RESEARCH ARTICLE



Redescription of Dynoides elegans (Boone, 1923) (Crustacea, Isopoda, Sphaeromatidae) from the north-eastern Pacific

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Abstract

Dynoides elegans (Boone, 1923) from southern California is reviewed, redescribed, and figured. The original species description did not include figures, making it difficult to attribute individuals to the species. *Dynoides saldanai* Carvacho and Haasmann, 1984 and *D. crenulatus* Carvacho & Haasman, 1984 from the Pacific Coast of Mexico and *D. brevicornis* Kussakin & Malyutina, 1987, from Furugelm Island, Peter the Great Gulf in the Sea of Japan, appear morphologically more similar to each other than to western Pacific species. A large pleonal process is present in about half of the *Dynoides* species, but is absent in this north-eastern Pacific clade and the north-western Pacific *D. brevicornis* and *D. brevispina. Dynoides dentisinus* Shen, 1929 possess a large pleonal spine. It is known from China, Japan, and Korea and is introduced in San Francisco Bay; it can be easily distinguished from *D. elegans* by the presence of a pleonal process in the former. A key to the Pacific West Coast *Dynoides* is provided.

Keywords

Isopoda, Sphaeromatidae, Dynoides, California, East Pacific, intertidal

Introduction

The genus *Dynoides* Barnard, 1914 was erected for *D. serratisinus* Barnard, 1914 from Natal and Mozambique (Kensley 1978) and currently has 20 accepted species (WoRMS, World Register of Marine Species, Bruce and Schotte 2013). A complete

synonymy for the genus was provided by Li (2000). In the north-eastern Pacific three species are known: *D. crenulatus* Carvacho & Haasman, 1984, *D. saldanai* Carvacho & Haasmann, 1984, both from the Pacific Coast off the Oaxacan State of Mexico, and the species redescribed here, *D. elegans* (Boone, 1923). Additionally, *D. dentisinus* Shen, 1929 originally described from the coast of North China also occurs in San Francisco Bay. Kussakin and Malyutina (1987) described *D. brevicornis* from Furugelm Island, Peter the Great Gulf in the Sea of Japan, (north-eastern Pacific). Additional species occur in the western Pacific (Japan, Korea, China, Singapore, India, and Australia).

Pearl Lee Boone described several new isopod genera and species from the California coast in her 1923 paper, all without figures. She erected the new genus *Clianella* Boone, 1923 for *C. elegans* from La Jolla, California based on six specimens collected in 1915 "from bunches of mussels along the outer ledge of rocks north of Scripps Institution of Biological Research." Of these she designated a male holotype and two male paratypes which are part of the United States National Museum of Natural History collections (Cat. Nos. 50421 and 1422085) and which were examined here. The other three paratypes were donated to the Scripps Institution of Biological Research (SIO). The SIO specimens could not be found in the SIO collections in 2016 and are presumed lost (pers. comm. Collection Manager, Harim Cha). Additionally, Boone included a single adult male specimen collected from "Point White, San Pedro, California, May 18, 1919, by Mr. E.P. Chace and donated to the U. S. National Museum" (USNM Cat. No. 1422085).

The individual designated by Boone as the holotype has previously had pleopods 1–4 removed. Some pleopods were recovered floating in the vial containing the specimen. One paratype had several broken pereopods, and its dorsum is cracked. The second paratype was complete and in as good a condition as can be expected of a 97-year-old specimen. Permission was granted for dissection and this individual is figured here.

The composition of *Dynoides* and its relationship to *Clianella* was reviewed by Li (2000) and the generic name *Clianella* placed into junior synonymy. The genus *Dynoides* is distinguished by "presence of pleotelsonic slit that may or may not have an anterior lobe and internal teeth; a penial process basally fused for half its length and an appendix masculina elongate, twice as long as the endopod and strongly reflexed" (Li 2000). Species of the genus are known from intertidal habitats.

Abbreviations

LACM – Natural History Museum of Los Angeles County; LMU – Loyola Marymount University; MBPC – Marine Biodiversity Center; USC – University of Southern California; USNM – United States National Museum, Smithsonian Institution; RS – robust seta/e; PMS – plumose marginal setae; SEM – scanning electron microscopy. Latitudes and longitudes denoted with "~" are approximate and estimated from Google Earth.

Material and methods

Descriptions are based on the male paratype and additional material as noted. Specimens examined have USNM or LACM catalog numbers. Numbers preceded by "RW" are field station numbers. Collections so labelled are readily retrieved in the LACM collections. Setal terminology broadly follows Watling (1989). We provide images of additional material from White Point (Boone's "Point White") and Pt. Fermin. Both localities are on the Palos Verdes Peninsula less than 5 km apart. Additionally, we examined material from Santa Catalina, San Cruz Islands (California Channel Islands) and Cedros Island (Baja California Norte, Mexico).

Specimens are prepared for SEM as described in Wall et al. (2015). Drawings were made with the aid of a *camera lucida* and illustrations were electronically "inked" with Affinity Designer, Serif Labs. Whole body illustrations were made with a Wild M5D stereo dissecting scope. Appendages were illustrated by dissecting off the appendage and placing them in glycerol on a depression slide and then imaged using a Nikon Labophot-2 compound scope. Specimens were measured with a micrometer. The lengths given in the "Material Examined" are of the largest specimen of each species and sex. Not all specimens were measured. If a length is provided and multiple specimens were present in a lot, the length refers to the largest specimen. In all species mature males appear larger than females, but body lengths for mature adults are similar. Males have broader and longer uropods than females, which contributes to this illusion.

Molecular data were generated for this species according to the protocols described in Wetzer et al. (2013). Voucher specimens are held in the LACM collections.

Taxonomy

Key to the north-eastern Pacific species of *Dynoides* of the North American West Coast

This key is based on adult 3 characters. Also note that weak pereon tubercles are visible only with SEM and not necessarily evident with light microscopy.

2 Pleon without broad shelf-like ridge. Pleotelson in form of bilobed dome. Pleotelsonic slit with parallel sides; base of slit teardrop-shapedDynoides crenulatus Pleon with broad shelf-like ridge. Pleotelson vaulted, without bilobed dome. Pleotelsonic slit elongated teardrop- to completely heart-shaped. Base of ple-3 Pleotelsonic slit heart-shaped, without crenulate slit margins. Antennule with 9 flagellar articles, only 7 distalmost articles with aesthetascs. Antenna article 5 length 1.4 × width. Penes distal apex distinctly acute; basal half fused; apex pitch fork-shaped. Pleopod 3 exopod with suture Dynoides saldanai Pleotelsonic slit elongated teardrop- to heart-shaped, slit with weak crenulate margins. Antennule with 14 or more flagellar articles, only 12 distalmost articles with aethetascs. Antenna article 5 length $2.2 \times$ width. Penes distal apex rounded and blunt; basal third fused; apex tuning fork-shaped. Pleopod 3 exopod without suture Dynoides elegans

Dynoides Barnard, 1914

Type species. Dynoides serratisinus Barnard, 1914: 408; from South Africa by monotypy. Remarks. A diagnosis and comprehensive synonymy was provided by Li (2000). Readily recognizable characteristics include cephalon longer than broad, penes fused along proximal half of the length. Appendix masculina elongate, twice as long as endopod, strongly reflexed. Uropodal rami broad, lamellar, and subequal in length. The genus presently has ~20 species, is intertidal to shallow water, and is most speciose in the northern Pacific with twelve species. Additional species occur off Brazil, South Africa, Sri Lanka, and Australia (Li 2000). At present, the relationships between species remain unassessed.

Dynoides elegans (Boone, 1923)

Figures 1-8

Clianella elegans Boone, 1923: 153; Kussakin and Malyutina 1993: 1174. *Dynoides elegans*. Li 2000: 138.

Material examined. HOLOTYPE ♂ (7.04 mm), California, San Diego County, La Jolla, Scripps Institution for Biological Research, ~32.27°N ~117.61°W, 23 Oct 1915, USNM 50421 [RW16.020] designated by Boone.

2 \bigcirc PARATYPES (6.03, 5.36 mm, smaller specimen dissected and figured), same data as holotype, USNM 1422085.

Non-type material: 1 & (6.16 mm), California, Los Angeles County, White Point, San Pedro, ~33.715°N ~118.314°W, 18 May 1919. Coll. E.P. Chace, USNM 50422 [RW16.022].

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Figure 1. Dynoides elegans. A Holotype. USNM 50421. **A** dorsal **B** pleotelson. A Paratype. USNM 1422085. All from left **C** antennula **D** antenna.

2 3 (largest 3 5.36 mm, 2^{nd} male used for SEM), plus 8 non-gravid females, subadults and juveniles, California, Los Angeles County, Palos Verdes Peninsula, Pt. Fermin, shore at Paseo del Mar, ~0.5 mi. W of Gaffey Street, 33.71°N 118.30°W, mid-low intertidal, chipping overhanging rock with hammer and *Phragmatopoma* tubes on underside of rock, 0.99 m. Fixed and preserved in 95% ethanol. 27 Mar 2004. Sta. #2. Coll. R. Wetzer, N.D. Pentcheff, and LMU students. RW04.030. LACM-MBPC 17829.

Additional material examined.

1 male (5.36 mm), 3 ?females/subadults, 13 juv., Pt. Fermin, shore at Paseo del Mar, ~0.5 mi. W of Gaffey Street, eastern end of beach, ~33.71°N ~118.3°W, mid intertidal, scraping live barnacles off deeply crenulated rock shelf, fixed and preserved in 95% ethanol. 13 Jun 2006. Coll. R. Wetzer. RW06.063. LACM-MBPC 17831.

1 male (5.35 mm), 5 subadults, 2 juv., Los Angeles County, Santa Catalina Island, Big Fisherman Cove, in front of USC Wrigley Institute, 33.44°N 118.48°W, algal scrapings, ca. 1-2 ft. below low water, fixed and preserved in 95% ethanol. 7 Apr 2006. Acc. No. F.P.2.2006-6. Coll. N.D. Pentcheff, N.L. Bruce, R.Wetzer. RW06.006. LACM-MBPC 17830.

2 subadult males (largest individual 5.4 mm), 2 juvenile specimens, and posterior half of a gravid female, Santa Catalina Island, Avalon Harbor, ~33.35°N ~118.33°W, either rock or artificial substrate, subtidal scrapings, 3.05 m. Probably fixed in formalin, stored in 95% ethanol. 1 May 2011. Sta. 406. Coll. LACSD, rcvd. from D. Cadien. RW12.212. LACM-MPBC 17832.

9 specimens (largest 7.37 mm), Santa Barbara County, Santa Cruz Island, Pelican Bay, ~34.035°N ~119.703°W, under *Mytilus* beds, 18 Jul 1939. Coll. W.G. Hewatt. RW16.019. USNM 86407, Acc. No. 154967.

1 male (6.83 mm), Pacific, Mexico, Baja California Norte, Cedros Island, South Bay, Sta. 288-34, 10 May 1934. RW16.028. USNM 252317, Acc. No. 128938.

2 specimens (3.9 mm and 4.0 mm) photographed live, Los Angeles County, San Pedro, White Point, 33.72°N 118.32°W, rocky intertidal, hand, preserved in 95% ethanol. 23 Jun 2016. Coll. A. Wall, J. Wall, K. Omura, N.D. Pentcheff, L. Harris. RW16.051. LACM-MBPC 16919.

Description of male. *Body* length 2.4 × width; pereonites 1–5 smooth, pereonite 1 medially very slightly raised, pereonites 6–7 with very small tubercles; pleotelson covered with small tubercles; pleotelson length 1.2 × width, anterior of pleotelsonic sinus with prominent rounded tubercle barely overhanging base of sinus, sinus walls straight-sided, finely crenulate, and slightly raised. Coxal margins with setae appearing membranous, *membrana cingula*, (Figures 1A, B; 5B, C; 7A, B).

Antennula peduncle article 1 length 3.6 × width, anterior medial margin with 2 palm setae; article 2 as long as wide, inferior distal margin with 1 palm seta, superior margin with 1 palm seta; article 3 length 2.2 × width, proximal margin with 1 simple seta; flagellum with 14 articles, 12 distalmost articles with aesthetascs (Figure 1C). *Antenna* reaching anterior margin of pereonite 3; article 5 length 2.2 × width, flagellum with 17 articles (Figure 1D). *Clypeus* and *labrum* as in Figure 5E, F.

Left mandible incisor with 3 cusps; lacinia mobilis with 3 cusps; lacinia mobilis spine row comprised of 2 serrate and 3 simple spines; crushing surfaces strongly ridged; mandibular palp article 1 with 2 minute setae; article 2 with 2 palm setae and 2 plumose setae; article 3 with long, plumose setae (Figure 2A). *Maxillula* mesial lobe with



Figure 2. *Dynoides elegans.* ♂ Paratype. USNM 1422085. All mouthparts from left. A mandible B maxillula C maxilla D maxilliped.

about 7 spines; lateral lobe with about 10 spines (Figure 2B). *Maxilla* mesial lobe with 2 simple setae and 3 plumose RS on gnathal surface; middle lobe with 2 simple setae and 2 pectinate RS; lateral lobe with 2 pectinate RS (Figure 2C). *Maxilliped* endite distal surface with 5 plumose setae; distomesial margin with 1 coupling hook; palp article 2 distal apex with 9 long, (some broken) simple RS; article 3 distal apex with 8 long,



Figure 3. *Dynoides elegans.* ♂ Paratype. USNM 1422085. All appendages from left. **A** pereopod 1 **B** pereopod 2 **C** pereopod 3 **D** pereopod 4 **E** pereopod 5 **F** pereopod 6 **G** pereopod 7.

simple RS; article 4 distal apex with 6 long, simple RS, lateral distal angle with 1 long, simple RS; article 5 distal apex with 4 long, simple RS (Figures 2D; 5F).

Pereopods 1–7 (Figures 3A–G; 5F) all with one strong secondary unguis on the dactyl, ambulatory, and similar; merus, carpus, and propodus inferior margins more



Figure 4. Dynoides elegans. ♂ Paratype. USNM 1422085. All appendages from left. A pleopod 1
B pleopod 2 C pleopod 3 D pleopod 4 E pleopod 5 (endopod and exopod separated).

setose than superior margins (as figured). *Pereopod 1 basis* length $2.3 \times$ width; *ischium* length $2.8 \times$ width. *Pereopod 2 basis* length $3.6 \times$ width; *ischium* length $3.1 \times$ width. *Pereopod 1* more stout than *pereopods 2–7*. *Pereopod 7 basis* length $3.4 \times$ width, *ischium* length $4.0 \times$ width.

Penial process length 2.3 × basal width, basal third fused (Figure 5G).



Figure 5. *Dynoides elegans*. ♂, non-type. LACM-MBPC 17829. A anterior dorsal B posterior dorsal C pleotelson D lateral E clypeus, labrum F mouthfield G ventral with penes.



Figure 6. *Dynoides elegans.* \bigcirc , non-type. USNM 86407. **A** dorsal **B** pleotelson **C** lateral. \bigcirc , non-type. LACM-MBPC 17832 **D** posterior half of gravid individual with mancas and ventral view of pleotelson.

Pleopod 1 peduncle length 2.3 × width with 2 coupling hooks (Figure 4A); PMS extending to posterior margin of pleonal cavity (Figure 5G). *Pleopod 2* peduncle length 3.2 × width with 2 coupling hooks, *appendix masculina* proximally slightly swollen, distally narrowing, basal mesial margin with scales, distal third doubled back on proximal half (Figure 4B). *Pleopod 3* peduncle length 2.0 × width with 2 coupling hooks (Figure 4C). *Pleopods 1–3* exopods and endopods with PMS as figured (note: not all drawn, but indicated). *Pleopod 4* endopod and exopod subequal, exopod with transverse suture (Figure 4D). *Pleopod 5* endopod and exopod subequal, endopod length 1.4 × width with one distal scale patch and one smaller submedial scale patch, exopod length 1.6 × width (Figure 4E).

Uropod exopod proximolateral margin rolled, weakening distally; in the adult 3 holotype (USNM 50421) and 2 adult 3 paratypes (USNM 1422085) uropods extend well beyond posterior margin of pleotelson (as figured in Figure 1B), but do so otherwise only in the largest males (see Figures 5B; 7A, B).

Description of female. *Body* length 2.2 × width; (Figures 6A, B, C). Dorsal ornamentation as in the male. *Pleotelson* length 1.2 × width. *Uropodal* endopod longer than exopod, endopod just barely extending to posterior margin of pleotelson (Figure 6D). Dorsally uropodal exopod proximolateral margin weekly rolled, tapering to an evenly rounded distal margin. Gravid female estimated with 8–12 mancas. Figure 6D is the posterior half of female broken open exposing 3 mancas.



Figure 7. *Dynoides elegans.* \mathcal{J} , non-type. LACM-MBPC 16919. Photographs of live specimens by Leslie Harris. **A** (3.9 mm) and **B** (4.0 mm).

Size. Largest $\stackrel{\frown}{\rightarrow}$ to 7.37 mm, largest $\stackrel{\bigcirc}{\rightarrow}$ to 5.4 mm.

Color. When alive brightly colored, individuals highly varied (Figure 7A, B). When preserved in ethanol, specimens quickly become pale buff to whitish. Bright red coloration outlining pleotelsonic slit fades last.

Distribution. California: San Diego to Santa Barbara Counties.

Molecular data. Both 18S-rDNA and 16S-rDNA were generated from the same individual from Pt. Fermin (RW04.030), GenBank numbers JF699541, and KU248214, respectively. Locality information is provided above in Material Examined. This specimen came from the same lot from which the SEM specimen in Figure 4 was prepared.

Remarks. *Dynoides elegans* is morphologically most similar to *D. saldanai* and *D. crenulatus* (Pacific, Mexico, Oaxaca). These three species are easily distinguished from *Dynoides dentisinus*. Adult male specimens of *Dynoides dentisinus* are more robust than those of *D. elegans* and have a distinctive, prominent large process extending over the pleotelson (Figure 8A, B). The presence of a prominent pleonal process is polymorphic in *Dynoides* (Li 2000). The presence of a slit, sinus, notch, or foramen is also variable in the genus (Li 2000). A pleotelson slit of various shapes is present in all three eastern Pacific *Dynoides* and the north-western Pacific *D. brevicornis* (Kussakin and Malyutina 1987).



Figure 8. *Dynoides dentisinus. A* dorsal **B** lateral **C** ventral. California, Alameda County, San Francisco Bay, off Doolittle Road near Oakland Airport, 37.73°N 122.21°W, from low intertidal under rocks, associated with sponge, salinity 30 ppt, fixed and preserved in 95% ethanol. 5 Jun 2002. Coll. R. Wetzer, T. Haney, and S. Boyce. RW02.027. MBPC 17838.

A generic description of the "penes fused along proximal half of length" (Li 2000) is an easily recognizable character. In *D. elegans* penes may be considered fused closer to proximal third of length (Figure 5G). Of all of the material available for examination, we had only a single broken gravid female (Figure 6D). Gravid females are clearly rare. This may be attributed to our poor sampling during brooding episodes, which remain unknown. No specimens collected during the months January/February, August/September, or November/December were available for examination.

Dynoides elegans is most similar to the Oaxacan species, *D. saldanai*. They share pleonal characters which are known to change as individuals, especially males, mature. Penial processes, pleonal process, appendix masculina, pleotelson morphology and also pleotelson sinus morphology are characters that all change with age in males. A fully adult male (penes and appendix masculina developed) may not be at the final fully developed male stage, potentially with some further changes to the pleotelson morphology. We do know that in males the sinus will transition progressively from a simple slit to a quite complex structure. The body length of the *D. elegans* type specimens range from 5.36 to 7.04 mm. The subtle changes in morphology are readily observed in Figure 7, represented by specimens from the same collecting event. Note uropodal development and progression of a simple pleotelsonic slit to a heart-shaped slit. The largest male examined was 7.37 mm (Santa Cruz Island), and its pleotelsonic slit approaches heart-shape. The largest *D. saldanai* specimen is 4.45 mm in length and female 3.0 mm. The two male specimens in Figure 7A and 7B are 3.9 and 4.0 mm in length.

The figured male paratype (Figure 1A) has a body length 2.35 × width. We note that in all other specimens measured, adult male body length is closer to 2.2 × width. Non-empirical observations of this species and other Sphaeromatidae from the north-eastern Pacific indicate that sexually mature adult males reached larger body sizes in the past than they do today (RW pers. obser.). Specimens of *D. elegans* collected before the 1940s are among the largest individuals in the examined collections, with the largest males exceeding 7 mm body length. The largest specimens come from the oldest collections (specimens collected between 1915–1939). It appears that fully developed males in the past attained larger body sizes than more recently collected individuals (e.g., 2004–2016). To quantify this, populations of individuals appropriate to determine statistical significance need to be evaluated.

Dynoides elegans is known from San Diego County to Santa Barbara County, with a single male specimen (USNM 252317) recorded from Cedros Island off the Pacific Baja California coast. The Cedros Island specimen is most similar to White Point and Pt. Fermin specimens (Los Angeles County). These localities are roughly 700 km apart. To definitively confirm that Cedros Island is the southernmost locality in the species range, additional specimens are needed. Appropriate material for molecular analysis would greatly contribute to our understanding of the morphological diversity within species (e.g., varying amounts of membrane-like setae on the coxal margins, refer to Figure 7), across populations, and allow us to determine whether *D. saldanai* might be a junior synonym of *D. elegans.* The *D. saldanai* type series consists of 27 specimens: 2 adult males, 10 juvenile males, 11 females, and 4

undetermined junveniles. The male holotype (4.45 mm) and allotype were deposited at the Institute of Biology of the National Autonomous University of Mexico. The paratypes are alleged to be in the National Museum of Natural History in Paris (Carvacho and Hassmann 1984). Type numbers were not provided. When substantially more fresh material has been collected, it would be useful to clarify the status of *D. saldanai* by comparisons with the type material and any other specimens attributed to *D. saldanai* and *D. elegans*. Not examining *D. saldanai* types at this time does not effect the status of *D. elegans*.

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RESEARCH ARTICLE



Presumed filter-feeding in a deep-sea benthic shrimp (Decapoda, Caridea, Stylodactylidae), with records of the deepest occurrence of carideans

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Abstract

Using the remotely operated vehicle *Deep Discoverer*, we observed a large stylodactylid shrimp resting on a sedimented sea floor at 4826 m in the Marianas Trench Marine National Monument. The shrimp was not collected but most closely resembled *Bathystylodactylus bathyalis*, known previously only from a single broken specimen. Video footage shows the shrimp facing into the current and extending its upraised and fringed first and second pereopods, presumably capturing passing particles. The video footage is the first ever to show a living deep-sea stylodactylid and constitutes the deepest record for the family. We provide a list of the deepest reports of caridean shrimps world-wide.

Keywords

Deep-sea shrimp, Stylodactylidae, feeding, carideans, Marianas Trench

Introduction

Benthic caridean shrimps living at 1000 m or more are poorly known, for the most part represented by specimens taken by trawls. To the best of our knowledge, none of them has been brought to the surface alive. Often, the fragile pereopods and antennae are broken or torn off. The feeding modes and form of the appendages of vent shrimps (family Alvinocarididae) have been studied in detail (Komai and Segonzac 2008). Other carideans living on mud or hard substrates away from vents are poorly studied. It is difficult to maneuver collecting equipment among rocks without entanglement. Shrimps living on mud may be difficult to see because they burrow into the sediment or dart away if disturbed. In situ photographs often do not show the shrimp in sufficient detail for identification.

There are three species of *Bathystylodactylus*, the deepest known members of the family Stylodactylidae. These are known from six specimens: one each of *B. inflatus* from off Taiwan and *B. bathyalis* from the Coral Sea and four of *B. echinus* from the eastern Pacific (Hanamura and Takeda 1996; Cleva 1994; Wicksten and Martin 2004). All known specimens are damaged, missing at least some of the appendages. We report here on a living shrimp photographed in situ, provide the deepest report of a stylodac-tylid shrimp to date, and compare the depth records of the deepest known carideans.

