and is contained on a hapantotype slide HWML48465 (authors' slide JJH060120B). The paratype series comprises 61 slides containing trophozoites, gamonts, and associations deposited in 3 lots: HWML48466 (JJH060108, JJH060109A-C, JJH060111, JJH060112A, B, JJH060114, JJH060115A, B, JJH060116, JJH060117A, B, JJH060119, JJH060120A); HWML48467 (REC060002A-C, REC060005A, B, REC060007A-F, REC060009, REC060010, REC060015A, B, REC060072, REC060073A-C, REC060074, REC060075A-C, REC060076A, B, REC060077, REC060079A-D, REC060081, REC060082, REC060096, REC060100); HWML48468 (SJH060055A-D, SJH060056, SJH060057, SJH060059, SJH060060, SJH060061A-D). No specimen from the type series is retained by the authors.

Etymology: The specific epithet is given to mark this species as a pragmatic typotypical example of the genus.

Remarks

Species in *Geneiorhynchus* are distinguished based primarily on epimerite structure. In general, *G. monnieri* and *G. desportesi* (Figs. 4 and 6) are distinguished from other members of the genus by relatively small, roughly orbicular epimerites whose length is less than 10% that of the diamerite. *Geneiorhynchus monnieri* and *G. desportesi* are readily differentiated by multiple tufts of small epimeritic spines in the former and a single terminal circlet of larger spines in the latter. *Geneiorhynchus aeshnae* (Fig. 5) and *G. shteini* (Fig. 8) are distinguished from other members of the genus by relatively large, roughly orbicular epimerites whose length equals or exceeds that of the diamerite. They are distinguished from one another by sparse spiral rows of spines in the former and the distinct 4-band arrangement of spines in the latter. *Geneiorhynchus manifestus* and *G. baudoini* both possess epimerites that are approximately shallowly deltoid or trullate cones, but they differ in orientation: deltoid to trullate in the former and obdeltoid to obtrullate in the latter. The species also differ in the arrangement of their epimeritic spines.

As additional data become available, oocyst metrics may play an important role in species identification: Oocyst form covaries strongly with generic characters, but oocyst metrics tend to vary among species within a genus (Baudoin, 1969; Clopton, 2006).

DISCUSSION

Careful reconsideration of available data and observations of members of the genus *Geneiorhyn-*

chus reveal 3 previously unrecognized species: *G. desportesi*, *G. baudoini*, and *G. shteini*. In the comparative light of the complete data set reported herein for *G. manifestus*, it is possible to use epimeritic characters provisionally to distinguish species within the genus, assess the stability of member species, and set future collection and redescription priorities for *Geneiorhynchus*. Given the current state of gregarine systematics, such an approach should be undertaken on a broad scale to prepare the order for synthetic systematic revision.

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