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Revision of the Genus *Nubenocephalus* and Description of *Nubenocephalus secundus* n. sp. (Apicomplexa: Actinocephalidae) Parasitizing Adults of *Argia sedula* (Odonata: Zygoptera: Coenagrionidae) in the Primitive Texas Big Thicket, U.S.A.

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ABSTRACT: *Nubenocephalus secundus* n. sp. (Apicomplexa: Eugregarinida) is described from adults of *Argia sedula* (Odonata: Zygoptera: Coenagrionidae) collected from Harmon Creek, Sam Houston State University Center for Biological Field Studies, Walker County, Texas, U.S.A. This is the second species described in the genus and confirms the generic hypothesis of *Nubenocephalus*. The generic diagnosis of *Nubenocephalus* is revised to reflect common characters of its constituent species and a previously described Asian gregarine, *Nubenocephalus mutabilis* n. comb. (=*Ancyrophora mutabilis*) is recognized as a member of the genus.

KEY WORDS: Apicomplexa, Actinocephalidae, Acanthosporinae, gregarine, *Nubenocephalus nebraskensis*, *Nubenocephalus mutabilis* n. comb., *Nubenocephalus secundus* n. sp., damselfly, Odonata, Coenagrionidae, *Argia sedula*, *Argia bipunctata*, Platycnemididae, *Copera annulata*.

Known diversity of eugregarines parasitizing Nearctic damselflies (Richardson and Janovy, 1990; Clopton et al., 1993; Clopton, 1995, 2004a; Percival et al., 1995) is less than that of other biogeographical regions subject to more intense survey such as the Indian (Devdhar and Deshpande, 1971; Sarkar and Haldar, 1980a, b; Sarkar, 1981a, b; Sarkar, and Haldar, 1981a, b, c, d; Sarkar and Mazumder, 1983; Kori and Amoji, 1985, 1986; Amoji and Kori, 1992; Sarkar, 1995) and Oriental faunal regions (H. Hoshide, 1953; Obata, 1953; H. Hoshide, 1959; K. Hoshide, 1977). This disparity in gregarine diversity is probably a function of differential survey effort rather than a true reflection of paucity in the Nearctic gregarine fauna of damselflies. As part of an ongoing survey of the insect and eugregarine diversity of the Primitive Big Thicket region of east-central Texas, U.S.A., we collected an heretofore unknown gregarine species from adults of the Blue-ringed Dancer, *Argia sedula* (Hagen), (Odonata: Zygoptera: Coenagrionidae). The gregarines recovered are referable to the monotypic genus *Nubenocephalus* but taxonomically distinct from *Nubenocephalus nebraskensis* Clopton, Percival, and Janovy, 1993. Herein we describe the new taxon, recognize the congeneric status of a previously described gregarine from damselflies in Japan, and revise the genus to reflect common cardinal characters shared by the constituent species.

MATERIALS AND METHODS

Argia sedula adults ($n = 94$) were collected with aerial nets along Harmon Creek at the Sam Houston State University Center for Biological Field Studies, Walker County, Texas, U.S.A. (N 30°44′44.7″, W 95°28′46.2″), June to October 2006. Adult damselflies were placed in 1-liter plastic containers for transportation to the laboratory at Sam Houston State University, Huntsville, Texas, U.S.A.

Damselflies were isolated, abdomen-down, in 5-ml plastic test tubes with 1 ml of water. Twelve to 24 hr later fecal material in the water was examined for gregarine gametocysts. Shed gametocysts were freed from feces, triple rinsed in insect muscle saline (Belton and Grundfest, 1962), triple rinsed in deionized water, and transferred with ca. 50 µl deionized water to individual 4×12 mm glass microvials (BioQuip Products, Gardena, California, U.S.A.). Vials were sealed with white silicon stoppers and gametocysts held for maturation and dehiscence. Gametocysts were observed daily to determine time of dehiscence. Fresh preparations of oocysts were examined as wet mounts or as agar monolayer mounts (Clopton, 2004a). Observations were made using an Olympus B-Max 50 compound microscope with 10×, 20×, 40×, and 60× universal planapochromatic objectives with either phase contrast condensers or differential interference contrast prisms and an infinity-optics turret image-doubler. Digital photographs were taken with an Olympus DP-70 digital camera through the aforementioned microscope. Oocyst morphometrics were taken from the digitized images of oocyts using Image-Pro Discovery® v. 4.0 image analysis software (Media Cybernetics, L.P., Silver Spring, Maryland, U.S.A.).