Methods

We obtained photographs and video of the shrimp from the U.S. National Oceanographic and Atmospheric Administration (NOAA) Ship *Okeanos Explorer* (*OkEx*), administered through the Office of Exploration and Research. The ship is equipped with a 6,000 m-rated dual-body system comprising the remotely-operated vehicle (ROV) *Deep Discoverer* (*D2*) and *Seirios* camera sled. During operations, *Seirios* is tethered to the ship with a standard oceanographic armored, fiber-optic cable (1.73 cm diameter) and *D2* is linked to *Seirios* with a neutrally buoyant tether, thus isolating the ROV from the *OkEx* surface motion to allow precise maneuvering and steady imaging of deep-sea communities.

The ROV *D2* is outfitted with two maneuverable and four fixed video cameras; scientific observations are made primarily using two high-definition video cameras. Light is supplied by 26 LED lamps (195000 lumens total), with eight of these on four hydraulically positioned booms. Paired lasers (10 cm apart) mounted on the fixed, high-definition video camera provide size scale in the imagery. The ROV traversed the seafloor at a speed of approximately ~ 0.1-0.3 knots (1 knot = 0.514 m s-1) with the cameras generally set on wide-angle view, and zooms were initiated to obtain detailed imagery when objects of scientific or aesthetic interest were encountered. High-definition video was transmitted from the *D2* in HD-SDI 1080i format. *OkEx* is equipped with high-speed communication capabilities to enable scientists on the shore to participate in ship operations in time via telepresence (see http://oceanexplorer.noaa.gov/

okeanos/collaboration-tools/welcome.html). Scientists (and anyone with an Internet connection) are able to observe live video feeds from the ROV *D2* and participate in real-time via a private Internet chat room and satellite teleconference line.

Results

From 20 April to 10 July, 2016, the *OkEx* was engaged in the "2016 Exploration of the Marianas" Expedition, a baseline study of deep-water environments in and around the Commonwealth of the Northern Mariana Islands and the Mariana Trench Marine National Monument (MTMNM). *D2* Dive 13 of Leg 3 (30 June 2016) of this expedition explored a site informally named "Twin Peaks" on a seamount in the MTMNM. The *D2* spent 4 hours 48 min traversing the bottom, from 4840 meters depth upslope to 4787 m. The seafloor was mostly thickly sedimented with clay-like particles that were easily disturbed into clouds by the ROV thrusters; small outcroppings of sedimentary rocks were seen frequently as well as occasional large boulders.

Approximately 2 hours 17 min after the ROV reached the bottom and the benthic exploration began, an observation was made of a single individual stylodactylid shrimp (estimated total length 120 mm) at 4826 m depth (21.41774° N, 145.89294° E). No other stylodactylids were observed during the dive or on other dives during this expedition. Other benthic shrimps (Superfamily Penaeoidea) and thread-leg shrimps (Caridea: Nematocarcinidae) were observed on soft substrates, as well as other carideans associated with soft corals (Order Gorgonacea) and sponges (Hexactinellida). When initially observed, the shrimp was facing away from the ROV camera. Participating scientists noted this was an atypical shrimp species for the expedition, so the ROV settled to capture detailed images. After a couple of minutes the ROV was repositioned to get a lateral view of the shrimp. During the approximately 4 minutes of observation (including the ROV maneuver) the shrimp did not move from its initial position on the bottom, facing into the weak boundary layer current. The following environmental data were recorded during the observation: temperature 1.47236°C, salinity 34.69294 PSU, dissolved oxygen 4.96223 mg/L.

With anterior legs upraised, the shrimp faced into the current, presumably using its legs as a net to capture passing particles. The shrimp had first and second pereopods fringed with setae and with extremely slender chelae, characteristic of the family Stylodactylidae (Cleva 1990). The deepest species, belonging to the genus *Bathystylodactylus*, have a long toothed rostrum, eyes without pigment, and a carapace that is pubescent or studded with minute spinules (Hanamura and Takeda 1996, Wicksten and Martin 2004). The shrimp in the video appeared to most closely resemble *Bathystylodactylus bathyalis*, previously only known from a single broken specimen collected at 3515–3502 m in the Coral Sea (Cleva 1994). The present video footage is the first for any of the deep-water dwelling Stylodactylidae. Other invertebrates in the area included a large long-legged isopod (family Munnopsidae), an enteropneust (phylum Hemichordata), a swimming holothurian (Echinodermata), and a hermit crab

(*Parapagurus* sp.) with an associated commensal sea anemone (Actiniaria). The ROV was not equipped with collecting equipment that could capture any of these animals and so their species identification remains uncertain.

As in the euphausiaceans, the long, setose legs of the stylodactylid seem to form a "filter basket" that captures particles. The shrimp in the video was not seen to open and expel water by means of pumping, as can euphausiaceans, but instead relied on passive transfer of food particles by the boundary layer current. No other group of carideans is known to feed in this manner (Wicksten 2010). Other decapods filter-feed by means of long feathery antennae, as in the hermit crabs of the genus *Paguritta* and the mole crabs, family Hippidae; or setose third maxillipeds, as in crabs of the family Porcellanidae (Riisgard and Larsen 2010).

Discussion

Relatively few caridean shrimps live at bathyal depths, i.e. greater than 1000 m, with far fewer recorded at abyssal depths of 3000 m and deeper. As well as species of the Stylodactylidae, caridean shrimps reported from abyssal depths include species of the families Bythocarididae, Crangonidae, Disciadidae, Nematocarcinidae, Oplophoridae, Pandalidae and Pasiphaeidae (Table 1). The present observation of *Bathystylodactylus* sp. is the deepest report of a member of this family. The oplophorid *Heterogenys microphthalma* has been collected in trawls as deep as 5060 m (Crosnier 1987). Jamieson et al. (2009) included photographs of "*Acanthephyra* sp." from baited traps as deep as



Figure 1. *Bathystylodactylus* cf. *bathyalis*, 4826 m, in situ. Photo extracted from high-definition video captured using ROV *Deep Discoverer*. (Image courtesy of the NOAA Office of Ocean Exploration and Research 2016 Deepwater Exploration of the Marianas).

Table 1. Deepest family level records for caridean shrimp species living at depths bathyal and abyssal depths. Systematics follows De Grave & Fransen (2011), with modifications in De Grave et al. (2014, 2015). Depths as well as sampling or observation method are given.

| Acanthephyridae |
|---|
| Acanthephyra quadrispinosa Kemp, 1939: Crosnier (1987), 5040–5060 m, trawl. |
| Heterogenys microphthalma (Smith, 1885): Crosnier (1987), 5040–5060 m, trawl. |
| Alvinocarididae |
| Rimicaris hybisae Nye, Copley & Plouviez, 2012: 4960 m, TV grab and slurp gun. |
| Bathypalaemonellidae |
| Bathypalaemonella serratipalma Pequegnat, 1970: Cleva (2001), 2660–2750 m, beam trawl. |
| Bresiliidae |
| Bresilia pacifica Hendrickx, 2014: 2010–2046 m, benthic sledge. |
| Bythocarididae |
| Bythocaris cryonesus Bowman & Manning, 1973: 3803 m, minnow trap. |
| Crangonidae |
| Placopsicrangon formosa Komai & Chan, 2009: 4807–4824, beam trawl. |
| Disciadidae |
| Lucaya bigelowi Chace, 1939: 4773 m, open net. |
| Glyphocrangonidae |
| Glyphocrangon atlantica Chace, 1939: Holthuis (1971), 6364-6373 m, collecting method not specified. |
| Hippolytidae |
| Leontocaris amplectipes Bruce, 1990: Ahyong (2010), 2182–2119 m, sled. |
| Nematocarcinidae |
| Nematocarcinus challengeri Burukovsky, 2006: 5477 m, trawl. |
| Oplophoridae |
| Systellaspis debilis (A. Milne Edwards, 1881): Crosnier (1987), 4987–5025 m, trawl. |
| Palaemonidae |
| Periclimenes pholeter Holthuis, 1973: Bruce (2011), 2148 m, collecting method not specified. |
| Pandalidae |
| Stylopandalus richardi (Coutière, 1905): Hayashi & Miyake (1969), 3600 m, midwater trawl. |
| Pasiphaeidae |
| Parapasiphae compta Smith, 1884: Crosnier (1988), 4990 m, trawl. |
| Physetocarididae |
| Physetocaris microphthalma Chace, 1940: Wasmer (1985), 1200–2200 m, non-closing trawl. |
| Psalidopodidae |
| <i>Psalidopus tosaensis</i> Toriyama & Horikawa, 1993: 2765–2881 m, beam trawl. |
| Stylodactylidae |
| Bathystylodactylus sp.: present report, 4820 m, video observation. |
| Thoridae |
| Lebbeus laurentae Wicksten, 2010: Komai et al. (2012), 2640 m, slurp gun. |

6890 m in the Kermadec Trench, but their photographs (Fig. 1B, C) show a shrimp with a short upturned rostrum, characteristic of *H. microphthalma*. If confirmed this would be the deepest recorded caridean shrimp record, a record currently held by *Glyphocrangon atlantica* at 6364–6373 m (Holthuis 1971).

Video link: http://oceanexplorer.noaa.gov/okeanos/explorations/ex1605/dailyup-dates/media/video/0630-mudmonsters/0630-mudmonsters.html

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RESEARCH ARTICLE



Towards a revision of the genus Periclimenes: resurrection of Ancylocaris Schenkel, 1902, and designation of three new genera (Crustacea, Decapoda, Palaemonidae)

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Abstract

Based on recently published molecular phylogenies of Indo-West Pacific palaemonid shrimps and further morphological evidence, the systematic position of several species of the polyphyletic genus *Periclimenes* is revised. The generic name *Ancylocaris* Schenkel, 1902 is re-established for the anemone-associated *P. brevicarpalis. Actinimenes* gen. n., is proposed for the anemone-associated *P. inornatus*, *P. ornatellus* and *P. ornatus*, all of which have a subspatulate first pereiopod. *Cristimenes* gen. n., is designated for the echinoderm-associated species, *P. commensalis*, *P. cristimanus*, and *P. zanzibaricus*, all with a unique carpopropodal articulation of the second pereiopods. *Rapimenes* gen. n. is established for the hydroid and antipatharian-associated *P. brucei*, *P. granulimanus*, and *P. laevimanus*, for which the long, slender and unequal second pereiopods and prehensile ambulatory propodi are the main synapomorphic characters.

Keywords

Ancylocaris, Actinimenes, Cristimenes, Periclimenes, Rapimenes, symbiotic shrimps

Introduction

The apparently polyphyletic and highly diverse palaemonid shrimp genus *Periclimenes* O. G. Costa, 1844 (e.g. Bruce et al. 2005) has in recent decades undergone some splitting by the designation of new genera for several species groups, e.g. *Exoclimenella* Bruce, 1995, *Periclimenella* Bruce, 1995, *Manipontonia* Bruce, Okuno & Li, 2005, *Crinotonia* Marin, 2006, *Brucecaris* Marin & Chan, 2006, *Unguicaris* Marin & Chan, 2006, *Margitonia* Bruce, 2007, *Leptomenaeus* Bruce, 2007, *Rapipontonia* Marin, 2009, and *Ancylomenes* Okuno & Bruce, 2010. Equally, several synonymised genera were reestablished, e.g. *Harpilius* Dana, 1852, *Urocaris* Stimpson, 1860, *Laomenes* AH Clark, 1919 and *Cuapetes* AH Clark, 1919 (see Bruce 2004, 2007a, b, c, Okuno and Fujita 2007, Okuno 2009). However, the genus *Periclimenes* as presently delineated still represents a heterogeneous assemblage of taxa of unresolved systematic status.

Although several molecular studies were recently constructed (Kou et al. 2013, Gan et al. 2015, Horká et al. 2016) to examine intrageneric relationships of the genus *Periclimenes*, a full resolution has not been achieved yet, partly due to incomplete coverage of species diversity, partly due to the low basal support of some clades within the analysis. Excluding the species recently allocated to *Echinopericlimenes* Marin & Chan, 2014 and *Bathymenes* Kou, Li & Bruce, 2016, only about 25 species of *Periclimenes* are involved in the analyses representing about 20% from the almost 130 species presently in the genus.

Periclimenes is clearly a genus which will see a further, strong reduction of its species diversity in the future. The type species, *P. amethysteus* (Risso, 1827) is a member of a clade of four sea anemone associated species distributed in the Mediterranean Sea and neighbouring part of the eastern Atlantic Ocean. It seems quite probable that only those species, with perhaps a few allied Atlantic species, will remain in *Periclimenes*, while all other species are likely to require allocation to further new or indeed resurrected genera. As indicated from the phylogenetic reconstruction provided by Horká et al. (2016), this group of anemone shrimps may be related to the majority of other Atlantic *Periclimenes* species, including the western Atlantic anemone shrimps, as well as Atlantic and Indo-Pacific deep-water *Periclimenes, Echinopericlimenes, Altopontonia* Bruce, 1990, and *Bathymenes* species. As the systematic relationship of these taxa still remains poorly supported in the recent phylogenies, and due to the lack of inclusion of many other Atlantic taxa, the exact composition of *Periclimenes* (*s.s.*) thus remains unclear.

Nevertheless, it is evident from the phylogeny in Horká et al. (2016) that most Indo-West Pacific representatives of the genus (as currently defined) are unrelated to the Atlantic *Periclimenes* taxa as a whole, and some natural groups can easily be separated from the genus based on molecular and morphological support. This report is a contribution to a series of revisions of the genus, resurrecting a synonym and establishing three new genera for some species of Indo-West Pacific *Periclimenes* species.

Abbreviations: fcn, field collection number; MHNG, Muséum d'Histoire Naturelle, Geneve; MNHN, Muséum National d'Histoire Naturelle, Paris; MTQ, Museum of Tropical Queensland, Townsville; RMNH, Naturalis Biodiversity Centre (formerly Rijksmuseum van Natuurlijke Historie), Leiden; spm(s), specimen(s); sp./spp., species (single/plural); UO, University of Ostrava.

Systematics

Superfamily Palaemonoidea Family Palaemonidae Rafinesque, 1815

Genus Ancylocaris Schenkel, 1902

Type species. Ancylocaris brevicarpalis Schenkel, 1902, by monotypy.
 Included species. Ancylocaris brevicarpalis Schenkel, 1902 (Figs 1, 3A, B).
 Gender. Feminine.

Diagnosis. Subcylindrical body form. Carapace smooth; rostrum well developed, subequal to antennular peduncle and moderately high, dorsal margin convex, dentate, with first tooth postorbital, ventral margin convex, with 1-2 teeth on distal third of rostrum length. Inferior orbital angle produced, without reflected inner flange, supraorbital and epigastric teeth absent, antennal and hepatic teeth present. Fourth thoracic sternite with broad transverse ridge subdivided by deep narrow median incision. Pleon smooth, third tergite non-carinated or posteriorly produced, pleura 1-5 posteroventrally rounded; telson with 2 pairs of minute dorsal spines on distal third of telson length and 3 pairs of short posterior marginal spines. Ophthalmic somite without interocular process. Antennule and antenna as usual for the family; upper ramus of antennular flagellum biramous, with fused basal part; scaphocerite moderately broad, with small distolateral tooth falling short of anterior margin of lamina; carpocerite short. Eyes with small accessory pigment spot dorsally on corneal margin. Mandible without palp; molar and incisor processes normal. Maxilla with basal endite distinctly bilobed, coxal endite obsolete, scaphognathite normal; first maxilliped with endites fused, exopod well developed, with multiple terminal setae, caridean lobe normal, epipod feebly bilobed; second maxilliped with normal endopod, exopod as in first maxilliped, without caridean lobe, epipod small, simple, without podobranch; third maxilliped with slender endopod, ischiomerus fused or feebly separated from basis, exopod as in second maxilliped, coxa with semi-circular lateral plate, single arthrobranch present. First pereiopods slender, coxa with distomedial setose lobe, fingers of chelae elongate, with lateral cutting edges. Second pereiopods moderately stout, similar and subequal, chelae with fingers kept laterally; fingers subequal to palm, cutting edges with simple lamina and 2 low proximal teeth, carpo-propodal articulation simple, carpus much shorter than palm in adults, feebly cup-shaped. Ambulatory pereiopods slender, propodus without ventral spines, dactyli with minute or reduced distoventral tooth on stout corpus, unguis elongate, curved. Endopod of male first pleopod simple, elliptic, with



Figure 1. Holotype of *Palaemonella amboinensis* Zehntner, 1894, adult female, MHNG (photo: L Monod; scale bar 5 mm).

multiple spinules medioproximally and multiple pappose setae distally. Male second pleopod with appendix masculina slender, with several simple terminal and lateral setae. Uropods normal.

Figures (selected). Schenkel (1902: Pl. 13, fig. 21), Kemp (1922: figs 40–42, Pl. 6, fig. 8), Kubo (1940: figs 13–14), Miyake and Fujino (1968: fig. 4), Bruce (1978: fig. 6; 1979: Pl. 1, fig. A), Fransen (1989: fig. 1a–c).

Systematic position. Ancylocaris brevicarpalis (under the name Periclimenes brevicarpalis), together with P. inornatus Kemp, 1922, P. nevillei Bruce, 2010, P. ornatus Bruce, 1969, P. ornatellus Bruce, 1979, and P. albolineatus Bruce & Coombes, 1997, were previously believed to be members of a "P. brevicarpalis" group (see Bruce and Svoboda 1983, Bruce and Coombes 1997, Bruce 2010) some of which are sea anemone associated species. On the contrary, Fransen (1989) stated that only three of those species, i.e. P. inornatus, P. ornatellus, and P. ornatus, are closely related to each other and comprise a "P. inornatus" group (see Actinimenes gen. n., below), rather than belong in the "P. brevicarpalis" group. The available comprehensive molecular phylogenies (Gan et al. 2015, Horká et al. 2016) show that at least A. brevicarpalis (under the name P. brevicarpalis) occupies a position away from the P. inornatus group.

While the species of the "*P. inornatus*" group share with *Ancylocaris* the general shape of the body, especially of the rostrum and the second pereiopods, they may easily be distinguished from *A. brevicarpalis* by the presence of deeply subspatulate chelae of the first pereiopod, but also by the more numerous proximal teeth on the fingers of the second pereiopod, as well as larger and more anteriorly placed dorsal telson spines (the first pair before mid-length). The propodal segment of the second maxilliped in *A. brevicarpalis* is broader than the dactylus and distomesially expanded, while sub-equally broad in the "*P. inornatus*" group (e.g. Kubo 1940, Bruce 1979).

The sister taxon for Ancylocaris, as revealed by the analyses of Gan et al. (2015) and Horká et al. (2016), is actually a pair of Periclimenes species, the crinoid-associated P. affinis (Zehntner, 1894) and P. kallisto Bruce, 2008, which is symbiotic with antipatharian corals. The significant genetic distance of this pair however indicates that their position is most likely quite distant from Ancylocaris. Both those species show some resemblance to A. brevicarpalis in the size and position of the dorsal telson dentition, and in the distomedial coxal lobe and fingers on the first pereiopods. Periclimenes affinis also has a short carpocerite and a similar carpus of the second pereiopod, and similar male pleopod shape and setation. Periclimenes kallisto has feeble dentition of the fingers of the second pereiopod and the ambulatory dactyli with a minute distoventral tooth. These two species are more slender and smaller than A. brevicarpalis and bear a slender rostrum with obsolete ventral carina, unequal second pereiopods, ventrally spinulose ambulatory propodi, and the endopod of the male first pleopod has a distomedial lobe (Holthuis 1958, Bruce 1980, 2008a). A close affinity between these two species was suggested by Bruce (2008a), who highlighted a group of species of a similar morphology, additionally including P. canalinsulae Bruce & Coombes, 1997, and P. jugalis Holthuis, 1952. Some other taxa, for instance P. novaffinis Bruce & Coombes, 1997, *P. albolineatus* and *P. nevillei*, may also belong to this group. The systematic relation of this assemblage as well as of each particular member to the genus Ancylocaris remains to be resolved.

Remarks. The earliest report on the present species was published by Zehntner in 1984. However, Holthuis (1952) places Palaemonella amboinensis Zehntner, 1894 into the synonymy of Ancylocaris brevicarpalis Schenkel, 1902 under the name Periclimenes brevicarpalis (Schenkel, 1902), as he considers the drawing of the scaphocerite and the antennular peduncle in Zehntner (1894) not to be entirely correctly drawn. After the examination of a photograph of the holotype (Fig. 1) kindly provided by L. Monod (MHNG) we fully concur with this position. Palaemonella amboinensis Zehntner (1894) should thus have priority over Periclimenes brevicarpalis (Schenkel, 1902); however as stated by Holthuis (1952) the latter name is preoccupied by Periclimenes amboinensis (De Man, 1888), originally described as Anchistia amboinensis De Man, 1888. For some time now both taxa are no longer considered congeneric, as Anchistia amboinensis De Man, 1888 was placed in the genus Laomenes AH Clark, 1919, resurrected for a group of crinoid dwelling species by Okuno and Fujita (2007). Conversely, Ancylocaris brevicarpalis Schenkel, 1902 was maintained in the genus Periclimenes up to now, although now returned to the resurrected genus Ancylocaris. This creates some ambiguity as to what is the correct name for the taxon currently known as Periclimenes brevicarpalis (Schenkel), a rather widespread, well-known and often photographed species.

Article 60.1 (ICZN 1999) specifies that a junior homonym must be rejected and replaced either by an available and potentially valid synonym or, for lack of such a name, by a new substitute name. We herein interpret Holthuis's (1952) action in proposing to use a junior synonym, *Ancylocaris brevicarpalis* Schenkel, 1902, for *Palaemonella amboinensis* Zehntner, 1894 as a "substitute name". In which case, Art. 59.3 specifies "that a junior secondary homonym replaced before 1961 is permanently invalid

unless the substitute name is not in use and the relevant taxa are no longer considered congeneric, in which case the junior homonym is not to be rejected on grounds of that replacement". Clearly, the substitute name, *Periclimenes brevicarpalis* (Schenkel) is in widespread use, throughout the scientific literature as well as popular accounts, as it is one of the most photographed shrimp species. Even though both taxa have not been considered congeneric since the resurrection of the genus *Ancylocaris* makes *Ancylocaris brevicarpalis* Schenkel, 1902 the valid name for the species in question.

Distribution. The single species in the genus is widely distributed throughout the whole Indo-West Pacific, from South Africa and Red Sea to Japan and Polynesia.

Ecology. *Ancylocaris brevicarpalis* is obligatory associated with sea anemones (Cnidaria: Actiniaria) (cf. Fransen 1989, Müller 1993), although juveniles may also occur on alcyonarian and scleractinian corals.

Actinimenes gen. n.

http://zoobank.org/A1D1A9D6-406C-4EB3-B750-494A81EEAF9A

Type species. Periclimenes ornatus Bruce, 1969, by present designation.

Included species. Actinimenes inornatus (Kemp, 1922), comb. n. (Fig. 3C); A. ornatus (Bruce, 1969), comb. n. (Fig. 3D); and A. ornatellus (Bruce, 1979), comb. n.

Diagnosis. Carapace smooth; rostrum well developed, compressed, dorsal and ventral margins convex, with 7-10 dorsal teeth (posterior tooth behind orbits) and 0-2 ventral teeth, lateral carinae and orbit feebly developed, epigastric and supraorbital spines absent, inferior orbital angle usually produced, rounded, antennal tooth marginal, hepatic tooth close to level of latter. Pleon smooth, third segment not posteriorly produced, pleura rounded. Telson with two pairs of moderately large dorsal marginal spines situated on anterior and posterior thirds of telson length; three pairs of posterior spines, lateral spines smaller than dorsal spines. Eyes with globular cornea, small additional pigment spot dorsally on corneal margin. Antennule well developed. Antennal basicerite armed with lateral tooth; scaphocerite well developed, moderately broad, with distolateral tooth small, not reaching distal end of lamella. Mandible without palp, molar process robust, incisor process as usual for the family. Maxillula with bilobed palp, laciniae as usual for the family. Maxilla with simple palp, basal endite slender, deeply bilobed, coxal endite obsolete, scaphognathite moderately broad. First maxilliped with simple palp, basal endite fused with coxal endite, exopod with large caridean lobe, flagellum slender with several plumose distal setae, epipod feebly bilobed. Second maxilliped with normal endopod, propodus not produced distomesially, exopod similar to first maxilliped, without accessory lobe, coxa with oval epipod without podobranch. Third maxilliped with slender endopod, ischiomerus fused to basis, exopod as in second maxilliped, coxa with oval lateral plate, arthrobranch rudimentary or lacking. Fourth thoracic sternite with broad transverse ridge subdivided by median incision. First pereiopods moderately slender, chela with fingers subequal to palm, deeply subspatulate with entire cutting edges, coxa with setose distoventral lobe.