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Damselflies were eviscerated and their alimentary canals dissected in insect muscle saline (Belton and Grundfest, 1962). Permanent parasite preparations were made following the techniques described by Clopton (2004a). Observations of trophozoites, sporonts, and gamonts were made using an Olympus B-Max 41 compound microscope with 10×, 40×, and 100× universal planapochromatic objectives with either bright field or phase contrast condensers. Digital photographs were taken using an Olympus DP-12 digital camera through the aforementioned microscope. Measurements were taken from digitized images of preserved specimens using Image Pro Express v. 4.5 image analysis software (Media Cybernetics, L.P., Silver Spring, Maryland, U.S.A.). Images of preserved specimens used in the photographic plates were taken using the Olympus DP-70 digital camera attached to the Olympus B-Max 50 compound microscope described above. Photographic plates were processed and assembled using Adobe® PhotoShop® v. 7.0.1 software (Adobe Systems Inc., San Jose, California, U.S.A.).

Terminology for developmental stages generally follows that of Levine (1971) for Apicomplexa with one notable exception. Sporont is used herein to indicate a mature individual lacking an epimerite that remains attached to the host epithelium prior to forming an association (Clopton et al., 1993). Terminology for shapes of planes and solids follows Clopton (2004b). Morphometric terminology follows Clopton (1999), Kula and Clopton (1999), and Clopton and Nolte (2002). The following metric characters used herein are consistent with those outlined and illustrated for the Acanthosporinae by Clopton (2004a): diamerite length (DiaL), dimaerite width (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), length of oocyst dorsal or polar spine (DSL), width of deutomerite at equatorial axis (DWE), maximum width of deutomerite (DWM), epimerite length (EpiL), epimerite width (EpiW), length of oocyst equatorial spine (ESL), distance from nucleus to protomerite-deutomerite septum (NDS), length of nucleus (NL), width of nucleus (NW), length of oocyst (OL), diameter of oocyst residuum (OrD), width of oocyst at equator (OW), width of oocyst at polar truncation (OWP), 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), and total length (TL).

As suggested by Filipponi (1949) and implemented by Clopton (1999), the holdfast of the taxon described herein is considered a compound structure composed of a terminal epimerite or holdfast proper and a diamerite intercalated between the protomerite and epimerite. The shape and relative proportion of structures in mature trophozoites, particularly the epimerite, comprise an important diagnostic character suite among the Actinocephalidae. However, significant developmental variation within taxa precludes the use of absolute metrics taken from trophozoites (Watwood et al., 1997; Clopton, 1999, 2006). Relative trophozoite morphometrics used herein are consistent with those proposed by Clopton (2006). Measurements are presented in μm as mean values followed parenthetically by range values, standard deviations, and sample sizes.

Nubenocephalus Clopton, Percival, and Janovy, 1993

Revised diagnosis

Eugregarinorida Léger, 1892, sensu Clopton (2002); Septatorina Lankester, 1885, sensu Clopton (2002); Actinocephalidae Léger, 1892, sensu Clopton (2002); Acanthsporinae Léger, 1892, sensu Clopton (2002); with the characters of the genus *Nubenocephalus* Clopton, Percival, and Janovy, 1993 revised as follows: Oocysts dipyramidic with polar truncations, hexagonal in equatorial cross section, without equatorial faces, with equatorial and terminal spines. Epimerite a tumidus with longitudinal pleats, petals, or lobes not forming hooks, spines, digitiform or rhizoid processes; diamerite present. Anterior margin of sporont protomerite expanded to form a broad crateriform adhesive disk.

Taxonomic summary

Type species: Nubenocephalus nebraskensis Clopton, Percival, and Janovy, 1993.

Remarks

Among gregarine genera whose members parasitize odonates, a transmutable protomerite that serves as an attachment sucker is observed only within *Nubenocephalus*, *Prismatospora* Ellis, 1914, and 2 members of *Ancyrophora* Léger, 1892. All 3 genera share a spined dipyramidic oocyst morphology. The genera are distinguished primarily by the form of the epimerite, which is unarmed in *Nubenocephalus* but armed with hooks in *Prismatospora* and digitiform processes in *Ancyrophora* (see Ellis, 1914; Tuzet, Ormières, and Théodoridès, 1968; Baudoin, 1971; Clopton et al., 1993; Clopton, 2002).

This work expands and confirms the previously monotypic *Nubenocephalus* with the recognition of 2 additional species within the genus. The generic diagnosis is revised to reflect cardinal character states evident in all 3 constituent species.

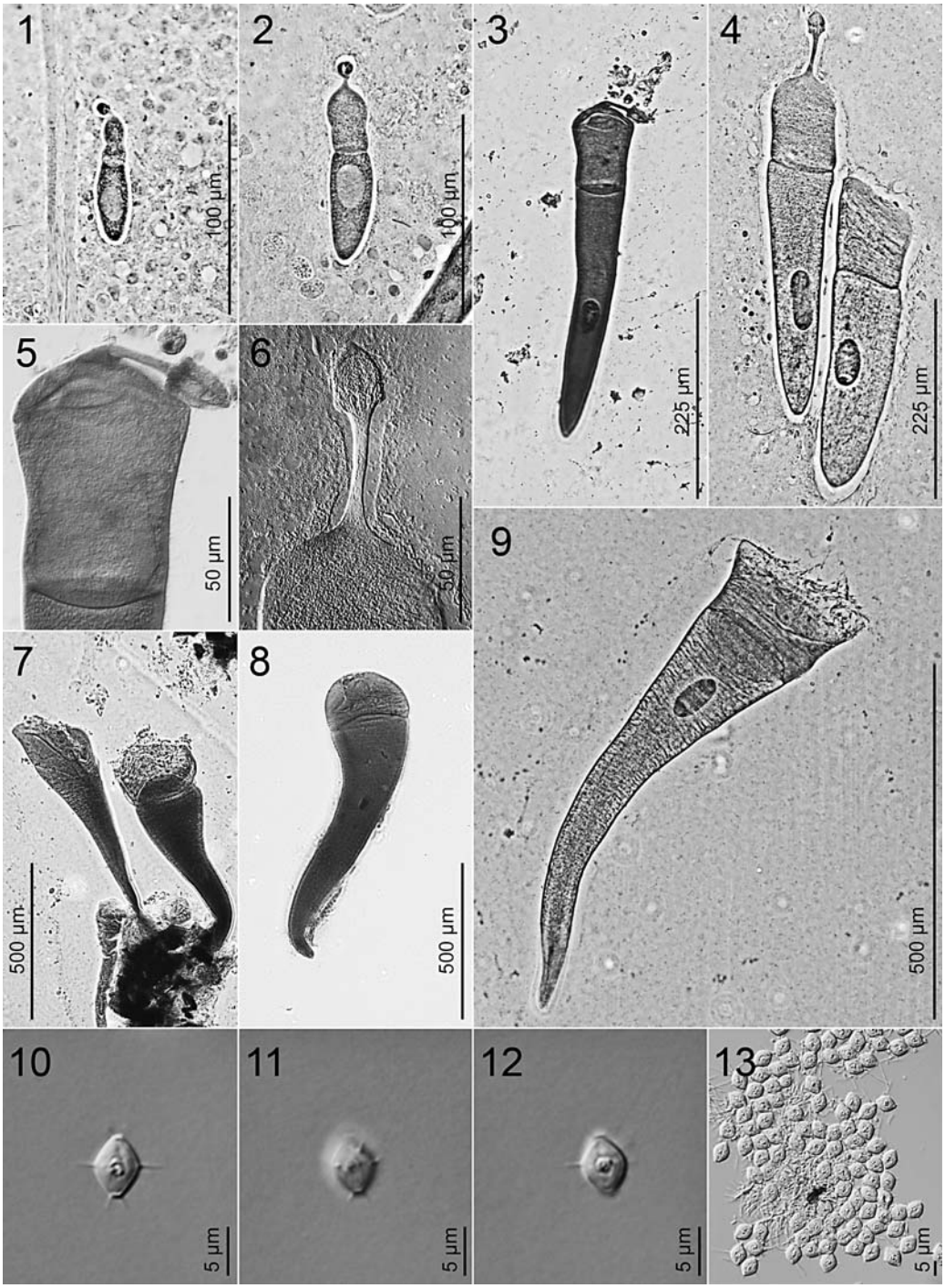
Nubenocephalus mutabilis n. comb. (K. Hoshide, 1977) Clopton and T. J. Cook