Second pereiopods well developed, smooth, similar and equal, fingers with several small recurved teeth on proximal half, palm subcylindrical, longer than fingers, carpo-propodal articulation terminal, carpus much shorter than palm, merus unarmed, coxa without distoventral lobe. Ambulatory pereiopods moderately slender, propodus without ventral spines, dactyli with stout unarmed corpus, unguis elongate, curved. Endopod of male first pleopod simple, elliptic, feebly spinulose medioproximally, with several setulose setae distolaterally. Male second pleopod with appendix masculina slender, with several simple terminal and lateral setae. Uropods normal, exopod with small distolateral tooth and normal movable spine.

Etymology. From Actiniaria, the order of Anthozoa which comprises the host sea anemones for the genus, and *Periclimenes* to which genus the species previously belonged; gender masculine.

Figures (selected). Kemp (1922: figs 43–46), Bruce (1976: 10–11; 1979: figs 3B, 4–7, Pl. 1: fig. B–E; 1982: figs 11–12), Fransen (1989: figs 2–3).

Systematic position. Based on recent molecular studies (Gan et al. 2015, Horká et al. 2016), species of the genus *Actinimenes* gen. n. show a close phylogenetic relationship to two groups of taxa, *Zenopontonia* Bruce, 1975 and some other echinoderm-associated taxa on the one hand, and to the *Periclimenes diversipes* species group on the other hand. While the latter are also cnidarian associates, they are distinctly smaller species with more slender ambulatory pereiopods and dactyls, but mainly with very distinctive second pereiopods with both or at least one of the chelae of a specific subspatulate shape, with fingers generally longer than palm. Further, the species of the latter group share a similar shape of rostrum, and position of the carapacial teeth, subspatulate first pereiopod chela, short carpus of second pereiopods, simple ambulatory dactyli with elongate sharp unguis, and the shape and spinulation of the male pleopods (Bruce 1989).

Zenopontonia as well as other related echinoderm-associated taxa, such as *P. colem*ani Bruce, 1975, and *Lipkemenes lanipes* (Kemp, 1922), are generally also very similar to *Actinimenes* by the position of antennal and hepatic teeth, an incised transverse ridge on the fourth thoracic sternite, the deeply subspatulate chelae of the first pereiopod, the shape of the chela of the second pereiopod and the very short carpus, and by the shape and spinulation of the male pleopods (Bruce 1989). These species however differ from *Actinimenes* spp. by a more down curved rostrum, more posteriorly situated and smaller dorsal telson spines, fine pectination on the fingers of the first pereiopod, and the ambulatory dactyli having small distoventral tooth on the corpus, sometimes also fully reduced (Marin 2012). Some mollusc- or ascidian-associated genera, e.g. *Anchistus* Borradaile, 1898, *Paranchistus* Holthuis, 1952, or *Dasella* Lebour, 1945, show some phylogenetic relationship to these echinoderm associated taxa (Gan et al. 2015, Horká et al. 2016), and thus more remotely also to *Actinimenes* gen. n. All species of these genera differ however from *Actinimenes* gen. n. by specialized biunguiculate ambulatory dactyli.

The three species of *Actinimenes* gen. n. were previously thought to be part of the '*Periclimenes brevicarpalis* group' (Bruce and Svoboda 1983, Bruce 2010), although

Fransen (1989) regarded them as comprising a '*Periclimenes inornatus* group' of identical composition of the new genus (see also Remarks for *Ancylocaris brevicarpalis* comb. n., above).

Distribution. Widely distributed in the Indo-West Pacific from the Red Sea and Kenya to Japan, Marshall Islands, and Fiji.

Ecology. The species of the present genus are all obligate associates of sea anemones (Cnidaria: Actiniaria) (see Fransen 1989, Müller 1993).

Key to species identification of Actinimenes gen. n.

Cristimenes gen. n.

http://zoobank.org/4A7068CC-CB18-4D6B-A9B0-FD518F4B3F19

Type species. *Periclimenes (Cristiger) commensalis* Borradaile, 1915, by present designation.

Included species. Cristimenes commensalis (Borradaile, 1915), comb. n. (Figs 2A, B, 3F); C. cristimanus (Bruce, 1965), comb. n. (Figs 2C, D, 3E); and C. zanzibaricus (Bruce, 1967), comb. n.

Diagnosis. Carapace smooth; rostrum well developed, subequal to antennular peduncle, compressed, usually with 5–7 low dorsal and 0–3 ventral teeth, lateral carinae with depressed supraorbital tooth, orbit feebly developed, epigastric tooth absent, inferior angle distinct, hepatic tooth close to antennal tooth and slightly lower positioned. Pleon smooth, fourth and fifth pleura posteroventrally angulate. Telson with two pairs of small dorsal spines on posterior half, and with three pairs of posterior spines. Eyes with globular cornea. Basal antennular segment with 2–3 acute distolateral teeth. Antenna with basicerite unarmed, scaphocerite moderately broad, with distolateral tooth small, not reaching distal level of lamina. Epistome with pair of lateral rounded tubercles. Mandible without palp, molar process robust, incisor process normal, with 3–4 terminal teeth; maxillula with bilobed palp, laciniae moderately broad; maxilla



Figure 2. Second pereiopod of species of the genus *Cristimanus* gen. n. showing specific carpo-propodal articulation. **A, B** *Cristimenes commensalis* (Borradaile, 1915), comb. n., MTQ 33230, Lizard Island, Great Barrier Reef **C, D** *Cristimenes cristimanus* (Bruce, 1965), comb. n., UO 103-Vn08, Nhatrang Bay, Vietnam. (**A, C** medial aspect; **B, D** lateral aspect; scale bars 1 mm).

with simple palp, basal endite slender, feebly bilobed or simple, coxal endite obsolete, scaphognathite moderately broad; first maxilliped with simple palp, basal and coxal endites fused, exopod with distinct caridean lobe, flagellum slender with 4 plumose distal setae, epipod bilobed; second maxilliped with normal endopod, propodus feebly produced medially, exopod similar to flagellum of first maxilliped, coxa with elongate epipod without podobranch, arthrobranch rudimentary; third maxilliped with slender endopod, ischiomerus distinct from basis, exopod as in second maxilliped, coxa with large subcircular lateral plate, arthrobranch rudimentary. Fourth thoracic sternite without median process. First pereiopods slender, chela with fingers tapering distally and feebly or distinctly subspatulate with entire cutting edges, coxa with obsolete distoventral lobe. Second pereiopods similar and subequal; cutting edges of fingers dentate or denticulate; palm elongate, subequal or longer than fingers, subterminally articulated to short cup-shaped carpus, with pair of proximal lobes fitting dorsally to carpal cavity; carpus and merus unarmed. Ambulatory pereiopods slender, dactyli bi- or triunguiculate (i.e. with or without dorsal spinule behind unguis), unguis long, almost subequal to corpus length; propodus with ventral spinules and tufts of soft setae. Uropodal exopod elongate, laterally straight, with small distolateral tooth with mobile spine medially.

Etymology. A combination of the subgeneric name *Cristiger* (see below) proposed by Borradaile, 1915 and *Periclimenes* in which genus the species were previously placed;



Figure 3. Examples of species from the genera reported in this study. **A**, **B** Ancylocaris brevicarpalis Schenkel, 1902: ovigerous females, MNHN-2014-558 and -156 (resp.), Kavieng, Papua New Guinea **C** Actinimenes inornatus (Kemp, 1922), comb. n., MNHN-IU-2014-315, with bopyrid parasite, Kavieng, Papua New Guinea **D** Actinimenes ornatus (Bruce, 1969), comb. n., ovigerous female, UO 80-Vn08, Nhatrang Bay, Vietnam **E** Cristimenes cristimanus (Bruce, 1965), comb. n., UO 103-Vn08, Nhatrang Bay, Vietnam **F** Cristimenes commensalis (Borradaile, 1915), comb. n., MTQ 33230, Lizard Island, Great Barrier Ree **G** Rapimenes laevimanus (Ďuriš, 2010), comb. n., ovigerous female holotype, RMNH D.53129, Nhatrang Bay, Vietnam **H** Rapimenes granulimanus (Bruce, 1978), comb. n., ovigerous female, MNHN-IU-2013-509, Madang, Papua New Guinea. (Photos: **A–G** Z Ďuriš; **H** A Anker).

gender masculine. As suggested by Holthuis (1993), the etymology of the name *Cris-tiger* (Latin = crest-bearer) was possibly in reference to the convex upper margin of the rostrum in the type species (from *crista* = crest, and *gero* = to bear).

Figures (selected). Holthuis (1952: figs 18–19), Miyake and Fujino (1968: fig. 2e–g), Bruce (1965: figs 1–2; 1967: figs 26–29; 1982: fig. 2).

Systematic position. The present new genus is closely related to three crinoidassociated genera, Araiopontonia Fujino & Miyake, 1970, Laomenes AH Clark, 1919, and Unguicaris Marin & Chan, 2006. This was already suggested by Marin and Chan (2006), and later supported by phylogenetic analyses (Kou et al. 2013, Gan et al. 2015, Horká et al. 2016). All these echinoderm-associated shrimps have a well-developed, somewhat downturned rostrum, generally dentate both dorsally and ventrally; the epistome is with a pair of lateral lobes (low, rounded in Cristimenes gen. n. and Araiopontonia, but acutely produced in the remaining genera); similar and subequal second pereiopods, and ambulatory legs possessing a specific type of 'triunguiculate' dactylus with a long main unguis. Such dactyli are secondarily reduced to a more biunguiculate state by the reduction of the dorsal spinule in the echinoid-associated species C. cristimanus and C. zanzibaricus, as well as in the crinoid associated genus Laomenes. The depressed supraorbital teeth associated with the lateral rostral carina are a synapomorphic character for the group, however, secondarily lost in Unguicaris. Such a reduction of the supraorbital teeth and lateral carinae was illustrated in some specimens of C. commensalis by Monod (1976), or Bruce (1982).

Cristimenes gen. n., together with *Araiopontonia*, can be distinguished from the genera *Laomenes* and *Unguicaris* by the rounded lateral lobes on the epistome (vs. acute projecting lobes). The new genus differs from all the three genera by a 3-dentate mandibular incisor (vs. distally expanded, multidentate), and by the unique carpopropodal articulation of the second pereiopods, with the subterminal proximo-ventral articulation on the propodus leaving a distinctive posterior part of the propodus dorsally overhanging the articulation (Fig. 2). This lobe is deeply subdivided by a short but deep longitudinal groove into a pair of lobes which smoothly fit into the dorsal cavity of the short cup-shaped carpus when the propodus is extended anteriad. The proximal end of the propodus is then well hidden inside the carpus from dorsal view.

Range. Widely distributed throughout the whole Indo-West Pacific region.

Ecology. The genus *Cristimenes* comprises a single crinoid-associated species, *C. commensalis* comb. n., with the other two species, *C. cristimanus* comb. n., and *C. zanzibaricus* comb. n., living on echinoids (Echinodermata: Crinoidea, Echinoidea).

Remarks. The genus *Cristimenes* is established here for three species, with *Periclimenes* (*Cristiger*) *commensalis* as the type species. This species was designated as the type species of the subgenus *Cristiger* Borradaile, 1915 by Holthuis (1955) since the previous designation of *Alpheus scriptus* Risso, 1822 by Borradaile (1917) as the type was invalid. As pointed out by Holthuis (1955, 1993), the name *Cristiger* Borradaile is a junior homonym of *Cristiger* Gistel, 1848 (Hymenoptera), and thus not available to be used for the present genus.

Key to species identification of Cristimenes gen. n.

1 Ambulatory dactyli triunguiculate; associated with crinoids (basal antennular segment with 2-3 acute teeth distolaterally; first pereiopod fingers simple, subequal to palm; second pereiopods with cutting edges of fingers dentate proximally and denticulate distally) C. commensalis (Borradaile, 1915), comb. n. Ambulatory dactyli biunguiculate; associated with echinoids2 2 Palm and dactylus of first pereiopod strongly compressed, palm tuberculate dorsally, dactylus carinate medially; second pereiopods with cutting edges of fingers dentate throughout; basal antennular segment with 3 acute teeth distolaterally C. cristimanus (Bruce, 1965), comb. n. Palm and dactylus of first pereiopod normal, smooth dorsally, uncarinate; second pereiopods with cutting edges of fingers dentate proximally and denticulate distally; basal antennular segment with rounded lobe and 2 acute

Rapimenes gen. n.

http://zoobank.org/5157C46E-9EC0-4D4A-A34E-CBA986D443A9

Type species. Periclimenes granulimanus Bruce, 1978, by present designation.

Included species. *Rapimenes brucei* (Ďuriš, 1990), comb. n.; *R. granulimanus* (Bruce, 1978), comb. n. (Fig. 3H); and *R. laevimanus* (Ďuriš, 2010), comb. n. (Fig. 3G).

Material examined. In addition to the type series (Ďuriš 2010), the following specimens were subsequently examined: *R. granulimanus* – 6 spms, (MNHN-IU-2013-10931), 1 spm. (IU-2013-11097), 2 spms (IU-2013-11077), *Papua Niugini Expedition* 2012, Madang Lagoon, Papua New Guinea, Dec. 2012, coll. Z Ďuriš. — *R. laevimanus* – 3 spms (UO-Jp2012), Nago-city, Okinawa, Japan, 26°33,6'N, 127°57.6'E, 10 May 2012, depth 30 m, on sea pen cf. *Stylatula* sp. [Pennatulacea]; coll.: N Sirakawa & Y Yamada, lgt. R Minemizu.—1 spm. SW Taiwan, coll. C-W Lin (fcn 20130202-08).

Diagnosis. Medium sized shrimps. Carapace smooth, with antennal and hepatic teeth; epigastric tooth lacking or, if present, clearly separated from them; hepatic tooth subequal and situated posteriorly of antennal tooth and slightly below. Rostrum slender, dorsal lamina bearing 6–10 teeth, ventral lamina obsolete, with 1–2 subterminal teeth. Inferior orbital angle produced, rounded. Pleon smooth, pleura posteroventrally rounded; telson slender, tapering distally, with 1–2 pairs of small dorsal spines and three pairs of posterior marginal spines. Ophthalmic somite without interocular process. Antennula and antenna normal, scaphocerite 3–4 times longer than broad. Eye with globular cornea and small accessory pigment spot, stalk distinctly longer than corneal diameter. Mandible without palp, incisor and molar processes
stout. Maxillula with bilobed palp, upper and lower laciniae well developed. Maxilla with slender palp, well developed scaphognathite, distal (basal) endite bilobed; proximal (coxal) endite lacking. First maxilliped with simple palp, basal endite broad, coxal endite feebly demarcated, exopod well developed, caridean lobe normal, epipod distally bilobed. Second maxilliped with normal endopod and exopod, epipod small, simple, without podobranch. Third maxilliped with slender segments, ischiomerus and basis fused; exopod well developed, coxa with rounded lateral plate, single small arthrobranch present. Fourth thoracic sternites without special structures. First pereiopods slender, fingers narrow, simple, with dense tufts of long setae on sides, coxa with or without distoventral setose process, basis unarmed. Second pereiopods long and slender, distinctly unequal in length; major pereiopod overreaching scaphocerite by distal part of merus in adults; fingers simple, cutting edges entire or with 1-2 feebly developed teeth on proximal third of minor chela, and with 2-4 obtuse proximal teeth on major chela fingers; major pereiopod with palm 2.5-5 times longer than fingers. Ambulatory pereiopods slender, propodus with prehensile structure of long straight distoventral spines arranged to 2-5 pairs, spines longer than distal propodal depth; dactyli slender and curved, simple, or with distinct or minute distoventral tooth. Endopod of first male pleopod with angulate apex and distinct medial lobe; second male pleopod with appendix masculina with 3 terminal serrated setae and 2 lateral setae. Uropods normal; distolateral angle of exopod with small tooth and movable spine medially.

Etymology. Combination of *rapina*, Latin for claw, to point on the prehensile structures on the ambulatory legs, and the name of the genus *Periclimenes* Costa, 1844, from which the new genus is separated; gender masculine.

Figures (selected). Bruce (1978: figs 16–19), Ďuriš (1990: figs 1–2; 2010: figs 1–8).

Systematic position. Based on the recent molecular phylogeny in Horká et al. (2016), the therein included two species of *Rapimenes* gen. n. are closely related to the genus Phycomenes Bruce, 2008, and to a pair of further Periclimenes spp., i.e. P. affinis, and P. kallisto, positioned near to A. brevicarpalis comb. n. From Phycomenes, the species of the genus Rapimenes gen. n., can be easily distinguished by their larger size, distinctly unequal second pereiopods, prehensile ambulatory legs, and lack of a triangular process on the fourth thoracic sternum (see Bruce 2008b, Ďuriš 2010). Morphologically, the new genus (i.e. the previous "P. granulimanus group") is phylogenetically close to the "P. obscurus group", as already indicated by Eilbracht and Fransen (2015) who also listed the characters distinguishing all species of those two groups. Included in the "P. obscurus group" are some species which show distinct similarities to Rapimenes, such as P. macrorhynchia Eilbracht & Fransen, 2015, P. nomadophila Berggren, 1994, and P. tonga Bruce, 1988 (the latter synonymized with P. granulimanus by Marin 2012, but regarded as valid by Eilbracht and Fransen 2015), particularly in the shape and proportions of the pereiopods and rostrum. These species have biunguiculate walking dactyli, sternal thoracic ridges, and distinct setose coxal lobe on the first pereiopod, i.e. the characters typical for the "P. obscurus group". The ambulatory dactyli vary in Rapimenes spp. from simple to bearing a minute additional

tooth; the latter is true for *R. brucei*, new comb., for which a coxal setose lobe also was reported (Ďuriš 1990). It is thus possible that both species groups represent a common evolutionary clade which inner diversity is still to be resolved.

Distribution. Madagascar; Maldive Islands; Indonesia; Vietnam and Taiwan, South China Sea; Japan; Heron Island, Great Barrier Reef, Australia.

Ecology. The species of the present genus have been recorded as associated with antipatharians, hydroids, pennatularians, and scyphozoans (Cnidaria) (Bruce 1978, 1988, Ďuriš 1990, 2010, Minemizu 2013, Eilbracht and Fransen 2015).

Remarks. The generic name *Rapimenes* was used as a *nomen nudum* by Marin (2009: 15) in reference to the then undescribed species *Periclimenes laevimanus* Ďuriš (2010), as "*Rapimenes laevimanus* Ďuriš & Petrusek (in press)". The name is herein validly reinstated for the genus, indeed now containing *Rapimenes laevimanus*.

Key to species identification of *Rapimenes* gen. n. (modified from Duriš 2010).

| 1 | Major second pereiopod extremely long and slender, overreaching scapho- |
|---|---|
| | cerite by proximal merus, carpus longer than both chela or merus; walking |
| | dactyli feebly biunguiculate with small distoventral tooth on corpus, propodi |
| | with long spines arranged to 4 distoventral pairs |
| | <i>R. brucei</i> (Ďuriš, 1990), comb. n. |
| _ | Second pereiopods unequal, slender, at least overreaching scaphocerite by |
| | distal merus, carpus subequal or distinctly shorter than both chela or mer- |
| | us; walking dactyli simple or with rudimentary distoventral tooth, propodi |
| | with 1-3 single proximal spines in addition to 2-4 distoventral pairs of long |
| | spines |
| 2 | Major second pereiopod with palm granulate; minor second chela with 1-2 |
| | teeth on cutting edges |
| _ | Major second pereiopod with palm smooth; minor second chela with cutting |
| | edges entir R. laevimanus (Ďuriš, 2010), comb. n. |
| | |

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RESEARCH ARTICLE



New species of *Habronattus* and *Pellenes* jumping spiders (Araneae, Salticidae, Harmochirina)

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Abstract

The harmochirine jumping spiders include the New World *Habronattus*, notable for their complex courtship displays, and *Pellenes*, found throughout the Old World and North America. Five new species of *Habronattus* and one new species of *Pellenes* are here described from North America: *Habronattus aestus*, **sp. n.**, *H. chamela* **sp. n.**, *H. empyrus* **sp. n.**, *H. luminosus* **sp. n.**, *H. roberti* **sp. n.**, and *Pellenes canadensis* **sp. n.** For each of the new species, photographs of living specimens are given, as well as notes on habitat. The new subgenus *Pellenattus* is described for the subgroup of *Pellenes* restricted to North America, with type species *Pellenes peninsularis* Emerton, 1925. Species placed in *Pellenes (Pellenattus)* are *Pellenes apacheus* Lowrie & Gertsch, 1955, *P. canadensis* **sp. n.**, *P. crandalli* Lowrie & Gertsch, 1955, *P. dorsalis* (Banks, 1898b), *P. grammaticus* Chamberlin 1925, *P. levii* Lowrie & Gertsch, 1955, *P. limatus* Peckham & Peckham, 1901, *P. longimanus* Emerton, 1913, *P. peninsularis* Emerton, 1925, *P. shoshonensis* Gertsch, 1934, and *P. washonus* Lowrie & Gertsch, 1955. *Pellenes wrighti* Lowrie & Gertsch, 1955 is synonymized with *P. peninsularis*. Attention is drawn to an undescribed species of *Habronattus* from Canada whose only known specimen is apparently lost.

Keywords

Araneae, Salticidae, Plexippini, Harmochirina, jumping spider

Introduction

The two jumping spider genera *Habronattus* F.O. Pickard-Cambridge, 1901 and *Pellenes* Simon, 1876 are closely related within the subtribe Harmochirina (Maddison and Hedin 2003a, b; Maddison 2015). While *Habronattus* species are confined to the Americas (Griswold 1987) and known for their complex courtship ornamentation and behaviour (Peckham and Peckham 1890; Griswold 1987; Elias et al. 2003, 2012), *Pellenes* are distributed throughout the Old World, along with North America, and show considerably less sexual dimorphism and courtship complexity. The phylogeny of *Habronattus* has been studied by both morphological (Griswold 1987) and molecular data (Maddison and Hedin 2003b), but many ambiguities remain — thus, an ongoing phylogenetic study seeks to use genomic data. To offer names for 6 taxa used in that phylogenomic study, five new species of *Habronattus* and one new species of *Pellenes* are described from North America. In addition, a new subgenus is erected to house the North American group of *Pellenes*.

Methods

Specimens are deposited in the Spencer Entomological Museum of the University of British Columbia (UBC-SEM), the Colección Nacional de Arácnidos, Instituto de Biología, Universidad Nacional Autónoma de México (CNAN-IBUNAM), the Museum of Comparative Zoology, Harvard University (MCZ), or the American Museum of Natural History (AMNH).

Preserved specimens were examined under both dissecting microscopes and a compound microscope with reflected light. Drawings (except that of *Pellenes peninsularis* habitus and palpi from Ontario) were made with a drawing tube on a Nikon ME600L compound microscope.

Terminology is standard for Araneae. The descriptions were written with primary reference to the focal specimen indicated, which was used for measurements and carefully checked for details, but they apply as far as known to the other specimens examined. All measurements are given in millimeters. Carapace length was measured from the base of the anterior median eyes not including the lenses to the rear margin of the carapace medially; abdomen length to the end of the anal tubercle. Rotation of the bulb of the palp expressed in degrees counterclockwise from distal. Thus, 0° is distal (12:00 on an analog clock face); 90° is prolateral (9:00); 180° is proximal (6:00); 270° is retrolateral (3:00). The following abbreviations are used: AME, anterior median eyes; ALE, anterior lateral eyes; PLE, posterior lateral eyes; PME, posterior median eyes (the "small eyes"); RTA, retrolateral tibial apophysis. The apophysis accompanying the embolus of the male palp was called the conductor by Lowrie and Gertsch (1955), the tegular apophysis by Griswold (1987), and the compound terminal apophysis by Logunov et al. (1999). It is here called the "terminal apophysis", abbreviated "TmA", following Edwards (2015).

Taxonomy

Genus Habronattus F. O. Pickard-Cambridge, 1901

Type species. Habrocestum mexicanum Peckham & Peckham, 1896

Notes. Most of the approximately 100 species (Griswold, 1987) of *Habronattus* are found in Mexico and the United States, extending into arctic Canada and to southern South America. *Habronattus* as a whole is easily recognized by the 90° bend ("elbow") on the long thin TmA of the palp, though the elbow is lost secondarily in the *H. coecatus* species group. Several clades of species are recognized as species groups (Griswold 1987; Maddison and Hedin 2003b), some referred to here in the descriptions.

Two of the new species were studied by Maddison and Hedin (2003b): *H. chamela*, called "*H.* sp. (CHMLA)" by Maddison & Hedin, and *H. roberti*, called "*H.* sp. (ROBRT)". For the other new species we used informal names in field and lab notebooks: *H. aestus* as "peñasco" or "ESTU", *H. empyrus* as "blondie" or "BLNDI", *H. luminosus* as "sunglow" or "SUNGL", and *P. canadensis* as "*P.* cf. *levii*". Images and mentions of *H. luminosus* have appeared on news reports in connection with Zurek et al.'s (2015) study of colour vision, under the name "*Habronattus sunglow*".

Habronattus aestus Maddison, sp. n.

http://zoobank.org/43D988D1-AA30-45F6-8A90-15D67B59EAA7 Figs 1–12

Holotype. Male in CNAN-IBUNAM, with data: México: Sonora: Puerto Peñasco, Estero Morúa, 31.30°N 113.46-113.48°W, 22–23 February 2003, W. Maddison, WPM#03-001.

Paratypes. (3 3 3 3 9 9): Same data as holotype (1 3 in UBC-SEM, 1 3 in AMNH). México: Sonora: Puerto Peñasco, Estero Cerro Prieto, 31.418° N 113.626°W, 1 m elev., 18 August 2013, W. Maddison & A. Meza López, WPM#13-086 (1 3 [specimen AZS13-7854, Figs 5–7] 2 2 9 in UBC-SEM, 1 9 in AMNH).

Etymology. From the Latin, in reference to the tides and the heat of its habitat.

Diagnosis. This species can be placed in the *americanus* group by male ornamentation (shelf of projecting setae under the AME, Fig. 7; darkened first tarsus, Fig. 6) and the relatively short and pointed terminal apophysis (TmA) arising at about 120°. However, unlike other members of the group (Griswold 1987, figures 184–186), the TmA of *H. aestus* is thin at the base (Fig. 1), more or less lacking the elbow typical of *Habronattus*. The male's scantiness of ornamentation is also distinctive — the first males found were not recognized as adult initially — as is the habitat of saline negative estuaries. Both male and female have the first tibia reddish brown, contrasting against a darker patella (Figs 6 and 9).

Description. *Male* (focal specimen: holotype). Carapace length 1.9; abdomen length 1.8. Palp (Figs 1–2) with bulb little rotated, embolus arising at about 140°;



Figures 1–12. *Habronattus aestus* sp. n. **I** Left male palp, ventral view (holotype) **2** Same, retrolateral view of palp tibia **3** Epigynum, ventral view (paratype described) **4** Epigynum, cleared, dorsal view, same female **5–7** Male AZS13-7854 (paratype) **8** Female AZS13-7889 **9–10** Female AZS13-7885 **11** Female AZS13-7874 **12** Juvenile AZS13-8283. All specimens are from Estero Cerro Prieto (WPM#13-086) except holotype, from Estero Morúa (WPM#03-001). Figures 5–12 are copyright © 2015 W. P. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.

TmA thin and with only a hint of an elbow. RTA triangular. First leg with tarsus and metatarsus thicker than usual. Colour: Chelicerae pale, covered with erect white setae. Palp femur, patella, tibia with partially erect white setae, especially long prolaterally. Distal 3/4 of cymbium with fine dark hairs. Legs light to medium brown in alcohol, though darker in life. First leg metatarsus and tarsus dark, with extended dark scopula. Clypeus covered with cream coloured scales, with prominent row of long cream-coloured setae extending forward, forming a shelf (Fig. 7). Carapace dark brown with bronze scales. Abdomen similar to that of the juvenile in Fig. 12, reddish brown with broad paler basal band, two distinctive cream triangles centrally, and lateral cream bands made of paired crescents.

Female (focal specimen: paratype, specimen from Estero Cerro Prieto, Figs 3–4). Carapace length 2.3; abdomen length 3.0. Epigynum with semicircular atria; central pocket broad posteriorly (Fig. 3). Colour: Chelicerae medium brown. Legs medium to pale brown, the first pair darkest. Clypeus covered with white scales, with (as in male) shelf of long white setae projecting forward (Fig. 10). Carapace and abdomen covered with cream-coloured scales except for orange-tan patches on abdomen. Central pale triangles (chevrons) on dorsum connected to lateral bands, as in Figs 8 and 10.

Additional material examined. Two juveniles and 3 females from the type locality.

Natural history. Found only in the negative tidal estuaries of Sonora, México. These unusual habitats have salt-tolerant plants (such as *Salicornia*) on soil that is constantly wet with salt water, as the tides enter then drain to cut stream-like channels (Figs 95–96). Fresh water is rarely available in this harsh desert. Although *H. aestus* was found at Estero Morúa, in 2013 it was considerably more common at Estero Cerro Prieta. There, it was found either in retreats in the larger salt-tolerant plants along the edges of the channels, about 20-40 cm above the substrate, or on the mud/sand of the slopes of these channels after shaking the overhanging salt-tolerant plants. The court-ship involves behaviours similar to those seen in other *americanus*-group members, though of weak amplitude. A video of the courtship of male AZS13-7854 is available at https://youtu.be/JUkULLdOZ0w.

Habronattus chamela Maddison, sp. n.

http://zoobank.org/65A538DC-EAEC-482F-978D-29CF544AA9D8 Figs 13–25

Holotype. Male specimen JAL14-9837 in CNAN-IBUNAM, with data: México: Jalisco: Estación de Biología Chamela, 400-650 m on Calandria Trail, 19.5038 - 19.5045°N 105.0334 - 105.0344°W, 19 Feb. 2014, W. Maddison & H. Proctor WPM#14-034.

Paratypes (5 ? ? ? ?). Same data as holotype (1 ? specimen JAL14-9844 in CNAN-IBUNAM. 1 ? specimen JAL14-9840 in UBC-SEM, 1 ? in AMNH). México: Jalisco: Estación de Biología Chamela, 19.498° N 105.045° W, 1-2 June 1998,



Figures 13–25. *Habronattus chamela* sp. n. **13** Left male palp, ventral view (paratype male) **14** Same, retrolateral view of palp tibia **15** Epigynum, ventral view (paratype female) **16** Male JAL14-9795 **17–18** male JAL14-9812 **19** Male JAL14-0138 (paratype) **20** male JAL14-0224 **21** male JAL14-0587 **22** male JAL14-0213 **23** female JAL14-9844 (paratype) **24–25** female JAL14-8947. All specimens are from Estación de Biología Chamela or Chamela Estuary except Fig. 21, from El Tuito (WPM#14-047). Figures 16–25 are copyright © 2015 W. P. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.

W. Maddison et al, WPM#98-071 (13 in AMNH, 13 in MCZ, 233299 in UBC-SEM). México: Jalisco: Estación de Biología Chamela 400-850 m on Calandria Trail, 19.5023-19.5045°N 105.0328-105.0344°W, 19 Feb. 2014, W. Maddison & H. Proctor, WPM#14-033 (19 specimen JAL14-9847 in UBC-SEM). México: Jalisco: Estación de Biología Chamela, Calandria Trail, 19.501 - 19.505°N 105.035°W, 130 m elev., 23 Feb. 2014, W. Maddison & R. Sosa, WPM#14-038 (13 specimen JAL14-0138 Fig. 19 in UBC-SEM, 19 in MCZ).

Etymology. The name of the type locality is placed as a noun in apposition.

Diagnosis. This little-ornamented species appears to be close to *H. nahuatlanus* Griswold 1987. The male's white clypeus is divided by one or two central dark bands beneath and between the AME (Figs 18, 19, 21), separating it from most other *Habronattus* except *H. nahuatlanus* and *H. banksi* (Peckham & Peckham, 1901), from which it differs in having a much less rotated bulb of the palp. In some specimens of *H. chamela*, the dividing bands are absent (Fig. 20). The bulb of the palp is unusually little rotated (Fig. 13), with the base of the TmA pointing prolaterally (to 90°) as in *H. paratus, H. moratus*, and the *americanus* group, from which *H. chamela* differs in many aspects of markings and form.

Description. Male (focal specimen: holotype). Carapace length 2.0; abdomen length 1.8. Palp with bulb little rotated, with embolus arising at 150° and the base of TmA directed prolaterally (Fig. 13). RTA long with fingerlike projection (Fig. 14). Colour (Figs 16-21): Chelicerae dark with a patch of white scales (Figs 18–21). Palp femur and patella pale yellow, contrasting against dark tibia and cymbium. Femora of legs pale centrally, with black annulae proximally and distally. Other segments medium brown (with cream scales) with black annulae distally. Prolateral side of first tibia and metatarsus black. Clypeus covered with white scales except for two vertical black lines near the midline. Extending from clypeus is a broad marginal band of white scales, reaching to the back of the carapace where it contacts the narrow longitudinal bands descending from just inside the PME. Carapace otherwise mostly black or dark brown, except for faint inverted "V" between PME and two small spots in the middle of the ocular area (Fig. 17). Abdomen dark above with a cream sword-shaped longitudinal band along the midline, and with lateral cream lines. The dark areas are black in the anterior third, but reddish in the posterior two-thirds.

Female (focal specimen: paratype, specimen JAL14-9844, Fig. 23). Carapace length 2.1; abdomen length 2.7. Epigynum with central pocket long (Fig. 15); atria separate, not joined anteriorly. Colour: Chelicerae dark with a few white scales on basal half. Legs medium brown but with distinctly paler area centrally on femora. Clypeus dark except for white scales along the margin, extending upward at the midline. Carapace and abdomen as in the male but with lower contrast. The central longitudinal band of the abdominal dorsum is usually broken into two cream-coloured spots.

Geographical variation. Males from the area of El Tuito, north of the type locality, have a continuous red patch in the centre of the clypeus (Fig. 21), instead of two vertical lines. Additional material examined. 123319 in UBC-SEM: México: Jalisco: El Tuito, Rancho Primavera, $20.3447^{\circ}N$ 105.3537°W, 700 m elev., 3 March 2014, W. Maddison, WPM#14-047 (433); México: Jalisco: Sierra Manantlan, 19.7013°N 104.3918°W, 1550 m elev., 1 June 1998, W. Maddison et al., WPM#98-067 (73319). México: Jalisco: Estación de Biología Chamela, 19.498°N 105.045°W, 1-2 June 1998, W. Maddison et al., WPM#98-071 (133).

Natural history. Known from the tropical deciduous forests along the southern coast of Jalisco, México (Fig. 101), typically found on leaf litter or sticks on the ground that receives sun but is somewhat shaded (Fig. 99) — in contrast to the more open sunny ground on which *H. roberti* lives nearby. The courtship involves the male standing at a distance from the female with first legs spread; he walks in bursts toward the female, sidling somewhat. On each burst forward, the front legs are flicked upward and the palps lowered to expose the face. A video of male courtship is available at https://youtu.be/mgXhB61u0mA.

Habronattus empyrus Maddison, sp. n.

http://zoobank.org/1FCF2BA2-B4E8-4C5C-B384-7198F62E5D17 Figs 26–37

Holotype. Male in CNAN-IBUNAM, with data: México: Sonora: Puerto Peñasco, Estero Morúa, 31.293 - 31.295°N 113.456 - 113.459°W, 17 August 2013, Maddison/ Proctor/Evans/Leduc-Robert/Meza, WPM#13-084.

Paratypes $(5 \textcircled{3} \textcircled{3} 4 \clubsuit \clubsuit)$. Same data as holotype $(1 \clubsuit$ specimen AZS13-7828 in CNAN-IBUNAM, $1 \textcircled{3} 1 \clubsuit$ in UBC-SEM, $1 \textcircled{3} 1 \clubsuit$ in MCZ, $1 \textcircled{3} 1 \clubsuit$ in AMNH). México: Sonora: Puerto Peñasco, Estero Morúa, $31.293 - 31.294^\circ$ N 113.456 - 113.458°W, 1 m elev., 16 August 2013, Maddison/Proctor/Evans/Leduc-Robert, WPM#13-079 (2 3 3 in UBC-SEM specimens AZS13-7562 [Fig. 30] and AZS13-7582 [Fig. 31]).

Etymology. From the Greek *empyros*, burning, referring to the male's flaming colors: a brilliant red face against a pale yellow-orange body and legs. Also, to the author's synesthesia, the dominant letters of the name match the colours of males perfectly: "e" for the green first legs, "r" for the red face, and "y" and "s" for the pale yellow-orange of the body and legs.

Diagnosis. A member of the *coecatus* group distinctive for its pale colours. The male's red face and form of the third legs (Figs 29–31, 33, 34) distinguish it from all other members of the *coecatus* group except *H. pyrrithrix*, from which it differs in having a much paler body, the green first legs paler in life, and the red facial band narrower. The third leg is much like that of *H. pyrrithrix*, *H. carpus* and *H. mexicanus*, with an orange tuft on the dorsal distal side of the femur and a dark patella with pale speckles, a bright white dorsal-basal tuft, and a moderate but thin thumb-like dorsal-distal apophysis (Figs 29–31; compare to Griswold 1987 figures 84–85). However, the femur of *H. empyrus* has an additional black streak just ventral to the prominent macroseta on the prolateral distal face of the femur (Fig. 29). Typical *H. pyrrithrix*



Figures 26–37. *Habronattus empyrus* sp. n. **26** Left male palp, ventral view (holotype male) **27** Same, retrolateral view of palp tibia **28** Epigynum, ventral view (paratype female AZS13-7828) **29** Femur, patella and tibia of third leg, prolateral view (holotype male) **30** Male AZS13-7562 (paratype) **31** Male AZS13-7582 (paratype) **32–33** Male AZS13-7575 **34** Male AZS13-7834 **35** Female AZS13-7617 **36–37** Female AZS13-7828 (paratype). All specimens are from Estero Morúa (WPM#13-084) except Figs 30–33, 35 from Estero Cerro Prieto (WPM#13-079). Figs 30–37 are copyright © 2015 W. P. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.

were found only 6 km away from the type locality, lessening concerns that *H. empyrus* might be a only a geographical variant.

Description. Male (focal specimen: holotype). Carapace length 2.2; abdomen length 2.1. Palp typical for *coecatus* group, with sickle-shaped TmA. Embolus arises at 180° (Fig. 26). Colour and ornaments in alcohol: Chelicerae dark at base, paler at tips. Palp femur and tibia pale except dark patch prolaterally and ventrally. Cymbium pale yellow-brown with long white hairs. Legs pale yellowish except for dorsal black stripe on first femur and markings of third leg. First leg with fringes and modified spatulate setae typical of *coecatus* group. Third femur with longitudinal black lines on dorsal and ventral edges of prolateral face, up to the expanded distal area which bears two black spots and a dorsal tuft of orange setae (Figs 29, 30). Third patella with a typical expanded triangular ridge above and a thumb-like apophysis distally. Clypeus red, transitioning abruptly to black between the AME and ALE. The black is a fairly narrow region beneath the ALE. Otherwise, the carapace is covered fairly uniformly with cream to light yellowish-brown scales, with the usual coecatus-group markings indistinct. Abdomen with standard *coecatus*-group markings of a central pale chevroned longitudinal band with a transverse band cutting across it, but less distinct than usual, because the background is light brown rather than black. In life (Figs 30-34), the palp femur is light brown, not red as in *H. pyrrithrix*. The integument of the first leg is light green. The third tibia is also green.

Female (focal specimen: paratype, specimen AZS13-7828; Figs 28, 36–37). Carapace length 2.6; abdomen length 2.7. Structure (including epigynum, Fig. 28) typical for *coecatus* group. Colour (Figs 35–37) typical for *coecatus* group, pale beige to light brown. Clypeus white (Fig. 37). Abdomen shows only a trace of the markings of the male.

Additional material examined. $10\Im$ 799 in UBC-SEM: México: Sonora: Puerto Peñasco, Estero Morúa, 31.293°N 113.452°W, 1 m elev., 16 August 2013, S.C. Evans, WPM#13-078 (1 \Im). México: Sonora: Puerto Peñasco, Estero Morúa, 31.293 - 31.294°N 113.456 - 113.458°W, 1 m elev., 16 August 2013, Maddison/Proctor/Evans/Leduc-Robert, WPM#13-079 (3 \Im). México: Sonora: Puerto Peñasco, Estero Morúa, 31.293 - 31.295°N 113.456 - 113.459°W, 17 August 2013, Maddison/ Proctor/Evans/Leduc-Robert/Meza, WPM#13-084 (3 \Im 799). México: Sonora: Puerto Peñasco, Estero Morúa, 31.296 - 31.297°N 113.487 - 113.493°W, 17 August 2013, Maddison/ Proctor/Evans/Leduc-Robert, WPM#13-085 (2 \Im). México: Sonora: Puerto Peñasco, Estero Cerro Prieto, 31.418°N 113.626°W, 1 m elev., 18 August 2013, W. Maddison & A. Meza López, WPM#13-086 (1 \Im).

Natural history. Found with *H. aestus* in the negative tidal estuaries of Sonora, México. *H. empyrus*, however, was found in the flatter areas with short salt-tolerant plants including *Salicornia* (Fig. 97), unlike *H. aestus* which was associated with large salt-tolerant plants along the tidal channels. Individuals of *H. empyrus* were found on the wet sand/mud, or hopping from one short plant to another like little monkeys. A portion of courtship was observed, and appears typical for the *H. coecatus* species group (https://youtu.be/Lwa678NVC3U).

http://zoobank.org/DB648F11-9FE1-41A9-9FBB-A6FA1E8D2352 Figs 38–49

Holotype. Male in UBC-SEM, with data: U.S.A.: Arizona: Santa Cruz Co., Mt. Hopkins Road, Amateur Astronomy Vista, 31.6775°N 110.9288°W, 7 May 2014, N. Morehouse & D. Zurek.

Paratypes $(1 \swarrow 2 \heartsuit \heartsuit)$. U.S.A.: Arizona: Santa Cruz Co., Mt. Hopkins Rd, Amateur Astronomy Vista, 31.6759 - 31.6762°N 110.9289 - 110.9293°W, 1430 m elev., 7 August 2013, W. Maddison & H. Proctor, WPM#13-056 ($2 \heartsuit \heartsuit$ specimens ASZ13-7108 and AZS13-7081 in UBC-SEM). Arizona: Cochise Co., Sunglow, west side Chiricahua Mts., 12 July 1977, B. & V. Roth ($1 \circlearrowright$ in AMNH).

Etymology. Latin, "full of light", in reference to the pale coloring of the body, especially in the yellow-white juveniles, as well as to the name of the locality of the first known specimen, Sunglow, Arizona.

Diagnosis. A large-bodied species, covered extensively with pale scales in both males and females. The male is distinctive for the red face with a blue central patch (Figs 43, 46), though in alcohol the blue patch appears as metallic green. The tibial apophysis of the palp has a distinct bump projecting retrolaterally, proximal from the tip (Figs 38, 39). The epigynum is distinctive, with the central pocket for the RTA very small, on a mound in front of which the openings are adpressed (Fig. 40).

Description. *Male* (focal specimen: holotype, Figs 41–43). Carapace length 3.1; abdomen length 3.2. Palp (Figs 38-39): bulb moderately rotated, with embolus arising at about 290°. RTA with a notable bump dorsally near the tip. Legs: unornamented, as in the female. Carapace: At the back of the carapace is a small stridulatory file, as is seen in various *Habronattus* species (Maddison and Stratton 1988). The file is similar in form to that of the *H. agilis* species group, but much narrower. Colour in alcohol: Chelicerae brown with fine glistening hairs. Palp femur light brown with some white scales; tibia with white scales; cymbium brown with a few pale setae. Legs without distinct markings, light to medium brown, with pale scales. Clypeus brown, with a central patch just over the chelicerae of metallic green setae — this contrasts with the appearance in life of a rust-coloured clypeus with a central blue patch (Figs 43, 46). Carapace dark brown with patches of cream-coloured scales in the ocular area, below the PLE, and on the thorax (Figs 41–42, 44). Abdomen dark brown above with a longitudinal band of cream scales medially, wider at front. Sides also covered in cream scales. Venter medium gray-brown.

Female (focal specimen: paratype, specimen AZS13-7108, Figs 47–48). This is the most intact female, as specimen AZS13-7081 (= genetic voucher GLR218) was mostly consumed for RNA extraction. However, an acrocerid fly from ASZ13-7108 emerged about 7 weeks after capture, and thus the abdomen is collapsed. While acrocerid parasitism can affect development, the epigynum of the parasitized specimen (Fig. 40) is apparently natural, as it matches closely to that of AZS13-7081. Carapace length 3.1. Epigynum (Fig. 40) with very small central pocket (the guide for the RTA) embedded



Figures 38–49. *Habronattus luminosus* sp. n. **38** Left male palp, ventral view (paratype male from Sunglow) **39** Same, retrolateral view of palp tibia **40** Epigynum, ventral view (paratype female AZS13-7108 from Amateur Astronomy Vista WPM#13-056) **41–43** Male holotype (photographed by Daniel Zurek) **44–46** Male from Mt. Hopkins Road 31.6697°N 110.9147°W (photographed by Thomas Shahan) **47, 48** Female paratype AZS13-7108 from Amateur Astronomy Vista WPM#13-056 **49** Juvenile AZS13-6951 from Mt. Hopkins Road WPM#13-054. Figs 41–43 are ©2016 Daniel Zurek, released under a Creative Commons Attribution (CC-BY) 4.0 license. Figs 44–46 are ©2016 Thomas Shahan, released under a Creative Commons Attribution-NonCommercial-ShareAlike 3.0 Unported license. Figs 47–49 are copyright © 2015 W. P. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.

within a sclerotized mound. Openings just in front of this mound, almost hidden by it. Colour: Markings indistinct; appendages and body pale yellowish to medium brown, darkest in the ocular area, covered with cream-coloured scales. Abdomen with hint of markings of male (Fig. 48). Clypeus (Fig. 47) covered in cream scales.

Additional material examined. 1Å, 8 juveniles, all from southeastern Arizona. U.S.A.: Arizona: Santa Cruz Co., Mt. Hopkins Rd, Amateur Astronomy Vista, 31.6759 - 31.6762°N 110.9289 - 110.9293°W, 1430 m elev., 7 August 2013, W.Maddison & H. Proctor, WPM#13-056 (2 juveniles in UBC-SEM). U.S.A.: Arizona: Santa Cruz Co.: Mt. Hopkins Road, 31.6705°N 110.9137°W, 1640 m elev., 6 August 2013, W.Maddison & H. Proctor, WPM#13-054 (3 juveniles in UBC-SEM). Arizona: Pima Co.: Madera Canyon, near Proctor Road, 31.7417°N 110.8847°W, 9 August 2013, W. Maddison, WPM#13-062 (3 juveniles in UBC-SEM). Arizona: Santa Cruz Co., Mt. Hopkins Road, 31.6697°N 110.9147°W, 19 June 2012, M. Girard (1Å in UBC-SEM, DNA voucher d436 and Figs 44-46).