(=*Ancyrophora mutabilis* K. Hoshide, 1977)

Taxonomic summary

Type host: Copera annulata (Selys) (Odonata: Zygoptera: Platycnemididae), adults.

Type locality: Yamaguchi, Yamaguchi Prefecture, Japan.



Figures 1–13. *Nubenocephalus secundus*, n. sp., fixed and stained specimens. **1, 2.** Young trophozoites, phase contrast microscopy. **3, 4.** Mature trophozoites, phase contrast microscopy. **5, 6.** Detailed structure of epimerite and diamerite in mature trophozoites, differential interference contrast microscopy. **7.** Sporonts, phase contrast microscopy. **8.** Gamont, phase contrast microscopy. **9.** Sporont, phase contrast microscopy. **10–12.** Optical sections through oocyst demonstrating residuum and spines, differential interference contrast microscopy. **13.** Oocysts, differential interference contrast microscopy.

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

Disposition of other specimens: No permanent specimen is known.

Remarks

A complete description of the taxon is given by K. Hoshide (1977). Hoshide (1977) placed the taxon within *Ancyrophora* based solely on oocyst and epimerite morphology, both of which are consistent with *Nubenocephalus*. Hoshide (1977) also described and illustrated the transmutable crateriform protomerite characteristic of *Nubenocephalus*. The epimerite of *N. mutabilis* takes the form of an ovoid tumidus with 12–14 longitudinal petaloid processes.

***Nubenocephalus secundus* n. sp. Hays, Clopton, and T. J. Cook (Figures 1–17)**

Description

Trophozoite (Figs. 1–6): Solitary, attached to host ventricular epithelium, with epimerite complex. Epimerite ovoid to deeply deltoid, with longitudinal pleats (Figs. 5, 6). Diamerite narrowly oblong. Protomerite broadly ovoid in young trophozoites (Figs. 1, 2) becoming broadly obpanduriform in mature forms (Figs. 3, 4), truncated at protomerite-deutomerite septum; without distinct constriction at protomerite-deutomerite septum. Deutomerite spatulate in young trophozoites, becoming narrowly obtrullate in mature forms. Nucleus elliptoid. Relative morphometric ratios: EpiL $<$ DiaL, EpiW $>$ DiaW, EpiL $<$ PL, DiaL $<$ PL, PWM $>$ DWM, PL $\approx$ PWM, DL/PL $\approx$ 3.5, DL/DWM $\approx$ 4.5.