Natural history. After this species was first found by Barbara and Vince Roth in the Chiricahua Mountains in 1977, it went uncollected for many years, despite my many attempts to find it in southern Arizona when I resided there for 13 years. It was then rediscovered in 2012 by Madeline Girard in the high desert scrub/grassland just below the oak woodlands in the Santa Rita Mountains. Subsequent collecting has revealed an unusual habitat: it is found hidden in tall clumps of grass in the desert scrub near the lower edge of the oak woodlands (Figs 102–103). It can be found by lifting up the overhanging grass of the clump, or pushing apart the clump to reveal specimens hidden near its core. Although we did not find many adults in August, small yellowish juveniles with prominent black spots (Fig. 49) were reasonably common. A few were raised for several moults, and by their change in markings, they do appear to be *H. luminosus*, supported also by the fact that they cannot be assigned to any other known localities and grassy habitat, its range might be expected to extend into the Chihuahan Desert grasslands.

Habronattus roberti Maddison, sp. n.

http://zoobank.org/A92F955E-13Ā9-4EDE-A707-F49C6253041C Figs 50–68

Holotype. Male specimen JAL14-0175 in CNAN-IBUNAM, with data: México: Jalisco: Estación de Biología Chamela, Calandria Trail, 19.501 - 19.505°N 105.035°W, 130 m elev., 23 Feb. 2014, W. Maddison & R. Sosa, WPM#14-038.

Paratypes $(5 \textcircled{0} \textcircled{0} 7 \clubsuit \clubsuit)$. Same data as holotype (2 0 0 specimens JAL14-0184 and JAL14-0152 in UBC-SEM). México: Jalisco: Chamela estuary, 19.5290°N 105.0770°W, 2 June 1998, W. Maddison et al., WPM#98-070 (1 🖓 Fig. 52 in UBC SEM, 1 🍄 in AMNH). México: Jalisco: Estación de Biología Chamela, 19.498°N 105.045°W, 1-2 June 1998, W. Maddison et al., WPM#98-071 (1 \textcircled{0} specimen W257



Figures 50–62. *Habronattus roberti* sp. n., typical (coastal) populations. **50** Left male palp, ventral view (paratype male W257 from WPM#98-071) **51** Same, retrolateral view of palp tibia **52** Epigynum, ventral view (paratype female from WPM#98-070) **53, 56** Male JAL14-8934 from WPM#14-015 **54, 57** Male JAL14-9737 from WPM#14-034 **55** Male JAL14-9777 from WPM#14-034 **58** Male from WPM#98-070 **59** Femur, patella and tibia of third leg, prolateral view, of male from WPM#98-070 **60** Same, in alcohol, of male paratype #257 from WPM#98-071 **61–62** Female paratype JAL14-9239 from WPM#14-015 All specimens are from the area of Chamela, Jalisco; WPM collecting codes are those indicated in specimen records in description. Figs 53–59, 61, 62 are copyright © 2015 W. P. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.

Figs 50–51 in UBC SEM). México: Jalisco: Estación de Biología Chamela, Chachalaca Trail, 19.496°N 105.042°W 10 Feb. 2014, W. Maddison & H. Proctor, WPM#14-015 (1 3° specimen JAL14-9252 and 1 $^{\circ}$ specimen JAL14-9239 in UBC-SEM). México: Jalisco: Estación de Biología Chamela, Viveros, 19.499°N 105.043°W, 90 m elev., 16 - 27 Feb. 2014, W. Maddison & H. Proctor, WPM#14-028 (1 $^{\circ}$ specimen JAL14-0120 in UBC-SEM, 1 3° in AMNH). México: Jalisco: Estación de Biología Chamela, Viveros, 19.499°N 105.043°W, 90 m elev., 28 Feb. - 1 March 2014, W. Maddison, WPM#14-042 (1 $^{\circ}$ in CNAN-IBUNAM, 1 $^{\circ}$ in MCZ, 1 $^{\circ}$ in MCZ).

Etymology. Named after my late father, Robert John Maddison, who introduced me to the small things in nature through fishing bait and saturniid cocoons. When my brother and I developed interests in beetles and spiders, he offered to take the family on long collecting trips. His gentle encouragement let me find my own love for the riches of biodiversity.

Diagnosis. Belonging within the clade whose males have modified first and third legs (*coecatus, viridipes* and *clypeatus* groups), but not clearly belonging to any of the subgroups. Shows similarities to the *viridipes* species group (a ridge of raised scales between the PLE; courtship behaviour) but also to the *clypeatus* group (red-purple third patella; checkered or striped pattern visible in male AMEs). Unlike relatives with green legs, the yellow-green of the first leg of northern populations is weakly green and is restricted to the underside of the femur. Modifications of the third patella are small, in that respect resembling several species of the *viridipes* and *clypeatus* groups, but differing from those in having two small bumps dorsally on the patella (Figs 59–60, 67–68). Like *H. moratus* (Gertsch & Mulaik, 1936), the raised ridge of scales between the PME appears from in front as a tuft over the PME (white arrow Fig. 66) and a broader raised ridge that is bimodal (lower at the midline; black arrow Fig. 66). Unlike *H. moratus*, the palp's bulb is reasonably well rotated (*H. moratus*, TmA base pointing to 90°; *H. roberti*, TmA base pointing to 190°).

Description. Male (focal specimen: holotype). Carapace length 2.3; abdomen length 2.3. Palp's bulb well rotated, with embolus arising at 310° (Fig. 50). Tip of RTA in ventral view curves toward the prolateral, forming a hook, like that seen in H. arcalorus Maddison & Maddison, 2016 and other clypeatus-group members. In retrolateral view, the RTA is more robust than usually seen in the *viridipes* group. Colour: Chelicerae light brown with a glabrous black patch in basal prolateral portion (Fig. 58). Palp femur pale brown with white setae distally; patella covered with white setae; tibia darker but with long white setae retrolaterally; cymbium covered with white setae. First leg with long fringe of white setae on ventral-retrolateral edge, longest distally; weak fringe ventrally and retrolaterally on patella and tibia; no prolateral fringe. One prolateral macroseta on tibia longer than usual, and only very slightly flattened. First leg black above, brown otherwise, palest beneath the femur where it is covered with white setae expanded at the tip (Figs 57-58). (In life, the integument of the femur shows no obvious green.) Other legs medium to dark brown with cream coloured scales. Second leg with prolateral side distinctly darker. Third femur with faint transverse bands of cream scales as in viridipes and clypeatus group (Fig. 56). Patella with a black spot on the prolateral side, and two protuberances dorsally, red-purple in life (Figs 59-60). (In some speci-



Figures 63–68. *Habronattus roberti* sp. n., El Grullo and Nayarit populations. **63, 65** Male from Jalisco: Los Yesos, near El Grullo 19.750°N 104.067°W WPM#98-065 **64, 66** Male from Nayarit: Singaita, just E of San Blas **67, 68** Femur, patella and tibia of third leg, prolateral view, of male from Los Yesos (WPM#98-065); Fig. 68 is of the right leg, digitally flipped horizontally. Figs 63–66, 68 are copyright © 2015 W. P. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.

mens, the proximal half of the patella is yellowish-green, Fig. 69.) The prolateral face of the tibia has a narrow strongly white band proximally, then a black region, then a rising band of cream scales. Clypeus and sides of carapace brown. Ocular area dark, covered in grey-brown scales that grade to black between the PME. On the thorax, broad bands of cream scales extend from beneath PME and PLE to the posterior margin; these two bands are contiguous with the inverted V of cream scales between the PME. The integument underlying these thoracic bands is pale. Abdomen black to dark brown above with a broad cream basal band, and a central longitudinal band that is widest at front, sometimes contacting the basal band (Fig. 54). Venter with three longitudinal dark bands.

Female (focal specimen: paratype, specimen JAL14-9239, Figs 61, 62). Carapace length 2.3; abdomen length 2.4. Epigynum (Fig. 52) with central pocket parallel-sided, as typical for *clypeatus* and *viridipes* groups. Atrium small, crescent shaped, in front of a central pocket that has more or less parallel sides. Colour (Figs 61-62) pale except for dark patches on chelicerae in the same places as male. In alcohol there is a faint hint of the abdominal markings of the male.

Geographical variation. Males from the coast of Jalisco, including the type locality and El Tuito, have brown faces (Fig. 58) and a third patella with a red-purple protuberance (Fig. 59). Males from north of the coastal mountain range, near El Grullo, have white hairs on the chelicerae and the border of the clypeus (Fig. 63), a third patella with no black spot and reduced protuberances that lack the red-purple colour (Fig 68), and a first femur that is more obviously greenish (Fig. 63). Males from further north, in Nayarit, have an extensively white clypeus, a greenish first femur (Fig. 64), and a third patella with the black spot and protuberances that are black rather than red-purple. No difference was noted in the palpi, nor were striking differences noted in



Figures 69–70. *Habronattus* males with checkered and striped patterns in the AME. **69** *H. roberti* male JAL14-9777 from WPM#14-034 **70** *H. aztecanus* male JAL14-8782 from Jalisco: Puerto Vallarta, Bocanegra beach, 20.670°N 105.274°W, 3 m elev., 8 Feb. 2014, WPM#14-012. Figures 69–70 are copyright © 2015 W. P. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.

their courtship behaviours (see below, Natural History). It is possible that these forms represent separate species, but they are here retained together pending more data.

Additional material examined. 3533722 in UBC-SEM: Coastal (typical) form: México: Jalisco: Chamela estuary, 19.5290°N 105.0770°W, 2 June 1998, W. Maddison et al., WPM#98-070 (5승경). México: Jalisco: north of El Tuito, 20.337°N 105.316°W, 3 June 1998, W. Maddison et al., WPM#98-072 (5♂♂ 1♀). México: Jalisco: Estación de Biología Chamela, Chachalaca Trail, 19.496°N 105.042°W, 10 Feb. 2014, W. Maddison & H. Proctor, WPM#14-015 (1d). México: Jalisco: Estación de Biología Chamela, Viveros, 19.499°N 105.043°W, 90 m elev., 16 - 27 Feb. 2014, W. Maddison & H. Proctor, WPM#14-028 (13). México: Jalisco: Estación de Biología Chamela, 400-650 m on Calandria Trail, 19.5038 -19.5045°N 105.0334 - 105.0344°W, 19 Feb. 2014, W. Maddison & H. Proctor, WPM#14-034 (2♀♀). México: Jalisco: El Tuito, Rancho Primavera, 20.341°N 105.350°W, 600 m elev., 2 - 4 March 2014, W. Maddison & H. Proctor, WPM#14-044 (233). El Grullo form: México: Jalisco: Apulco, 19.737°N 103.903°W, 920 m elev., 31 May 1998, W. Maddison et al., WPM#98-064 (1⁽¹⁾). México: Jalisco: Los Yesos, near El Grullo, 19.750°N 104.067°W, 900 m elev., 1 June 1998, W. Maddison et al., WPM#98-065 (5♂♂ 1♀). México: Jalisco: Los Yesos, near El Grullo, 19.7508°N 104.0595°W, 870m elev., 1 June 1998, W. Maddison et al., WPM#98-066 (23312). *Nayarit form:* México: Nayarit: north of Compostela, 25 km S of Tepic, 21.323°N 104.921°W, 1000 m elev., oak woodland, 4 June 1998, W. Maddison et al., WPM#98-077 (533 12). México: Nayarit: few km W of Compostela on highway 200, 21.2233°N 104.9382°W, 820 m, 4 June 1998, W. Maddison et al., WPM#98-078 (6 $\bigcirc 12$). México: Nayarit: few km W of Compostela on highway 200, 21.212°N 104.949°W, 870 m, 4 June 1998, W. Maddison et al., WPM#98-079 (2合合).

Natural history. Collected in the tropical deciduous forests in Jalisco and Nayarit, México. It occurs on leaf litter (Fig. 100) along trails and small clearings (Fig 101), exposed to the sun but with shade nearby. Courtship resembles that of the *viridipes* group, with an early stage in which the palps are waved in small circles and the first leg

tips pointed at the female, followed by two transitional waves of the front leg, followed by a long period of asymmetrical flickers of the first legs. Coastal and Nayarit populations have similar displays (Coastal: 3w259 https://youtu.be/rL24mLEkUxE, 3w257 https://youtu.be/ty6p7NioFnU; Nayarit: 3w261 https://youtu.be/i79aw5ju1EA, 3w262 https://youtu.be/JV8AjMAgO58).

The pattern of light and dark spots or bands visible inside the male's AME (Fig. 69) is an intriguing feature of *H. roberti* and members of the *clypeatus* group. Maddison and Maddison (2016) discussed such visible patterns in the male eye as characteristic of the *clypeatus* group (Fig. 70; see also https://www.youtube.com/watch?v=Dq5ky7vjPYo). As one looks into the AME of most living salticids with translucent carapaces, one sees the colour changing from honey to black smoothly as the eye moves inside the prosoma and our line of sight moves from the side walls of the eye to the retina itself. The pattern of dark spots in *H. roberti* and the *clypeatus* group is therefore unusual. It is unclear whether other *Habronattus* have such a pattern; the eye simply appears dark. In *H. roberti*, as in the *clypeatus* group, the integument underlying the thoracic bands is unusually pale, which may permit light to enter the prosoma thus revealing the pattern. Given that this pattern is at the same focal plane as the ornamented third legs (Figs 69, 70), it is conceivable that the visibility of the eye pattern itself is a courtship ornament, enabled by the depigmented thorax.

Habronattus sp. near *carolinensis* (Peckham & Peckham, 1901) Fig. 71

Note. At the Royal Ontario Museum in 1978 I saw a male specimen of Habronattus from Lake Temagami, Ontario, from whose label I recorded the collecting data "Ontario: Temagami. Island 1027. 24 June 1939. #5669", although the museum reference notes indicated the date as 27 June 1937. It was notable for the brush of longer setae on the dorsal distal surface of the cymbium, and the twisted and tufted tarsus of the first leg. In both of these features it resembled the two described species H. carolinensis (Peckham & Peckham, 1901) (from the southeastern U.S.) and H. venatoris Griswold, 1987 (from the southern Rocky Mountains of Wyoming, Colorado, and New Mexico), both of which are notable for the twisted and tufted tarsus and metatarsus of the first leg (Chamberlin and Ivie 1944, figure 210). I drew the palp (Fig. 71), which differs distinctly in rotation of the bulb from those two species (embolus arising at 225°, compared to 270° for H. venatoris and 290° for H. carolinensis), and thus represents a new species. I did not draw the cymbial brush or the first leg, and my memory does not retain their details except that there was a clear resemblance to H. carolinensis in these ornaments. Recent attempts to locate the specimen at the museum have failed, and it may have been loaned for a project on *Pellenes* (which was never completed) and not returned. In 1995 I travelled to the exact island in Lake Temagami on the label, but no specimens were found. However, the island was rock of perhaps 5 meters by 2 meters, unlikely to sustain any permanent population, and so either the specimen bal-



Figure 71. Habronattus cf. carolinensis, from Lake Temagami, Ontario, male left palp, ventral view.

looned in, or the label was incorrect. We are thus left with a biogeographically puzzling new species with no specimen on which to describe it. Two possible habitats might be productively searched: the rock outcrops of the Canadian Shield, or exposed sand of glacial deposits in Northern Ontario and Québec.

Genus Pellenes Simon, 1876

Type species. Aranea tripunctata Walckenaer, 1802

Notes. Currently 84 species are assigned to *Pellenes* (World Spider Catalog, 2016). There are five subgenera: the nominate, three described by described by Logunov et al. (1999) and one by Prószyński (2016). These are:

Pellenes Simon 1876. Logunov et al. (1999) included three species in the nominate subgenus. The TmA is massive, much larger than the embolus. Logunov et al (1999) diagnosed *Pellenes s. str.* by "a raised epigynal median septum in females ... and the tibial apophysis appressed in the cymbial groove in males".

Pelpaucus Logunov, Marusik & Rakov, 1999 (type species *Pellenes limbatus* Kulczyński, 1895). Six species are assigned to *Pelpaucus*. Their TmA is a more or less straight flat blade, wide especially at the tip, parallel to the embolus and as long as it. Logunov et al (1999) diagnosed *Pelpaucus* by the RTA very short or absent, an apical spine on the TmA, a recessed epigynal atrium, and a one-chambered spermatheca.

Pelmultus Logunov, Marusik & Rakov, 1999 (type species *Attus geniculatus* Simon, 1868). Twenty-three species are assigned to *Pelmultus*. They are compact-bodied (not elongate), with contrasting markings and a somewhat-ornamented male first leg, resembling in habitus to some extent the *Habronattus dorotheae* species group. The TmA is as long as the embolus but wider, with a complex pointed tip. Logunov et al (1999) diagnosed *Pelmultus* by the heavily sclerotized epigynal flaps and the subparallel tips of the embolus and the TmA.

Pelmirus Logunov, Marusik & Rakov, 1999 (type species *Pellenes dilutus* Logunov, 1995). Four species are assigned to *Pelmirus*, having a large complex TmA that

curls distally at the tip, like a tongue. Logunov et al. (1999) diagnosed *Pelmirus* by the embolus and TmA perpendicularly orientated to each other and the peculiar elevated central pocket of the epigynum.

Pellap Prószyński, 2016 (type species implied to be *Pellenes lapponicus* Sundevall 1833). *P. lapponicus* has a long embolus and TmA, the latter much wider. Prószyński (2016) characterizes *Pellap* by the long needle-like embolus sheathed in the thick TmA, trapezoidal RTA, medial groove behind the central pocket of the epigynum, and spiral spermathecae.

In all of these subgenera, the TmA is distinctly larger than the embolus. Many other species of *Pellenes* are not yet assigned to a subgenus, including many African species whose TmAs are small or (apparently) absent.

Although two Holarctic species are known from the Americas, *P. (Pellap) lapponicus* and *P. (Pelpaucus) ignifrons* (Grube, 1861), the remaining species of New World *Pellenes* form a distinctive group not known to occur in the Old World. The subgenus *Pellenattus* is here described to contain them.

Pellenattus subgen. n.

http://zoobank.org/18078E5C-998D-4498-8D42-86536F0D6FF7 Figs 72–94

Type species. Pellenes peninsularis Emerton, 1925

Diagnosis. Differs from the other described subgenera of *Pellenes* in having the TmA smaller than the embolus. The TmA of *Pellenattus* is often reduced to a small protuberance (Figs 72, 73, 75, 77, P. peninsularis), or if as long as the embolus, then it is narrower than it (Fig. 86, P. canadensis). In Old World species placed in described subgenera, the TmA is distinctly broader and larger than the embolus proper. The breadth of their TmA could be considered a synapomorphy of the four described subgenera, thereby excluding Pellenattus. Alternatively, the narrowness of the TmA in Pellenattus could be considered a synapomorphy with Habronattus. Those Old World species with a small TmA are primarily African (e.g., P. bulawayoensis Wesołowska, 1999) and as yet unplaced to subgenus. *Pellenattus* species have a relatively narrow body and a simple medial longitudinal band, often divided into chevrons, on the abdomen (Figs 82-85), in contrast to Pelmultus and the African *Pellenes* which are more compact-bodied and have more contrasting markings. Strong transverse or oblique pale abdominal bands as seen in many Old World species (e.g., P. tripunctatus, P. bulawayoensis, P. nigociliatus (Simon, 1875)) are absent from the American species. Molecular data currently being prepared for publication also support the distinctiveness of the American Pellenes.

The species here placed in *Pellenattus* are: *Pellenes (Pellenattus) apacheus* Lowrie & Gertsch, 1955!, comb. n. *Pellenes (Pellenattus) canadensis* sp. n.! *Pellenes (Pellenattus) crandalli* Lowrie & Gertsch, 1955!, comb. n.



Figures 72–81. *Pellenes peninsularis.* **72** Bulb of left palp, holotype of *Pellenes peninsularis* Emerton, 1925 **73–74** Left palp, holotype of *Pellenes wrighti* Lowrie & Gertsch, 1955 **75–76** Left palp, male from Nova Scotia (DRM02.103) **77–78** Left palp, male from east-central Ontario (WPM#76-133) **79** Male from east-central Ontario (WPM#76-133) **80** Epigynum, ventral view, female from Nova Scotia (DRM02.103) **81** Epigynum, cleared, dorsal view, same female. DRM and WPM collecting codes are those indicated in specimen records.

Pellenes (Pellenattus) dorsalis (Banks, 1898), comb. n. Pellenes (Pellenattus) grammaticus Chamberlin 1925!, comb. n. Pellenes (Pellenattus) levii Lowrie & Gertsch, 1955!, comb. n. Pellenes (Pellenattus) limatus Peckham & Peckham, 1901!, comb. n. Pellenes (Pellenattus) longimanus Emerton, 1913!, comb. n. Pellenes (Pellenattus) peninsularis Emerton, 1925!, comb. n. Pellenes (Pellenattus) shoshonensis Gertsch, 1934!, comb. n. Pellenes (Pellenattus) washonus Lowrie & Gertsch, 1955!, comb. n.

Most of the described species of *Pellenes* (*Pellenattus*) were figured by Lowrie and Gertsch (1955). I have examined the holotypes of those species marked with ! in the list above. Although Griswold (1987) considered *P. dorsalis* to be a *nomen dubium*, Banks's figure of the palp almost certainly shows a *Pellenes* near *P. washonus*, given the context of the Sonoran fauna. The figure of *P. cinctipes* Banks, 1898 suggests it belongs here as well.

Logunov et al. (1999) placed one of these species within one of the Old World subgenera, *P. limatus* into *Pelmultus*, but *P. limatus* is a typical American species, differing from *Pelmultus* by the characters mentioned above.

Pellenes (Pellenattus) peninsularis (Emerton)

Figs 72-82

Pellenes peninsularis Emerton, 1925: p 68, fig. 6 (Dm) (male holotype in Museum of Comparative Zoology, Harvard, examined, Fig. 72)

Pellenes wrighti Lowrie & Gertsch, 1955: p. 23, fig. 19, 20, 27 (Dmf), **syn. n.** (male holotype in American Museum of Natural History, examined, Figs 73–74)

Notes. The vial of *P. wrighti*'s holotype includes the labels "Pellenes wrighti Lowrie & Gertsch \Diamond holotype", "Pellenes peninsularis \Diamond , Ill., Kankakee Col, Pembroke TWP. SEC, Sept 8 1936, Coll. & Det. D.C. Lowrie", and "Pellens [sic.] sp. nov. $\Diamond \ \Diamond \ \varphi \ \varphi$ from Ind. Porter Co., Tremont. 8 June 1929". The second (contradictory) locality label matches that expected for the female allotype of *P. wrighti*, and may have been inserted or retained in error.

Lowrie and Gertsch (1955) compared *P. wrighti* to *P. apacheus* but made no comment about its differences from *P. peninsularis*, despite the *P. wrighti* holotype having been originally identified as *P. peninsularis*. The holotypes of *P. peninsularis* and *P. wrighti* and other specimens from throughout the range bear no known features that would justify distinguishing two species. The bodies of specimens from Ontario and Nova Scotia are primarily black; those from the prairies of Minnesota, Montana and South Dakota are dusted with tan to orange scales, corresponding to their different substrates (dark rock outcrops in the eastern Canadian populations; prairies further west). There may be a small genitalic difference, in the size of the dorsal lobe of the cymbium, which appears to be larger in eastern than western populations (Figs 76, 78 versus Fig. 74). However, any difference would be slight, within the usual variability of a single species, and there is no indication of an abrupt transition in form in specimens arrayed from Nova Scotia through Montana. Otherwise, the male palp is consistent



Figures 82–85. Female *Pellenes (Pellenattus)* species. **82** *P. peninsularis* from Ontario: Muskoka District: Dwight **83** *P. apacheus* from Arizona: Apache Co.: Mt. Baldy Wilderness, 33.92°N 109.63°W **84** *P. limatus* Arizona: Pinal Co.: Three Buttes, 8.9 mi N of Oracle Junction along highway 79 **85** *P. longimanus* from Texas: Hidalgo Co.: Bentsen-Rio Grande Valley State Park 26.178°N 98.391°W. Figs 82–85 are copyright © 2015 W. P. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.

from west to east, with the TmA a small rounded flange pendant from the tip of the embolus (Figs 72, 73, 75, 77), the tibial apophysis leaning dorsally, and the cymbium with a prominent dorsal proximal lobe (Figs. 74, 76, 78). It is possible that *P. apacheus* is also conspecific, extending the trend to an even smaller cymbial lobe toward the southwest, but confirmation would require further study.