Sporont (Figs. 7, 9, 14–17): Solitary, attached to host ventricular epithelium by modified protomerite, epimerite lacking. Protomerite trapezoidal to campanulate, anterior margin expanded to form a broad crateriform adhesive disk; not or only slightly constricted at protomerite-deutomerite septum; PL 198 (97.9–349.3, ±63.67, 40); PWE 208.4 (116.5–422.4, ±74.2, 40); PWM 218.7 (1,27.2–441.7, ±75.55, 40); PLAM 71.9 (21.9–171.6, ±32.6, 40); PLPM 122.2 (59.8–237.2, ±45.17, 40); PDSW 173.2 (96.3–378.3, ±62.12, 40); PL/PWE 1 (0.4–1.9, ±0.37, 40); PL/PWM 1 (0.4–1.9, ±0.34, 40); PL/PDSW 1.2 (0.5–2.5, ±0.49, 40); PLAM/PL 0.4 (0.2–0.7, ±0.11, 40); PLAM/PLPM 0.6 (0.2–2.2, ±0.36, 40); PWM/PWE 1.1 (1–1.2, ±0.06, 40); PWM/PDSW 1.3 (1–1.8, ±0.18, 40). Deutomerite narrowly to very narrowly obtrullate; DL 790.2 (552.6–1,360.2, ±203.23, 40); DWE 116.2 (62.1–221.1, ±38.45, 40); DWM 172.7 (92.7–372.3, ±68.2, 40); DLAM 66.7 (26.2–168.7, ±33.57, 40); DLPM 723.6 (440.3–1,299, ±195.02, 40); DL/DWE 7.1 (4.8–12.2, ±1.47, 40); DL/DWM 4.9 (3–8.6, ±1.27, 40); DL/PDSW 4.8 (3.1–7.5, ±1.15, 40); DWM/DWE 1.5 (1.1–1.9, ±0.21, 40); DWM/PDSW 1 (0.7–1.3, ±0.12, 40). Total length (TL) 987.2 (702.2–1,690.6, ±247.18, 40); TL/PL 5.2 (3–8, ±1.12, 40); DL/PL 4.2 (2.1–7.1, ±1.11, 40); DWM/PWM 0.8 (0.5–1.1, ±0.13, 40); TL/DL 1.3 (1.1–1.5, ±0.07, 40). Nucleus elliptoid, placement variable, predominately subequatorial; nuclear karyosomes present; NW 46.4 (30–80.1, ±10.79, 40); NL 72.5 (45–108.9, ±14.14, 40); NDS 411.5 (23.9–1,186.8, ±234.27, 40); NL/NW 1.6 (1.1–2.9, ±0.39, 40); DL/NL 11 (6.8–17.5, ±2.19, 40); TL/NL 13.8 (8.6–22.4, ±2.76, 40); DL/NDS 3.9 (1.1–34.7, ±6.4, 40).

Gamonts (Fig. 8): Solitary gamonts rare, isogamontic, similar in size and morphology to mature sporonts, but crateriform adhesive disk of sporont lost, protomerite becoming shallowly depressed ovoid.

Gametocysts: White in color, orbicular with hyaline coat. Gametocysts stored in water dehisced by simple rupture in 4 to 6 days.

Oocysts (Figs. 10–13): Axially symmetric, dipyramidic with slight polar truncations OL 6.5 (6.1–6.7, ±0.16, 30); OW 4.7 (4.4–5.2, ±0.16, 30); OWP 0.9 (0.6–1.3, ±0.17, 30); OL/OW 1.4 (1.3–1.5, ±0.05, 30); OL/OWP 7.2 (5.1–10.1, ±1.35, 30); OW/OWP 5.2 (3.6–7.2, ±0.97, 30); hexagonal in equatorial cross section, without equatorial faces, bearing 6 equatorial spines, 1 at each equatorial vertex, ESL 2.2 (1.7–2.5, ±0.21, 30); 3 terminal spines obliquely inserted at each pole, 1 at each vertex created by polar truncations, DSL 1.1 (0.6–1.5, ±0.22, 30); OL/ESL 3 (2.6–3.9, ±0.34, 30); OL/DSL 6.1 (4.1–10.5, ±1.4, 30); OW/ESL 2.2 (1.8–2.7, ±0.23, 30); OW/DSL 4.4 (3.1–7.3, ±0.99, 30); oocyst residuum orbicular, smooth, equatorial, and axial, OrD 1 (0.7–1.2, ±0.13, 30); OL/OrD 6.7 (5.1–9.4, ±1.07, 30); OW/OrD 4.9 (3.8–6.5, ±0.72, 30).

Taxonomic summary

Type Host: Argia sedula (Hagen) (Odonata: Zygoptera: Coenagrionidae), adults.

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

Figures 14–17. *Nubenocephalus secundus*, n. sp., live specimens demonstrating the nature of the anterior crateriform adhesive disk, bright-field microscopy. **14, 15.** Mature sporonts attached to host gut epithelium. **16.** Mature sporont freed from host intestine. **17.** Mature sporonts attached to host gut epithelium.