Additional material examined. $21\sqrt[3]{3}$ 1929 in UBC-SEM: Canada: Nova Scotia: Pictou Co., Barneys River at route 104, 45.58617° N 62.22710° W, 22 June 2002, L.J. Maddison, D.R. Maddison, A.E. Arnold, DRM02.103 ($1\sqrt[3]{3}92$). Ontario: Muskoka District, Dwight, 45.3384°N 79.0302°W, 22 May 1976, W. Maddison WPM#76-133 ($1\sqrt[3]{3}$). Ontario: Muskoka District, Dwight, 45.3384°N 79.0302°W, 17 May 1980, W. Maddison, WPM#80-020 ($15\sqrt[3]{3}1292$). Ontario: Kenora District, Percy Lake, few mi E of Hawk Lake on HWY 17, 29 May 1977, W. & D. Maddison, WPM#77-122 ($1\sqrt[3]{3}12$). U.S.A.: Minnesota: Anoka Co., Cedar Creek Natural History Area, Rg 23 W Twp 34 N Sect 34-35, 16 May 1977, D. & W. Maddison, WPM#77-025 ($1\sqrt[3]{2}2$). North Dakota: Stark Co., S of Belfield, 74 km N of Bowman along HWY 85, 31 May 1982, D. Maddison, WPM#82-164 ($1\sqrt[3]{3}$). South Dakota:

Pennington Co., 12 mi W of Interior on HWY 44, 19 May 1977, W. Maddison, WPM#77-051 (1 \bigcirc 1 \bigcirc).

Natural history. This species occurs on rock outcrops in Nova Scotia and on the Canadian Shield of Ontario. Further west it occurs among grasses on the ground of prairies.

Pellenes (Pellenattus) canadensis sp. n.

http://zoobank.org/1F25FF98-0859-41E1-A72F-F56771B28AD3 Figs 86–94

Holotype. Male (Figs 86, 87) in UBC-SEM, with data: Canada: British Columbia: Mt. Baldy. 49.099°N 119.156°W, 1180 m elev. 17 May 2013 W.Maddison & H. Proctor WPM#13-014.

Paratypes $(3 \textcircled{0} \textcircled{0} 2 \clubsuit \clubsuit)$. Same data as holotype (1 0 specimen NA13-6071 and 1 \clubsuit specimen NA13-6083 in UBC-SEM). Canada: British Columbia: W of Midway, along HWY 3, 3.0 km E of crossing of Kettle River with HWY 3, ca. 49.0°N 118.83°W, 2 May 1982, W. & D. Maddison, WPM#82-019 $(1 \textcircled{0} 1 \clubsuit)$ in CNC, 1 \textcircled{0} in AMNH).

Etymology. Named for the country of the type locality, in honour of the 150th anniversary of Canada's confederation.

Diagnosis. A typical member of *Pellenattus* with striped markings, more contrasting in males than females. *P. canadensis* can be distinguished by the TmA being only slightly smaller than the embolus, diverging from the embolus initially, then curving distally to touch the tip of the embolus. *Pellenes levii* has a similar palp, but its TmA is shorter and considerably narrower, only 1/4 to 1/3 the width of the embolus, and also is pressed against the embolus its entire length (Lowrie and Gertsch 1955, figure 17; holotype in AMNH examined).

Description. *Male* (focal specimen: holotype). Carapace length 2.0; abdomen length 2.1. Structure of body typical for *Pellenattus*. Embolus a short pointed blade, accompanied by a TmA of almost the same size, which opposes the embolus like a thumb against a forefinger (Fig. 86). The RTA is broad but pointed (Fig. 87). The cymbial lobe is small but distinct, projecting toward the retrolateral (e.g., visible behind the RTA in Fig. 86). Colour: Black except for paler femur, patella and tibia of palp, and coxae and trochanters of legs. Body with longitudinal stripes of white scales (Figs 90–91).

Female (focal specimen: paratype, specimen NA13-6083, Figs 88, 89, 93, 94). Carapace length 2.4; abdomen length 2.7. Structure of body typical for *Pellenattus*. Central pocket not on a raised sclerotized mound (it is in *P. peninsularis*). Openings posterior to central pocket (Fig 86), as in *P. levii* (Lowrie and Gertsch 1955, figure 29). Colour paler than male, with more distinct chevrons on the abdomen. Clypeus white except black patches below AME (Fig. 93).





Figures 86–94. *Pellenes canadensis* sp. n. **86** Left male palp, ventral view (holotype male) **87** Same, retrolateral view of palp tibia **88** Epigynum, ventral view (paratype female NA13-6083) **89** Epigynum, cleared, dorsal view (same female) **90–92** Male paratype NA13-6071 **93–94** Female paratype NA13-6083 All specimens are from the type locality. Figs 90–94 are copyright © 2015 W. P. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.

Additional material examined. U.S.A: Montana: Glacier Co., 1.3 mi SE of intersection of HWY U.S. 89, Cutbank River & HWY 445, 24 May 1977, D., W., L., & R. Maddison, WPM#77-099 (12 337224 juveniles in UBC-SEM).

Natural history. Collected at fairly high elevation on open ground with scattered small rocks, sticks and sparse vegetation (Fig. 98).



Figures 95–101. Habitats of new *Habronattus* and *Pellenes* species. 95–97 Negative estuaries near Puerto Peñasco, Sonora 95, 96 Habitat of *H. aestus*, type locality, Estero Cerro Prieto 97 Habitat of *H. empyrus*, type locality, Estero Morúa 98 Habitat of *P. canadensis*, type locality, Mt. Baldy, British Columbia 99–101 Tropical deciduous forest of Chamela, Jalisco at type locality for both *H. roberti* and *H. chamela* 99 Habitat of *H. chamela*, type locality 100 Habitat of *H. roberti*, type locality.



Figures 102–103. Habitat of *Habronattus luminosus*, Arizona, Amateur Astronomy Vista, 31.676°N 110.929°W.

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RESEARCH ARTICLE



A new species of the leafhopper genus Maiestas Distant from Australia (Hemiptera, Cicadellidae, Deltocephalinae, Deltocephalini)

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Abstract

A new leafhopper species *Maiestas irwini* **sp. n.** is described and illustrated from Australia. A checklist of the genus from the Australian region is provided together with a key to species for males.

Keywords

Auchenorrhyncha, morphology, new species, taxonomy

Introduction

The grassland leafhopper genus *Maiestas* was established by Distant (1917) with the type species *Maiestas illustris* Distant from the Seychelles. It belongs to the *Deltocephalus* group as reviewed by Webb and Viraktamath (2009), as part of a larger study of Old World Deltocephalini and re-assessment of *Maiestas* Distant. Subsequently, Zhang and Duan (2011) revised the group in China and currently the genus comprises 98 species. It differs from *Deltocephalus* Burmeister and *Recilia* Edwards by the aedeagal shaft being at most only slightly curved dorsally with its apex not notched and sometimes produced

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into a thin process or spine with the gonopore apical on the dorsal surface. In this paper, a new species of *Maiestas* Distant is described from Australia bringing the total for the Australian region to six species (see checklist). A checklist and a key to these species for males are provided. Images of all previously known Australian species can be seen on Fletcher's (2016) website.

Materials and methods

Morphological terminology follows Dietrich (2005). Digital photographs were taken with a QImaging Micropublisher 3.3 digital camera mounted on an Olympus BX41 stereo microscope and with a Nikon D1x digital SLR camera configured with lenses by Microptics, Digital Lab XLT system. Photographs were modified with Adobe Photoshop CS. Abbreviations used herein are INHS: Illinois Natural History Survey, Champaign Ill, USA; QDPI: Queensland Department of Agriculture and Fisheries, Brisbane, Australia; QM: Queensland Museum, Brisbane, Australia.

Taxonomy

Maiestas Distant

- Maiestas Distant, 1917: 312. Type species: Maiestas illustris Distant, 1917, by monotypy.
- *Togacephalus* Matsumura, 1940: 38. Type species: *Deltocephalus distincta* Motschulsky, 1859, by original designation.
- *Inazuma* Ishihara, 1953: 15. Type species: *Deltocephalus dorsalis* Motschulsky, 1859, by original designation.
- *Inemadara* Ishihara, 1953: 48. Type species: *Deltocephalus oryzae* Matsumura, 1902, by original designation.
- *Insulanus* Linnavuori, 1960: 303. Type species: *Stirellus subviridis* Metcalf, 1946, by original designation.

Distribution. The Old World.

Checklist of species of Maiestas Distant from the Australian region

Note: see Fletcher (2016) for full synonymy.

Maiestas dorsalis (Motschulsky, 1859) (Qld, NT, NSW, Oriental region) *Maiestas irwini* **sp. n.** (Qld)

Maiestas knighti Webb & Viraktamath, 2009 (ACT, NSW, NT, Tas, Vic, WA, New Zealand, Papua New Guinea, Fiji, Guam)

Maiestas lucindae (Kirkaldy, 1907) (Qld) Maiestas samuelsoni (Knight, 1976) (Norfolk Island, New Zealand (Kermadec Islands), Fiji, New Caledonia) Maiestas vetus (Knight, 1975) (ACT, NSW, NT, Vic, WA, NZ)

Key to species of *Maiestas* Distant from the Australian region (males)

Note: male genitalia of *M. lucindae* is unknown and this species is therefore omitted from the key.

| 1 | Forewing with dark zig-zag marking (Webb and Viraktamath 2009, fig. 36o) |
|---|---|
| | |
| _ | Forewing without zig-zag marking |
| 2 | Aedeagal shaft with ventral margin extending beyond gonopore by approxi- |
| | mately 5× apical width of shaft (Webb and Viraktamath 2009, fig. 35h) |
| | |
| _ | Aedeagal shaft with ventral margin extending beyond gonopore by approxi- |
| | mately apical width of shaft |
| 3 | Style apophysis robust (Fig. 2E) |
| _ | Style apophysis slim |
| 4 | Subgenital plate lateral margin slightly convex (Webb and Viraktamath 2009, |
| | fig. 39d) |
| _ | Subgenital plate lateral margin slightly concave (Webb and Viraktamath |
| | 2009, fig. 41d) |
| | 5 |

Maiestas irwini sp. n.

http://zoobank.org/439E3157-1A52-4847-9A0D-13D25C053D2C Figs 1–2

Length. Male: 2.6–3.0 mm.

Coloration and morphology. Ground color stramineous marked with orange and fuscous (Fig. 1A–C). Fore margin of head with fuscous marks and light fasciae extending to scutellum, coronal sulcus prominent (Fig. 1A–B). Face mostly brown, with paired white arcs corresponding to muscle scars of frontoclypeus (Fig. 1D). Pronotum with three pairs of fasciae. Scutellum with three fasciae (Fig. 1A–B). Forewing pale ochraceous, with two distinct, irregular fuscous maculae, one at the apex of the clavus and the other at the base of the central anteapical cell, veins contrastingly pale, veins of apex bordered with fuscous. Mesosternum light brown. Femora and tibiae with fuscous marks (Fig. 1C).

Head wider than pronotum, crown depressed, anterior margin distinctly angulate in dorsal view, slightly longer than distance between eyes (Fig. 1A–B). Ocellus closely adjacent to eye on anterior margin of vertex (Fig. 1A–C). Anteclypeus tapering toward the apex, not extended to ventral margin of face. Lorum semicircular, narrower than anteclypeus, well separated from lateral margin of face (Fig. 1D). Pronotum nearly as



Figure I. Maiestas irwini sp. n. A, B habitus, dorsal view C habitus, lateral view D face.

long as vertex (Fig. 1A–B). Forewing macropterous, with four apical and three anteapical cells, inner anteapical cell open basally, costal area with one cross vein (Fig. 1C).

Male genitalia. Pygofer lobe with numerous apical macrosetae, longer than its height, hind margin rounded (Fig. 2A–C). Subgenital plate subtriangular, lateral margin convex, length nearly as long as width. Valve rectangular (Fig. 2D). Style preapical lobe angulated, apophysis digitate, slightly laterally curved (Fig. 2E). Connective slightly longer than aedeagus. Aedeagal shaft short, stout, more or less of uniform width, curved dorsally with ventral margin produced into small spine beyond gonopore (Fig. 2F–G).

Material examined. Holotype: 1 male, 4km up Black Mountain Road, via Kuranda, 14.ix.–12.x.1982, malaise trap (QM, T234944, ex QDPI). **Paratypes:** 1 male, same data as holotype (QDPI); 2 males, same data as previous but 14.ix–12.x.1982, G. Simpson (QDPI); 1 male, 1 female, same data as holotype but 12–26.x.1982 (QDPI); 3 males, 3 females, Moggill State Forest, 26 km W Brisbane, Queensland, 17.x.1983, M. E. Irwin, malaise trap in gully in eucalyptus (INHS); 1 male, Mount Baldy Rd via Atherton, N Queensland, vi.1981, J. D. Brown, malaise trap (QDPI); 1 male, Tully Falls Rd, 10.iii.1956, J. L. Gressitt, light trap (BPB).

Remarks. The male genitalia of this species are similar to those of *M. scriptus* (Distant), from India (Webb & Viraktamath, 2009, Fig. 33) with a short and broad subgenital plate with lateral margin well rounded (Fig. 2D), style apophysis relatively long and straight (Fig. 2E), and aedeagal shaft short (Fig. 2F–G), but *M. irwini* differs in color pattern, the more strongly produced head (Fig. 1A–B), and less acute aedeagal apex in dorsal view (Fig. 2F). The new species differs from other Australian species (see Fletcher, 2016) in coloration and genital morphology.

Etymology. This species is named for M. E. Irwin who collected much of the type series.



Figure 2. *Maiestas irwini* sp. n. **A** male pygofer lobe, lateral view **B**, **C** male pygofer and segments X–XI, dorsal view **D** valve, subgenital plates and styles, ventral view **E** style, dorsal view **F**, **G** connective and aedeagus, dorsal and lateral view, respectively.

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RESEARCH ARTICLE



Review of Neopalpa Povolný, 1998 with description of a new species from California and Baja California, Mexico (Lepidoptera, Gelechiidae)

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| http://zoobank.org/3175884F-5A42-4662-8F09-7639C0FDE708 | |

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Abstract

The monotypic genus *Neopalpa* was described in 1998 by Czech entomologist Dalibor Povolný based on two male specimens from Santa Catalina Island, California, which he named *N. neonata*. The female of this species was discovered recently based on a DNA barcode match and is described. In addition, a new species with marked differences in morphology and DNA barcodes from southern California and Baja California Mexico is described as *Neopalpa donaldtrumpi* **sp. n.** Adults and genitalia of both species are illustrated, new diagnosis for the genus *Neopalpa* is provided, and its position within Gelechiidae is briefly discussed.

Keywords

Microlepidoptera, new species, nomenclature, taxonomy, Donald J. Trump

Introduction

The tribe Gnorimoschemini currently consists of 44 genera, only six of which have exclusively Nearctic distributions (Povolný 2002). The defining characters of Gnorimoschemini remain vague since it was defined based on genital morphology with no synapomorphies proposed (Povolný 1964, Huemer and Karsholt 2010), although the reduction of muscle m7 in male genitalia maybe a unifying trait (Kuznetsov and Stekolnikov 2001, Povolný 2002). A combination of characters have been suggested that weakly support the monophyly of Gnorimoschemini, namely the presence of a hook-like signum and a ventromedial zone of microtrichia near the ostial area of the female genitalia (Huemer and Karsholt 1999, Ponomarenko 2006); however, one or both of these traits are sometimes absent in some genera (e.g., *Symmetrischema*). The monophyly and higher classification of the tribe thus remains unresolved.

In November 2011, a non-descript female gelechiid moth collected by J.-F. Landry from Santa Cruz Island in 1984 (CNCLEP00077350) was submitted for DNA barcoding. This specimen yielded a unique 407 bp fragment COI barcode that, while clustering with other Gnorimoschemini specimens in Neighbour-Joining analyses, morphologically did not match any of the known species of Gnorimoschemini that I had studied. In May 2012 additional matching barcode sequences from a Malaise trap catch in California became available that contained samples from both sexes. The genitalia of the females from this series were identical to the CNC specimen, and dissection of the male revealed its identity as *Neopalpa neonata* as described and illustrated by Povolný in 1998. Subsequently I examined the holotype and the only paratype of this species and confirmed the identification. Many additional specimens were later collected and barcoded from California and Arizona, mainly through the continuous Malaise trapping initiative by the Biodiversity Institute of Ontario BioBus program.

The new species was initially discovered through dissection of Gnorimoschemini material borrowed from the Bohart Museum of Entomology, University of California, Davis (UCBME). Two males and one female from Algodones dunes in Imperial County, California, showed a unique genitalia and wing pattern that did not match known species of Gnorimoschemini. Based on similarities in genitalia of both sexes I associated these with *Neopalpa*, and this identification was further supported by DNA barcoding. A few additional male specimens were later discovered among the material borrowed from other institutions. In this paper I provide a new diagnosis for the genus *Neopalpa*, illustrate the previously unknown female of *Neopalpa neonata* Povolný, 1998, and describe this newly discovered species.

Materials and methods

Collections. Specimens were examined from the following collections:

| BIOUG | Biodiversity Institute of Ontario, University of Guelph, Ontario, Canada |
|-------|--|
| CNC | Canadian National Collection of Insects, Ottawa, Ontario, Canada |
| Albu | Research collection of Valeriu Albu, O'Neals, California, USA |
| CAS | California Academy of Sciences, San Francisco, USA |
| EMEC | Essig Museum of Entomology, University of California, Berkeley, USA |
| LACM | Natural History Museum of Los Angeles County, Los Angeles, California, USA |
| UCR | Entomology Research Museum, University of California, Riverside, Cali- |
| | fornia, USA |
| UCBME | Bohart Museum of Entomology, University of California, Davis, Cali- |
| | fornia, USA |

Dissections. Genitalia dissections and slide mounts followed procedures outlined in Landry (2007). Intact male genitalia were excised and photographed in lactic acid after cleaning and removal of scales. The unrolling technique (Pitkin 1986, Huemer 1988) was used for male slide preparations. The male genitalia slide of the holotype was dissolved, and genitalia also unrolled and remounted. Intact (in lactic acid) and slidemounted genitalia were photographed with a Nikon DS-Fi1 digital camera mounted on a Nikon Eclipse 800 microscope at magnifications of 100x. Nikon's NIS 2.3 Elements was used to assemble multiple photos of different focal planes into single deepfocus images. The descriptive terminology of genitalia structures generally follows Huemer and Karsholt (2010) and Kristensen (2003).

Photography. Pinned specimens were photographed with a Canon EOS 60D with a MP-E 65 mm macro lens. They were placed on the tip of a thin plastazote wedge mounted on an insect pin, with the head facing toward the pin and the fringed parts of the wings facing outward. This ensured that there was nothing between the fringes and the background. All specimens were photographed over a white background. Lighting was provided by a ring of 80 LED covered with a white diffuser dome (Fisher 2012 and references therein). The camera was attached to a re-purposed stereoscope fine-focusing rail. Sets of 20-35 images in thin focal planes were taken for each specimen and assembled into deep-focused images using Zerene Stacker and edited in Adobe Photoshop.

DNA sequence analysis. DNA extracts were prepared from one or two legs removed from each specimen. DNA extraction, PCR amplification of the barcode region of COI, and subsequent sequencing followed standard protocols at the Canadian Centre for DNA Barcoding (deWaard et al. 2008). Attempts to barcode the type specimens of N. neonata failed due to their old age. All resultant sequences, along with the voucher data, images, and trace files, are publicly available in the BOLD dataset "DS-NEOPALPA", dx.doi. org/10.5883/DS-NEOPALPA. Sequences > 600 bp are deposited in GenBank (for accessions, see Suppl. material 1). Uncorrected p-distances were calculated in MEGA5 (Tamura et al. 2011). To infer a phylogenetic framework for Gnorimoschemini, a nexus file of 35 sequences, including several outgroups and one representative from 32 Gnorimoschemini genera, together with the sequences from the two species of *Neopalpa*, was compiled using public sequences on BOLD and subjected to a Bayesian analysis of 50m generations in MrBayes v.3.2. (Ronquist et al. 2012) under the $GTR + \Gamma + I$ model with two simulations, independent Markov chain Montecarlo (MCMC) runs starting from different random trees, each with three heated chains and one cold chain.

Results

Neopalpa Povolný, 1998

Neopalpa Povolný, 1998a: 141, figs 1, 6.

Type species. *Neopalpa neonata* Povolný, 1998b (by original designation).

Diagnosis. *Neopalpa* can be defined by the combination of the following genitalia characters: male tegumen long and parallel sided, gnathos a short and delicate spine with distinct V-shaped arms, uncus tall and rounded, valvae sigmoid with antlershaped tip, saccus narrow and nearly as long as tegumen, phallus nearly as long as longitudinal axis of genitalia, with a subovate caecum and a sub-terminal projection. Female with a well-developed antrum and an aviform signum.

Remarks. Povolný (1998a) did not provide a differential diagnosis for *N. neo-nata*; instead he emphasized the "extremely characteristic" male genitalia, "… mainly reflected in the form of the curious bilobate paired process arising from the sacculus, in the shape of slender parallel-sided sigmoid valva with its curious tip, and in the long slender aedeagus with the specialized tip." As for the adult, he commented, "The moth shows the monotonous forewing coloration with indistinct blackish stigmata characteristic of the tribe." With the discovery of a new species of *Neopalpa* described here, none of these characters holds up as a synapomorphy for the genus. While comparable structures occur in other Gnorimoschemini (e.g., some species in *Ephysteris* or *Keiferia*), the "curious bilobate paired process arising from the sacculus" is significantly reduced in the new species. Also, the sigmoid bifurcating valve is not unique in Gnorimoschemini (present in some species of *Keiferia, Scrobipalpopsis* and *Symmetrischema*), and the new species show a highly-specialized phallus. In addition, the adults of the new species show a highly-contrasting wing pattern that is very distinct from *N. neonata*.

Description. *Head.* Scaled with light-yellow frons, scales on the vertex converging towards middle, often with darker tips, ocelli present, small, located behind the base of antenna. Labial palpi strongly up-curved, segment 3 acute, about 2/3 length of segment 2; antenna with more or less distinct dark and light rings.

Thorax. Grey to brown; wingspan 7–12 mm; forewing slender, discal and apical areas dark brown, termen with black-tipped white scales. Hindwing off-white to grey-ish with a well-developed tornal lobe and a pointed tip.

Abdomen. Male tergum 8 subtriangular, equilateral, weakly sclerotized and concave anteriorly; sternum 8 more than twice the size of tergum 8, subrectangular, broader than long, posterior margin broadly rounded, anterior margin bilobate with a deep ventral emargination. Female segment 7 trapezoidal, tergum 7 approximately twice the length of other abdominal segments; apodemes in both sexes well developed. Coremata absent.

Male genitalia. Characterized by elongate shape, long parallel-sided tegumen and slender, well-rounded uncus; gnathos a short spine; culcitula weakly developed; valva sigmoid, parallel sided with a bifurcating antler-shaped tip; sacculus parabasally located, short and cone shaped; vincular processes variously developed; saccus elongate, nearly as long as tegumen; phallus elongate with a subovate caecum and a distinct subterminal spine.

Female genitalia. Segment 8 with almost evenly sclerotized subgenital plate, moderately to strongly sculpted, ventromedial zone membranous; ostium bursae distinctly edged; antrum wide, tubular and weakly sclerotized, nearly ³/₄ length of apophysis anterioris; apophysis anterioris thin and parallel sided, about same length as segment 8; ductus bursae same width as antrum and same length as apophysis anterioris; corpus bursae clearly delineated, bulbous; signum aviform with a central spine (hook) and two wide subtriangular lobes.

Distribution. Western USA (California and Arizona) and Baja California, Mexico.

Biology. Both species specialize in xeric habitats. The host plant is unknown, but is probably in the Solanaceae (one specimen of *N. neonata* "collected in tomato foliage").

Key to species of Neopalpa

1

Review of species

Neopalpa neonata Povolný, 1998 Barcode Index Number: BOLD:ABW8320 Figs 1a–f, 2a, b, 3a–d, 4a, c, 5a

Neopalpa neonata Povolný, 1998a: 141, figs 1, 6.

Material examined. Holotype ♂, California: Los Angeles County, Santa Catalina Island, Middle Cyn. 5.ii.1978, J.A. Chemsak, specimen # EMEC82306, genitalia slide Pw1173 (EMEC). Paratype ♂, Mexico: Baja California Sur, 21 mi. W. La Paz, 8.9.1966, J.A. Powell, specimen # EMEC342305, genitalia slide Pw1173 (EMEC).

For a complete list of additional specimens examined from California, Arizona and Mexico (n = 386), see Suppl. material 1.

Diagnosis. Distinguishable from the species described below by dark forewing and frons, well-developed vincular processes that are more than 4× as long as sacculus, segment 8 in female genitalia heavily sculpted with microtrichea, and signum heavily granulated with small stubby spines.

Redescription. *Adult* (Figs 1a–f, 2a, b). Forewing length: male 3.6–4.9 mm (mean 4.2 mm, n=50); female 4.2–5.0 mm (mean 4.3 mm, n=50). Head, thorax and tegula covered with a mixture of grayish-brown scales with darker tips; scales on vertex and frons with darker tips, often appressed, converging towards middle. Labial palpi up-curved, annulated, segment 3 acute, about ²/₃ size of segment 2; antenna about ²/₃



Figure I. Adults of *Neopalpa* species. **a**–**f** *N. neonata* **g**–**j** *N. donaldtrumpi* sp. n. *N. neonata*: **a** holotype ♂ EMEC82306 (CA: Santa Catalina Island) **b** paratype ♂ EMEC342305 (Mexico: Baja California Sur) **c** ♀ CNCLEP00077350 (CA: Santa Cruz Island) **d** ♀ EMEC407544 (CA: Santa Cruz Island) **e** ♂ LAC-MENT326744 (CA: San Bernardino County) **f** ♀ EMEC408849 (CA: Modoc County); *N. donaldtrumpi* sp. n.: **g** Holotype ♂ UCBMEP0201628 (CA: Imperial County) **h** Paratype ♀ UCBMEP0201482 (CA: Imperial County) **i** Paratype ♂ UCBMEP0201629 (CA: Imperial County) **j** Paratype ♂ EMEC408498 (Mexico: Baja California Sur). For detailed specimen data see Suppl. material 1. Scale bar 2 mm.

length of forewing, with more or less distinct dark and light rings, scape covered with yellow and dark-brown scales. Mesoscutum grayish brown, tegulae greyish brown to brown. Forewing upper surface ground coloration consists of a mixture of grayish-brown scales with dark tips, the dorsal region and subterminal fascia distinctly paler partly mixed with orange scales; three to four obscure black tear-shaped stigmata situated axially, first near forewing base, second in wing center, third in cell; additional one or two stigmata in the dorsal forewing fold, the first near wing center, the second rather indicated by a group of chocolate-brown scales before external transverse band near forewing dorsum; apical area and fringes generally dark grey mottled with lighter suffusion. Hindwing deep grey, unmarked, slender, with distinctly protruding tip. Sexes similar.

Variation. Adult size and the intensity of forewing pattern variable. A large female specimen (wingspan=6.3mm, not included in mean wingspan calculation) from Cedar Pass Campground, Modoc County (EMEC408849, dissection VNZ 591, Fig. 1f) shows gray ground coloration on wings instead of dark brown, but the female genitalia are identical to those of *N. neopalpa* (Fig. 1f).

Male genitalia (Figs 3a–d, 4a) (seven preparations examined). Tergum 8 subtriangular, equilateral, weakly sclerotized and concave anteriorly; sternum 8 more than 2× the width of tergum 8, subquadrate, broader than long, posterior margin broadly rounded, anterior margin bilobate with a protruded anterolateral corner.

Tegumen slender, parallel-sided, the anterior margin laterally notched; uncus long and narrow with a round apex, finely setose; gnathos a short delicate spine with distinct V-shaped arms about same width; culcitula weakly developed. Valva sigmoid, long and slender, parallel-sided, bifurcating at about ½ length of valva towards tip into two equally-sized acute branches in form of antlers; sacculus parabasally located, short and cone-shaped, finely setose; posterior margin of vinculum with a striking paired bilobate process separated by a deep, narrow excision; this process with a shorter truncate lobe provided with a brush of long, stiff hairs, their tips extending over second (longer) lobe with obtuse upper edge and with rounded lateral side, both armoured with numerous short spinules; lateral side of the paired process fused basally with oblique wall of sacculus; (ventral) wall of sacculus strengthened basally by a distinct, paired, heavily-sclerotized curved ledge; saccus elongate, ligulate, nearly as long as tegumen, with distinctly-sclerotized lateral edge and a moderately rounded tip; phallus nearly as long as the longitudinal genitalia axis, moderately sigmoid, with a strongly-curved, rounded tip, a distinct subterminal hook-like spine, and an irregularly subovate caecum.

Female genitalia (Fig. 5a, c) (eight preparations examined). Segment 8 parallel sided on slide mounts, subgenital plate heavily sculpted with microtraechia, two distinct dense round patches of microtraechia on Segment 8 posterolaterally; ostium bursae subspherical, distinctly-edged anterolaterally; antrum wide, tubular, weakly sclerotized, nearly ³/₄ length of apophysis anterioris; apophysis anterioris thin, parallel sided, about the same length as segment 8; ductus bursae about same width and length of antrum, lightly sculpted with speckles; corpus bursae clearly deliniated, bulbous,



Figure 2. Close up of the head of male *Neopalpa* species. **a**, **b** *N. neonata* (LACMENT326885, Mexico: Baja California) **c**, **d** *N. donaldtrumpi* sp. n., holotype (UCBMEP0201628, CA: Imperial County). Left: lateral aspect, right: frontal aspect. Scale bar 1 mm.

lightly sculpted; signum aviform with a central spine and two subtriangular wings covered with several rows of spinules.

Distribution. Povolný's assumption that this species is a Channel Islands endemic is incorrect, as it seems to have a much wider distribution on the mainland. Examined specimens are from the USA: California (Imperial, Inyo, Los Angeles, Modoc, Riverside, San Bernardino, San Diego, Santa Barbara and Solano counties); Arizona (Cochise and Coconino counties), as well as Mexico (States of Sonora, Baja California, and Baja California Sur).

Biology. Adults fly throughout the year, probably in more than one generation. Studied specimens were collected in every month of the year in almost even numbers (the high number of samples collected in March is likely an artefact of high-volume Malaise trapping in one location). The two males that formed the type series of this species were collected in the "xeric maritime habitats extending from California Channel Islands." Additional specimens examined were collected in a variety of generally dry habitat types in canyons, creeks, campgrounds, microphyll forest, dry bush, dunes

and desert habitats. The life history and host plant remain unknown; nearly all specimens examined were collected at light or in Malaise traps, although one specimen (UCREM 4318, UCR) was "collected in tomato foliage."

Neopalpa donaldtrumpi Nazari, sp. n. http://zoobank.org/5FA78DB3-9FB8-409A-AD01-34567BB3C396 Barcode Index Number: BOLD:ACR1768

Figs 1g-j, 2c-d, 3e-h, 4b,d, 5b

Type material. *Holotype* 3: [label 1] "USA: CA: Imperial Co. | Algodones Dunes – Niland- | Glamis Rd. 7.4 km NW Glamis", [label 2] "33°02N 115°08.3W | 21-25 April 2009 AL173 | Bohart Museum Team", [label 3] "UC BME | P 0201628", [label 4] "Barcode of Life Project | Leg(s) removed | DNA extracted", [label 5] "genitalia slide | VNZ240 3." Condition of specimen: double mounted, wings partly spread, left antenna and part of right antenna missing, left hind- and all right legs missing, partly removed for DNA barcoding. Deposited at UCBME.

Paratypes. 5 males, 1 female. 1 ♂ same data as for holotype, specimen # UCB-MEP0201629 (CNC); 1 ♀ **USA:** CA: Imperial Co., Algodones Dunes, Mammoth Wash, Niland-Glamis Rd., 29 km N. Hwy 78, 2008AL20, 6-9.II.2008, Malaise trap, S.L. Heydon & T.J. Zavortnik, specimen # UCBMEP0201482, slide VNZ241 (UCBME); 1 ♂ CA: Riverside Co., P.L. Boyd Desert Research Center, 3.5 miles S. Palm Desert, 13–18.VI.1969, Malaise trap, Saul Frommer & R. Worley, specimen # UCREM 18373, slide VNZ580 (UCR); 1 ♂ *ibid*, 16–17.8.1970, P.L. Boyd, specimen # UCRC ENT 461717 (UCR); 1 ♂ CA: Imperial Co., Deep Canyon, Coyote Creek, 5.IV.1975, J.B. Tucker, specimen # UCIS 313268, slide VNZ556 (UCR). 1 ♂ **Mexico:** Baja California Norte, Arroya Catavina, Hwy 1, 35 mi S Progresso, 1.IV.1976, Blacklight, P.A. Rude, specimen # EMEC408498, slide VNZ327 (EMEC).

Diagnosis. The new species can be easily distinguished from *N. neonata* by its external appearance, the yellowish-white scales covering the frons of the adult head, and the distinctive orange-yellow coloration on the forewing dorsum. In the male genitalia, the valvae are strongly curved, the saccus has an acute tip, and the highly-developed bilobed processes of the vinculum, characteristic of *N. neonata*, are absent. In the female genitalia, the subgenital plate is simpler than in *N. neonata* and much less sculptured with microtrichea, and the signum wings are smooth.

Description. *Adult* (Figs 1g–j, 2c, d). Forewing length: male 3.0–4.6 mm (mean 3.6 mm, n=6); female 4.3 mm (n=1). Head and thorax off-white, tegula greyish brown to brown, scales on vertex and frons yellowish white, often rough, converging towards middle. Labial palpi strongly up curved, annulated, segment 3 slender and acute, about ²/₃ size of segment 2; antenna about ²/₃ length of forewing, with more or less distinct dark and light rings, scape covered with yellow and light-brown scales. Forewing upper surface with costal region dark brown with sparse, lighter speckles; dorsal region and discal fascia orange yellow to pale buff, the sinuous margin with two or three scallops;



Figure 3. Male genitalia of *Neopalpa* species. **a–d** *N. neonata* **e–h** *N. donaldtrumpi* sp. n. **a, b** ventral and lateral view of intact genitalia, unmounted, stored in lactic acid (LACMENT326710, CA: Riverside County) **c, d** Unrolled genitalia and phallus of the Holotype (EMEC82306, dissection Pw1168) **e, f** ventral and lateral view of intact genitalia, unmounted, stored in lactic acid (UCRC ENT 461717, CA: Riverside County) **g, h** Unrolled genitalia and phallus of the Holotype (UCBME021628; dissection VNZ241). Scale bar 100 μm.



Figure 4. Last abdominal segment of male *Neopalpa* species. **a** *N. neonata* (specimen BIOUG01860-D04, dissection MIC6545; CA: San Diego County) **b** *N. donaldtrumpi* sp. n. (UCIS 313268, dissection VNZ556; CA: Riverside County). Scale bar 100 μm.

apical area and fringes dark brown heavily mottled with lighter suffusion. Hindwing pale buff, unmarked, with slightly darker fringe. Sexes similar.

Male genitalia (Figs 3e–h, 4b) (four preparations examined). Tergum 8 subpentagonal, weakly sclerotized and concave anteriorly; sternum 8 more than 2× the width of tergum 8, subquadrate, broader than long, posterior margin broadly rounded, anterior margin bilobate with a protruded anterolateral corner. Genitalia comparatively smaller than for *N. neonata*, tegumen slender and parallel sided, anterior margin laterally notched, uncus long and narrow with a round tip; gnathos a short spine with distinct V-shaped arms about same width; culcitula weakly developed. Valva sigmoid, parallel sided, with a short spine at about ²/₃ length towards tip; sacculus parabasally located, short and cone shaped; vinculum with lateral projections spine shaped and about the same size as sacculus, vinculum posterior margin weakly developed with a shallow anteromedial incision; saccus elongate, nearly as long as tegumen, narrowing towards an acute tip; phallus elongate with a subovate caecum and a distinct subterminal spine.

Female genitalia (Fig. 5b, d) (1 preparations examined). Segment 8 with almost evenly sclerotized subgenital plate, with ventromedial zone membranous and moderately sculpted with microtraechia; ostium bursae subtriangular, distinctly edged anterolaterally; antrum wide, tubular and weakly sclerotized, nearly ³/₄ length of apophysis anterioris; apophysis anterioris thin and parallel sided, about same length as segment 8; ductus bursae about same width and 2× length of antrum, lightly sculpted with wrinkles; corpus bursae clearly deliniated, bulbous, lightly sculpted; signum aviform with a central spine and two smooth subtriangular wings.

Etymology. The new species is named in honor of Donald J. Trump, to be installed as the 45th President of the United States on January 20, 2017. The reason for this choice of name is to bring wider public attention to the need to continue protecting fragile habitats in the US that still contain many undescribed species. The specific epithet is selected because of the resemblance of the scales on the frons (head) of the moth to Mr. Trump's hairstyle. The name is a noun in the genitive case.



Figure 5. Female genitalia of *Neopalpa* species. **a** *N. neonata* (CNCLEP00077350, dissection MIC6530; CA: Santa Cruz Island) **b** *N. donaldtrumpi* sp. n. (UCBMEP0201482, dissection VNZ241; CA: Imperial County); Close-up of signa **c** *N. neonata* (UCBMEP0201495, dissection VNZ239; CA: Imperial County) **d** *N. donaldtrumpi* sp. n. (same as b). Scale bar 100 μm.

Distribution. So far only known from Riverside and Imperial counties in southern California and Baja California in Mexico.

Biology. Specimens collected at mercury-vapour light, black-light or Malaise trap in February, April, June and August, in dry or sandy habitats. Life history and host plant unknown.

Discussion

The two species of *Neopalpa* fly sympatrically in three localities in southern California (Deep Canyon and P.L. Boyd Desert Research Center in Riverside County, and Algodones dunes in Imperial County) (Fig. 6), although none of the examined specimens of *N. donaldtrumpi* were collected synchronically with *N. neonata* (see Suppl. material 1). The



Figure 6. Distribution of Neopalpa species. (Created using simplemappr.net, accessed December 2016)

DNA barcodes of *N. neonata* and *N. donaldtrumpi* are 4.9–5.1% divergent from one another and are placed in separate BINs on BOLD. A Bayesian analysis of DNA barcodes from representatives of all available Gnorimoschimini genera placed these two species together, and as a distant sister to *Ochrodia* Povolný, 1966 and *Ephysteris* Meyrick, 1908 with good support. The tree was rooted using representative from other tribes of Gelechiinae, and other subfamilies of Gelechiidae. Short mitochondrial fragments such as the DNA barcode region cannot resolve deeper relationships at the subfamily level, as evident by these results. In the inferred phylogeny, all genera currently recognized under Gnorimoschemini (*sensu* Povolný 2002) group together in a large unresolved clade with weak support, except *Kiwaia* Philpott, 1930; in addition, *Neofaculta* Gozmany, 1955 (Gelechiinae: Chelarini) appears within the Gnorimoschemini clade as sister to



Figure 7. Bayesian Inference of COI barcode sequences for selected Gnorimoschimini species. Values are posterior probabilities for each node.

Keiferia Povolný, 1967 (Fig. 7). *Ochrodia* has been treated as a valid genus (Povolný 2002, Huemer and Karsholt 2010) or a subgenus of *Ephysteris* (Karsholt and Sattler 1998, Li and Bidzylia 2008). These two taxa share the same "Ephysteroid" type of genitalia (*sensu* Povolný and Šustek 1988) with *Neopalpa*, and appear to be the most similar group to it within Gnorimoschemini.

The discovery of this distinct micro-moth in the densely populated and otherwise zoologically well-studied southern California underscores the importance of conservation of the fragile habitats that still contain undescribed and threatened species, and highlights the paucity of interest in species-level taxonomy of smaller faunal elements in North America. By naming this species after the 45th President of the United States, I hope to bring some public attention to, and interest in, the importance of alpha-taxonomy in better understanding the neglected micro-fauna component of the North American biodiversity.

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Supplementary material I

Material examined and GenBank accessions

Authors: Vazrick Nazari

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RESEARCH ARTICLE



Oreoglanis hponkanensis, a new sisorid catfish from north Myanmar (Actinopterygii, Sisoridae)

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Abstract

During a survey of the Mali Hka River drainage in Hponkanrazi Wildlife Sanctuary in December 2015, a new species was collected and is described herein as *Oreoglanis hponkanensis*. It is a member of the *O. siamensis* species group and can be distinguished from its congeners in having a unique combination of the following characters: lower lip with median notch and posterior margin entire, caudal fin emarginate, nasal barbel reaching about half the distance to eye, tip of maxillary barbel rounded, posterior margin of maxillary barbel entire, absence of pale elliptical patches on sides of body below adipose fin, absence of patch on base of first dorsal fin ray, caudal fin rays 2, vertebrae 40, pectoral fin surpassing pelvic fin origin, pelvic fin length 21–26% SL, caudal peduncle length 25–33% SL, caudal peduncle depth 3–5% SL, adipose fin base length 34–39% SL, and dorsal to adipose distance 12–16% SL.

Keywords

Hponkanrazi, Irrawaddy, Myanmar, Siluriformes

Introduction

The Sisoridae is the largest family of Asian catfish, with more than 200 species and 22 genera (Ferraris 2007; Ng 2015). Members are found along the entire southern arc of the Asian continent and comprise a significant portion of the hill-stream fauna in southern and eastern Asia (Ng and Jiang 2015). Recent morphological (Ng 2015) and molecular research (Ng and Jiang 2015) reconstructed the monophyly of Sisoridae and divided it into Sisorinae and Glyptosterninae subfamilies. The Sisorinae includes 12 genera in three tribes (Bagariini, Erethistini and Sisorini). The Glyptosterninae includes 10 genera in one tribe (Glyptosternini). The Glyptosterninae is well-supported as a monophyletic group with 15 synapomorphies, within which *Oreoglanis* is monophyletic and considered to be a sister group of *Pseudoexostoma* and *Exostoma*, with five synapomorphies (Ng 2015), and a sister group of *Creteuchiloglanis* and *Pseudoexostoma* (Ng and Jiang 2015).

The genus *Oreoglanis* was established by Smith (1933) for glyptosternine catfish characterized with a continuous postlabial groove in the lower jaw and an unusual dentition of pointed teeth in the upper jaw and posterior part of the lower jaw and truncate-spatulate teeth in the anterior part of the lower jaw (Ng and Kottelat 1999). There are currently 22 valid species of *Oreoglanis* (Ng and Rainboth 2001; Ng and Freyhof 2001; Ng 2004; Kong et al. 2007; Vidthayanon et al. 2009; Linthoingambi and Vishwanath 2011; Sinha and Tamang 2015). Among them, only *O. macropterus* and *O. insignis* have been recorded from the Irrawaddy River drainage of Myanmar and China. During a survey of the Mali Hka River drainage in Hponkanrazi Wildlife Sanctuary in December 2015, we collected specimens of *Oreoglanis*, which we identified as a new species and describe herein as *O. hponkanensis*.

Materials and methods

Measurements were made point to point with dial calipers and recorded to 0.2 mm. Counts and measurements were made on the left side of the specimens when possible. Subunits of the head were measured as proportions of head length (HL). Head length and body parts were measured as proportions of standard length (SL). Counts and measurements followed Ng and Kottelat (1999). Vertebral counts followed Roberts (1994). Images of tooth bands, maxillary barbels, and genital papillae were taken with an Olympus SZ61 and ToupCam microscope digital camera. Radiographs were obtained to count vertebrae using a digital Cabinet X-ray System (Kubtec Xpert 80). The examined specimens are deposited at the Kunming Institute of Zoology (KIZ), Chinese Academy of Sciences (CAS), Kunming, China, and the Southeast Asia Biodiversity Research Institute (SEABRI), Chinese Academy of Sciences, Nay Pyi Taw, Myanmar.

Results

Oreoglanis hponkanensis sp. n.

http://zoobank.org/A539FAAD-34D9-4370-ABCA-D6048BC54CA6 Figure 1

Holotype. KIZ2015006376 (CXY20150125), 102.14 mm SL; Myanmar: Kachin State, Hponkanrazi Wildlife Sanctuary, Zeyar Stream near Zeyar Dan Village, 27°34.2'N, 97°06.05'E; XY. Chen, T. Qin and SS. Shu, 14 Dec. 2015.

Paratypes.KIZ2015006375 (CXY20150124),KIZ2015006377 (CXY20150126), 2 ex., 78.88–99.26 mm SL; data as for holotype. SEABRI-CXY20150143, 1 ex., 110.68 mm SL; Myanmar: Kachin State, Hponkanrazi Wildlife Sanctuary, Ponyin Stream near Zeyar Dan Village, 27°33.86'N, 97°05.42'E; XY. Chen, T. Qin and SS. Shu, 14 Dec. 2015. SEABRI-CXY20150104, SEABRI-CXY20150106, KIZ2015006378, 3 ex., 70.6–120.64 mm SL; Myanmar: Kachin State, Hponkanrazi Wildlife Sanctuary, Zeyar Stream near Zeyar Dan Village, 27°34.2'N, 97°06.05'E; XY. Chen, T. Qin and SS. Shu, 9 Dec. 2015. SEABRI-CXY20150078, 1 ex., 88.78 mm SL; Kachin State, Hponkanrazi Wildlife Sanctuary, Monlar Stream near Warsar Dan Village, 27°29.82'N, 97°11.34'E; XY. Chen, T. Qin and SS. Shu, 7 Dec. 2015.

Diagnosis. Oreoglanis hponkanensis is a member of the O. siamensis species group, and can be distinguished from its congeners in having a unique combination of the following characters: lower lip with median notch and posterior margin entire, caudal fin emarginate, nasal barbel reaching about half the distance to eye, tip of maxillary barbel rounded, posterior margin of maxillary barbel entire, absence of pale elliptical patches on sides of body below adipose fin, absence of patch on base of first dorsal fin ray, caudal fin brown with two round, bright orange patches in middle, branched dorsal fin rays 5, branched anal fin rays 2, vertebrae 40, pectoral fin surpassing pelvic fin origin, pelvic fin length 21–26% SL, caudal peduncle length 25–33% SL, caudal peduncle depth 3–5% SL, adipose fin base length 34–39% SL, and dorsal to adipose distance 12–16% SL.

Description. Morphometric data are listed in Table 1. Head and body moderately broad and very strongly depressed. Mouth and gape inferior, with broad and thin papillate lips. Lower lip with median notch, posterior margin entire. Postlabial groove on lower jaw present and uninterrupted. Jaw teeth pointed, in a large broad band with small median indentation and rounded ends on both sides of upper jaw. Teeth on lower jaw present in two, well-separated patches of roughly triangular shape and of two kinds: anterior teeth truncate-spatulate, inner face curved; posterior teeth pointed like those of upper jaw (Figure 2). Eyes small, dorsolaterally situated and subcutaneous. Gill openings extending to middle of pectoral fin base. Maxillary barbels flattened, with surrounding flap of skin and rounded tip; ventral surface with numerous plicae; posterior margin of maxillary barbel entire (Figure 3D). Nasal barbel short, reaching about half the distance to eye.



Figure 1. Oreoglanis hponkanensis, SEABRI CXY20150104, paratype, male, 70.6 mm SL.

Dorsal fin without spine and with i, 5 (7) rays. Adipose fin with long base. Anal fin with i, 2 (7) rays. Caudal fin emarginate, with 6/6 (7) rays. Pelvic fin greatly enlarged, with convex distal margin and i, 5 (7) rays; first ray flattened, with numerous plicae on ventral surface; tip of pelvic fin surpassing anus, and anus at midpoint between posterior end of pelvic fin base and tip of pelvic fin. Pectoral fin greatly enlarged, without spine and with i, 16 (4) or i, 17 (3) rays; first ray flattened, with numerous plicae on ventral surface. Tip of pectoral fin reaching beyond pelvic fin origin; Vertebrae 25+15=40 (3), or 26+14=40 (1).