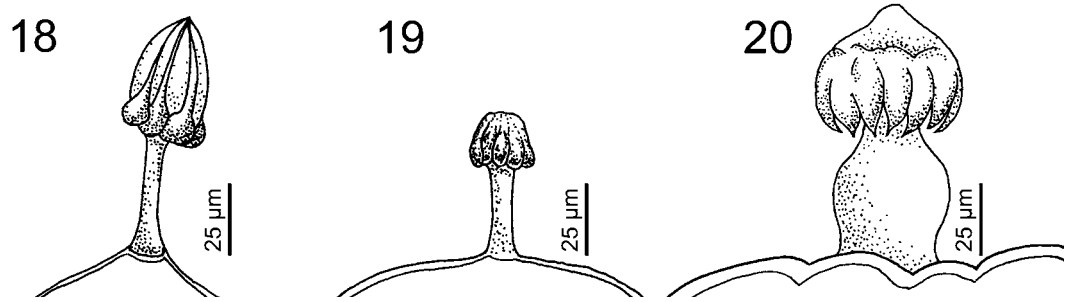
Symbiotype: Two symbiotype specimens (authors' specimens TJC060148 and TJC0600176) are deposited in the Sam Houston State University Insect Collection (SHSUIC), Department of Biological Sciences, Sam Houston State University, Huntsville, Texas, U.S.A. Individual accession numbers are not assigned by SHSUIC.

Other hosts: Argia translata (Selys), adults.

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

Prevalence: Seventy-eight of 94 individuals examined (83%).

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 a hapantotype slide HWML48469 (authors' slide JCG060709). The paratype series comprises 92 slides containing trophozoites, gamonts, and associations deposited in 9 lots as follows: HWML48470 (JCG060701, JCG060702, JCG060703, JCG060704, JCG060705, JCG060706, JCG060707, JCG060708, JCG060710, JCG060713); HWML48471 (JJH060455, JJH060456, JJH060457, JJH060458, JJH060459, JJH060460, JJH060461, JJH060462, JJH060464A, B); HWML48472 (JJH060466, JJH060467, JJH060 469A, B, JJH060470, JJH060471, JJH060472, JJH 060473, JJH060474, JJH060475A, B, JJH060476, JJH060477); HWML48473 (JJH060509); HWML 48474 (SXD060275, SXD060276, SXD060277, SXD060278); HWML48475 (SXD060279, SXD060 280, SXD060281, SXD060282, SXD060283); HWM L48476 (TJC060149, TJC060150A, B, TJC060151, TJC060154, TJC060155A, B, TJC060156, TJC060 157, TJC060159, TJC060161, TJC060162, TJC060 163, TJC060164, TJC060165, TJC060166, TJC0601 67, TJC060177, TJC060178, TJC060179, TJC060 181, TJC060182, TJC060183, TJC060184, TJC060



Figures 18–20. Comparative epimerite structure of *Nubenocephalus* spp. **18.** *Nubenocephalus secundus*, n. sp. **19.** *Nubenocephalus nebraskensis* (after Clopton et al., 1993). **20.** *Nubenocephalus mutabilis* n. comb. (after K. Hoshide, 1977).

187, TJC060190); HWML48477 (TJC060223, TJC 060224, TJC060225, TJC060228, TJC060229, TJC 060230, TJC060236A, B, TJC060237); HWML48 478 (TJC060335A, B, TJC060337A–C, TJC060343, TJC060344A–D, TJC060345A–C). No specimen from the type series is retained by the authors.

Etymology: The specific epithet is taken from the Latin to mark this as the second species described in the genus *Nubenocephalus*.

Remarks

Species of *Nubenocephalus* are most readily differentiated by the form of the epimerite (Figs. 18–20). *Nubenocephalus secundus* is differentiated from *N. mutabilis* by the form of the epimerite (deeply deltoid with longitudinal pleats in the former, Fig. 18; ovoid with 12–14 longitudinal petaloid processes in the latter, Fig. 20). *Nubenocephalus secundus* is differentiated from *N. nebraskensis* by both size of the sporont and the form of the epimerite. On average, sporonts of *N. secundus* are ca. 2/3 the length of *N. nebraskensis* sporonts (987.2 vs. 1,559.8). Trophozoites of *N. secundus* are characterized by a deeply deltoid epimerite with longitudinal pleats, but those of *N. nebraskensis* are characterized by a deltoid epimerite with longitudinal lobes (Fig. 19).

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