Males with small genital papilla located immediately posterior to anus (Figure 4A). Females with two flaps of skin on both sides of anus, and small genital papilla located in longitudinal groove immediately posterior to anus (Figure 4B).

Color. In life: brown on dorsal and lateral surfaces of head and body, light yellow on ventral region. Dorsal surfaces of head and body with series of small, light yellow

| Catalog number | Holotype | Range | Mean | SD |
|--------------------------------|----------|------------|------|------|
| Total length (mm) | 114.3 | 80.1-135.0 | _ | - |
| Standard length (mm) | 102.1 | 70.6–120.6 | - | - |
| Percentage of standard length | | | | |
| Head length | 18.5 | 16.5–22.9 | 20.0 | 2.53 |
| Head width | 18.3 | 17.4–23.2 | 19.8 | 2.28 |
| Head depth | 8.4 | 8.1–10.3 | 9.0 | 0.91 |
| Predorsal length | 25.6 | 24.2-30.9 | 28.3 | 2.61 |
| Prepectoral length | 12.5 | 11.2–16.4 | 13.4 | 1.92 |
| Prepelvic length | 32.3 | 29.2-34.6 | 32.7 | 2.28 |
| Preanal length | 61.3 | 61.3–69.3 | 66.2 | 2.93 |
| Body depth at anus | 9.6 | 9.3–12.0 | 10.3 | 1.05 |
| Caudal peduncle length | 29.9 | 25.4–33.2 | 29.7 | 2.99 |
| Caudal peduncle depth | 3.6 | 3.1–4.8 | 3.8 | 0.58 |
| Dorsal to adipose distance | 15.8 | 11.5–16.0 | 14.4 | 1.79 |
| Post adipose length | 11.2 | 8.4–11.9 | 10.4 | 1.27 |
| Dorsal fin base length | 9.0 | 7.8–10.6 | 9.3 | 1.11 |
| Adipose fin base length | 36.8 | 36.3–39.2 | 37.5 | 1.19 |
| Pectoral fin length | 25.0 | 23.4–29.0 | 26.3 | 2.28 |
| Pelvic fin length | 21.0 | 20.5-25.9 | 23.1 | 2.11 |
| Anal fin base length | 3.1 | 3.1–5.5 | 3.8 | 1.00 |
| Percentage of head length | | | | |
| Head width | 1.0 | 0.9–1.1 | 1.0 | 0.04 |
| Head depth | 0.5 | 0.4–0.5 | 0.5 | 0.03 |
| Snout length | 0.7 | 0.6–0.7 | 0.6 | 0.03 |
| Interorbital width | 0.3 | 0.3–0.3 | 0.3 | 0.02 |
| Eye diameter | 0.1 | 0.1-0.1 | 0.1 | 0.01 |
| Nasal barbel length | 0.2 | 0.2-0.2 | 0.2 | 0.03 |
| Maxillary barbel length | 1.0 | 0.8–1.1 | 0.9 | 0.08 |
| Outer mandibular barbel length | 0.2 | 0.2–0.2 | 0.2 | 0.01 |
| Inner mandibular barbel length | 0.2 | 0.1-0.2 | 0.2 | 0.03 |

Table 1. Morphometric data of *Oreoglanis hponkanensis* sp. n. (n = 8).

patches: two ovoid patches on occipital region, elliptical patches on anterior and posterior bases of adipose fin. Ovoid patch on base of first dorsal fin ray absent, and elliptical patch on lateral surface of body below middle part of adipose fin base absent. Dorsal fin brown, dorsal surfaces of pectoral and pelvic fins brown, anal fin and ventral surfaces of pectoral and pelvic fins light yellow. Adipose fin light yellow. Caudal fin brown with two round, bright orange patches in middle. Pectoral fin base occasionally with round yellow patch on inner and outer anterior sides, respectively. Dorsal surface of barbels brown, ventral surface light yellow.



Figure 2. Tooth band of Oreoglanis hponkanensis, SEABRI CXY20150106, paratype, male, 120.64 mm SL.



Figure 3. Comparison of posterior margin of maxillary barbel of *Oreoglanis* species. A *O. jingdongensis*, KIZ 200104003, holotype, 109.1 mm SL B *O. immaculatus*, KIZ 200261015, holotype, 54.2 mm SL C *O. insignis*, KIZ 9810191, holotype, 66.7 mm SL D *O. hponkanensis*, KIZ CXY20150126, paratype, 78.88 mm SL E *O. macropterus*, KIZ 2004000834, 79.6 mm SL F *O. setiger*, KIZ 2016000859, 90.0 mm SL.



Figure 4. Ventral view of anus and external genital papilla of *Oreoglanis hponkanensis*. A SEABRI CXY20150106, paratype, male, 120.64 mm SL B SEABRI CXY20150078, paratype, female, 88.78 mm SL.

Distribution. Known from high mountain streams of Mali Hka River drainage (upper Irrawaddy River drainage) in Hponkanrazi Wildlife Sanctuary, Kachin State, north Myanmar (Figure 5).

Habitat. Fast flowing mountain streams with stone, cobble, and sand beds (Figure 6A, B). Other associated fish species recorded from the type locality include: Cyprinidae: *Danio aequipinnatus, Barilius barnoides, Tor qiaojiensis, Neolissochilus* sp., *Garra salweenica, Garra bispinosa, Placocheilus dulongensis, Schizothorax meridionalis*; Nemacheilidae: *Paracanthocobitis adelaideae, Schistura malaisei*; Siluridae: *Pterocryptis berdmorei*; Amblycepitidae: *Amblyceps murraystuarti*; Sisoridae: *Exostoma vinciguerrae*; Channidae: *Channa burmanica.*

Etymology. From Hponkanrazi Wildlife Sanctuary, adjectival.

Discussion

Oreoglanis hponkanensis is a member of the *O. siamensis* species group (*sensu* Ng and Rainboth 2001) based on the presence of a lower lip with a median notch. There are 13 species in this group, including *O. hponkanensis. Oreoglanis hponkanensis* can be distinguished from its congeners in the *O. siamensis* species group by branched anal fin rays 2 vs. 3–6.

Oreoglanis hponkanensis shares with O. immaculatus, O. insignis, O. jingdongensis, O. laciniosus, O. majusculus, O. macropterus, O. pangenensis, O. setiger, and O. suraswadii in having the tip of the maxillary barbel rounded and the pectoral fin reaching or surpassing pelvic fin origin (vs. tip of maxillary barbel pointed and pectoral fin not reaching pelvic fin origin in O. siamensis, O. sudarai, and O. heteropogon).



Figure 5. Distribution map of Oreoglanis hponkanensis.



Figure 6. Habitat of *Oreoglanis hponkanensis*. **A** Zeyar Stream, Mali Hka drainage, Hponkanrazi Wildlife Sanctuary, north Myanmar **B** Monlar Stream, Mali Hka drainage, Hponkanrazi Wildlife Sanctuary, north Myanmar.

Oreoglanis hponkanensis is further distinguished from *O. siamensis* in having the posterior margin of lower lip entire (vs. with small laciniate projections), the posterior margin of the maxillary barbel entire (vs. lobulated), longer pelvic fin (surpassing vs. not reaching anus; length 21–26% SL vs. 15–16), absence (vs. presence) of pale patches on the sides of the body below the adipose fin, fewer branched dorsal fin rays (5 vs. 6), longer and more slender caudal peduncle (length 25–33% SL vs. 17–23; depth 3–5% SL vs. 5–6), shorter nasal barbel (16–25% HL vs. 28–37), and larger interorbital distance (28–34% HL vs. 23–27).

Oreoglanis hponkanensis can be further distinguished from *O. sudarai* in having the posterior margin of lower lip entire (vs. with lobulate projections), longer pelvic fin (greatly surpassing anus vs. slightly surpassing), absence (vs. presence) of pale patches on sides of body below adipose fin absent, longer caudal peduncle (length 25–33% SL vs. 17–23), shorter prepelvic length (29–35% SL vs. 37–43), shorter anal fin base length (3–6% SL vs. 6–9), longer pelvic fin length (21–26% SL vs. 13–17), and shorter nasal barbel (16–25% HL vs. 27–41).

Oreoglanis hponkanensis can be distinguished from *O. heteropogon* in having the nasal barbel reaching midway between its base and anterior orbital (vs. reaching anterior margin of orbit), the posterior margin of the maxillary barbel entire (vs. with crenulate projections), more branched dorsal fin rays (5 vs. 6), more vertebrae (40 vs. 38), shorter predorsal length (24–31% SL vs. 35), shorter prepectoral length (11–16% vs. 19), shorter prepelvic length (29–35% SL vs. 42), shorter preanal length (61–69% SL vs. 75), shorter dorsal to adipose distance (12–16% SL vs. 20), longer caudal peduncle (length 25–33% SL vs. 18), shorter post-adipose distance (8–12% SL vs. 13), longer adipose fin base (34–39% SL vs. 29), longer pelvic fin (21–26% SL vs. 13), shorter anal fin base (3–6% SL vs. 7), larger interorbital distance (28–34% HL vs. 22), and shorter nasal barbel (16–25% HL vs 33).

Oreoglanis hponkanensis differs from *O. jingdongensis* and *O. suraswadii* in having the caudal fin emarginate (vs. lunate). It can be further distinguished from *O. jingdongensis* in having the posterior margin of the maxillary barbel entire (vs. with crenulate projections, Figure 3A), more slender and narrower caudal peduncle (length 25–33% SL vs. 20–26, depth 3–5% SL vs. 5–8), pelvic fin surpassing anus for a longer distance (vs. just surpassing), less blunt snout, and fewer vertebrae (40 vs. 42–43). It can be further differentiated from *O. suraswadii* in having the pelvic fin greatly surpassing anus (vs. just surpassing), more vertebrae (40 vs. 36–38), absence (vs. presence) of pale patches on sides of body below adipose fin, longer caudal peduncle (25–33% SL vs. 19–25), shorter prepelvic length (29–35% SL vs. 36–40), and shorter dorsal fin base (8–11% SL vs. 11–14).

Oreoglanis hponkanensis can be distinguished from *O. laciniosus* in having the posterior margin of the lower lip entire (vs. with lobulate projections), absence (vs. presence) of pale patches on sides of body below adipose fin, shorter predorsal length (24–31% SL vs. 35–37), shorter prepelvic length (29–35% SL vs. 38–42), and longer adipose fin base (34–39% SL vs. 32–33).

Oreoglanis hponkanensis shares a similar color pattern with *O. immaculatus*, but differs in having the posterior margin of the lower lip entire (vs. with lobulate projections), the posterior margin of the maxillary barbel entire (vs. with laciniate projections, Figure

3B), more vertebrae (40 vs. 37–38), longer pelvic fin (21–26% SL vs. 18–21), pelvic fin far surpassing anus (vs. just surpassing), much slenderer caudal peduncle (length 25–33% SL vs. 17–21, depth 3–5% SL vs. 5–7), longer adipose fin base (34–39% SL vs. 26–33), and shorter dorsal to adipose distance (12–16% SL vs. 16–23).

Oreoglanis hponkanensis differs from *O. macropterus* in having the posterior margin of the maxillary barbel entire (vs. with lobulate projections, Figure 3E), absence (vs. presence) of pale patches on sides of body below adipose fin, fewer branched dorsal fin rays (5 vs. 6), fewer caudal fin rays (6/6 vs. 7/8, 8/7, or 8/8), shorter maxillary barbel (surpassing posterior edge of eye vs. closer to gill opening), much slenderer caudal peduncle (length 25–33% SL vs. 19–22 and depth 3–5% SL vs. 8–9), and shorter dorsal to adipose distance (12–16% SL vs. 18–19).

Oreoglanis hponkanensis can be distinguished from *O. majusculus* in having the posterior margin of the maxillary barbel entire (vs. with villiform projections), absence (vs. presence) of patches on sides of body below adipose fin, fewer branched pectoral fin rays (16–17 vs. 20), fewer caudal fin rays (6/6 vs. 7/8), and much slenderer caudal peduncle (with length 25–33% SL vs. 18–21 and depth 3–5% SL vs. 6).

Oreoglanis hponkanensis differs from *O. pangenensis* in having the posterior margin of the maxillary barbel entire (vs. with lobulate and laciniate projections), fewer branched dorsal fin rays (5 vs. 6), fewer caudal fin rays (6/6 vs. 7/8), absence (vs. presence) of pale patches on sides of body below adipose fin, slenderer caudal peduncle (with length 25–33% SL vs. 23 and depth 3–5% SL vs. 5), shorter head (17–23% SL vs. 26), shorter predorsal length (24–31% SL vs. 33), shorter preanal length (61–69% SL vs. 75), shorter prepelvic length (29–35% SL vs. 36), longer adipose fin base (34– 39% SL vs. 31), and shorter dorsal to adipose distance (12–16% SL vs. 21).

Oreoglanis hponkanensis can be differentiated from *O. setiger* in having the posterior margin of the lower lip entire (vs. with laciniate projections), the posterior margin of the maxillary barbel entire (vs. with laciniate projections, Figure 3F), fewer branched dorsal fin rays (5 vs. 6), anus much closer to snout tip than to caudal fin base (vs. vice versa), absence (vs. presence) of pale patches on sides of body below adipose fin, more vertebrae (40 vs. 36), much slenderer caudal peduncle (with length 25–33% SL vs. 15–16), shorter predorsal length (24–31% SL vs. 32–37), shorter prepelvic length (29–35% SL vs. 37–39), and larger eye diameter (8–12% HL vs. 7–8).

Oreoglanis hponkanensis can be distinguished from *O. insignis* in having the distance between anal fin origin and caudal fin base almost equal to distance between pelvic and anal fin origins (vs. almost equal to distance between posterior end of pelvic fin base and anal fin origin), anus much closer to snout tip than caudal fin base (vs. anus at midpoint between snout tip and caudal fin base), absence (vs. presence) of pale patches on sides of body below adipose fin, black (vs. yellow) tip of caudal fin, fewer branched dorsal fin rays (5 vs. 6), fewer caudal fin rays (6/6 vs. 8/7), more vertebrae (40 vs. 36–39), shorter predorsal length (24–31% SL vs. 31–35), shorter prepelvic length (29–35% SL vs. 36–40), and longer adipose fin base (34–39% SL vs. 29–34).

Within species of the *O. siamensis* group, *O. siamensis* and *O. sudarai* only occur in the Chao Phraya River drainage, *O. suraswadii*, *O. setiger*, and *O. jingdongensis* only occur in the Mekong River drainage, *O. heteropogon*, *O. laciniosus*, and *O. immaculatus* are found only in the Salween River drainage, *O. majusculus* and *O. pangenensis* only occur in the Brahmaputra River drainage, *O. macropterus* occurs in the Salween and Irrawaddy river drainages, and *O. insignis* and *O. hponkanensis* are only found in the Irrawaddy River drainage. Ng and Rainboth (2001) erroneously stated that *O. insignis* was distributed in the "upper Irrawaddy and Salween (Nu Jiang) river drainages in northern Myanmar and southwestern China" based on specimens from René Malaise's 1934 collection "Qushi, Baoshan, Yunnan, China from the Kambawti area, Kachin state, Myanmar and Tengchong area, Yunnan, China". Kambawti, Tengchong, and Qushi (a Tengchong Township) are located in the Irrawaddy drainage. Thus, *O. insignis* should be confined to the Irrawaddy drainage, as clarified by Chen (2013).

Key to Oreoglanis siamensis group

| 1 | Tip of maxillary barbel pointed; tip of pectoral fin not reaching pelvic fin |
|----|--|
| | origin2 |
| - | Tip of maxillary barbel rounded; tip of pectoral fin reaching or surpassing |
| 2 | Nasal barbel reaching midway between its base and anterior orbital margin |
| | |
| _ | Nasal barbel reaching anterior orbital margin |
| 3 | Pectoral fin not reaching pelvic fin origin |
| _ | Pectoral fin reaching pelvic fin origin O. sudarai |
| 4 | Caudal fin lunate |
| _ | Caudal fin emarginate |
| 5 | Upper and lower caudal fin first principal rays of approximately equal length |
| _ | Lower first principal ray of caudal fin much longer than upper O. jingdongensis |
| 6 | Posterior margin of lower lip with lobulate projections |
| _ | Posterior margin of lower lip entire |
| 7 | Posterior margin of maxillary barbel entire |
| _ | Posterior margin of maxillary barbel with lobulate or laciniate projections8 |
| 8 | Posterior margin of maxillary barbel with lobulate projections; yellow patch |
| | below adipose fin absent |
| _ | Posterior margin of maxillary barbel with laciniate projections; yellow patch |
| | below adipose fin present |
| 10 | Posterior margin of maxillary barbel entire11 |
| _ | Posterior margin of maxillary barbel with projections12 |
| 11 | Distance between anal fin origin and caudal fin base almost equal to distance |
| | between pelvic and anal fin origins; anus much closer to snout tip than caudal |
| | fin base; patches on sides of body below adipose fin absent |
| | |
| _ | Distance between anal fin origin and caudal fin base almost equal to distance |
| | between posterior end of pelvic fin base and anal fin origin; anus at midpoint |

| | between snout tip and caudal fin base; patch on sides of body below adipose |
|----|---|
| | fin presentO. insignis |
| 12 | Posterior margin of maxillary barbel villiform; ovoid patch on base of first |
| | dorsal fin ray absent |
| _ | Posterior margin of maxillary barbel lobulate; ovoid patch on base of first |
| | dorsal fin ray present13 |
| 13 | Posterior margin of maxillary barbel lobulate; caudal peduncle depth 8–9% |
| | SL O. macropterus |
| _ | Posterior margin of maxillary barbel with lobulate and laciniate projections; |
| | caudal peduncle depth 5% SL |

Comparative material

- Oreoglanis immaculatus. Holotype: KIZ 200261015, 54.2 mm SL, Paratypes: KIZ200261010, 012, 014, 016, 4 ex., 57.4–63.9 mm SL, Nanjing River (a tributary of the upper Salween), Yongde County, Yunnan, China; KIZ 794762, KIZ794763, 2 ex., 52.0–54.3 mm SL, Nangun River (a tributary of the upper Salween), Cangyuan County, Yunnan, China.
- Oreoglanis insignis. Holotype: KIZ 9810191, 66.7 mm SL, Longchuanjiang River (a tributary of the upper Irrawaddy), Tengchong County, Yunnan, China. KIZ 2006010198-217, 220-229, 30 ex., 41.–85.3 mm SL, upper Binglang River (upper Daying River, a tributary of the Irrawaddy), Tengchong County, Yunnan, China.
- *Oreoglanis jingdongensis.* Holotype: KIZ 200104003, 109.1 mm SL, Paratypes: KIZ 200104001-002, 004-008, 7 ex., 87.1–115.2 mm SL, upper Mengpian River (a tributary of the upper Mekong), Jingdong County, Yunnan, China.
- *Oreoglanis macropterus*. KIZ 2004000749-754, 825-840, 22 ex., 43.8–85.1 mm SL, a tributary of upper Dulong River (a tributary of the upper Irrawaddy), Gongshan County, Yunnan, China.
- Oreoglanis setiger. KIZ 2016000859, 868, 870, 874, 883, 5 ex., 74.7–95.0 mm SL, Nanbi River (a tributary of the upper Mekong), Mengsa Township, Gengma County, Yunnan, China.

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RESEARCH ARTICLE



A new species of Aspidophryxus (Isopoda, Dajidae), ectoparasitic on Mysidella hoshinoi (Mysidae) in Japan

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Abstract

A new dajid, *Aspidophryxus izuensis* **sp. n.**, is described from seven females and six males found infesting the dorsal carapaces of specimens of *Mysidella hoshinoi* Shimomura, 2016 (Mysidae: Mysidellinae) associated with an unidentified species of sea anemone (Haloclavidae) from Izu-Oshima Island, Sagami Sea, central Japan. *Aspidophryxus izuensis* sp. n. differs from its congeners in having a body length about as long as wide, widest at the anterior part in females; an elongate frontal part of the cephalon, half as long as wide in females; the frontal margin of the cephalon exceeding the anterior margins of lateral lamellae in females; an unsegmented, vermiform, elongate pleon in females; and a uropod composed of a protopod and an inner and outer ramus in males. A key to worldwide species in the genus is provided.

Keywords

Aspidophryxus, Dajidae, Izu-Oshima Island, Mysidella, parasite

Introduction

Dajidae, a family of the suborder Cymothoida, consists of 54 species belonging to 18 genera, all of which are exclusively ectoparasites of mysid, euphausiid and decapod crustaceans (Boyko and Schotte 2013; Shields and Gómez-Gutiérrez 1996; Williams and Boyko 2012). Dajidae exhibits highest diversity in the Antarctic (seven species) with

14 species in the North East Atlantic regions combined (Williams and Boyko 2012). Seven dajid species have so far been recorded from Japan: *Aspidophryxus japonicus* Shimomura & Ohtsuka, 2011 from the mysid *Holmesiella affinis* Ii, 1937, *Heterophryxus appendiculatus* G. O. Sars, 1885 from the euphausiid *Euphausia recurva* Hansen, 1905, *Holophryxus fusiformis* Shiino, 1937 from the sergestid *Sergestes prehensilis* Bate, 1881, *Notophryxus ocellatus* Shimomura & Ohtsuka, 2011 from the mysid *Rhopalophthalmus orientalis* O. S. Tattersall, 1957, *Prodajus bilobatus* Shiino, 1943 from the mysid *Anisomysis ijimai* Nakazawa, 1910, *P. curviabdominalis* Shimomura, Ohtsuka & Naito, 2005 from the mysid *Siriella okadai* Ii, 1964, and *Zonophryxus retrodens* Richardson, 1903 from the pandalid shrimp *Plesionika semilaevis* Bate, 1888 (Shimomura et al. 2010).

During a parasitological survey of invertebrates in Japanese waters, new parasitic isopods were found on the carapace of the mysid *Mysidella hoshinoi* Shimomura, 2016. The present paper describes a new species of *Aspidophryxus* and is the second occurrence of the genus from Japan.

Material and methods

Host mysids were collected by a local SCUBA diver using sealable plastic bags (20 cm × 20 cm) by scooping seawater from around a sea anemone (Haloclavidae sp). All specimens obtained were preserved in 80% ethanol. Dajids were removed from hosts under a stereomicroscope. Each individual was dissected and prepared for observation with a light microscope (Nikon E600). For SEM observation (Hitachi S-3000N), specimens were dehydrated through an alcohol series, freeze-dried and sputter-coated with platinum. Total length as indicated in "Material examined" was measured from the tip of the cephalon to the end of the body excluding the pleon. The authors and dates of dajid taxa are referenced but those of the hosts are not. The terminology follows Shimomura et al. (2005).

The type specimens are deposited in the Kitakyushu Museum of Natural History and Human History, Japan (KMNH).

Systematics

Aspidophryxus G. O. Sars, 1883

Aspidophryxus G. O. Sars, 1883: 72–73.

Type species. *Aspidophryxus peltatus* G. O. Sars, 1883 (by original designation).

Species included. *A. discoformis* Boyko & Williams, 2012; *A. frontalis* Bonnier, 1900; *A. izuensis* sp. n.; *A. japonicus* Shimomura & Ohtsuka, 2011; *A. peltatus* G. O. Sars, 1883.

Aspidophryxus izuensis sp. n.

http://zoobank.org/406F5790-697C-4411-8E0C-1FB94D4E26E6 Figs 1–4

Material examined. Holotype. Ovigerous Q (1.4 mm) (KMNH IvR 500908), Akinohama, Izu-Oshima Island, Sagami Sea, Japan, 23 August 2014, 35 m.

Allotype. 1 $\mathcal{J}(KMNH IvR 500911)$, obtained from the holotype.

Paratypes. 2 ovigerous $\bigcirc \bigcirc$, 1.3 mm (KMNH IvR 500909), 1.2 mm (KMNH IvR 500910), 2 $\bigcirc \bigcirc$, 0.5 mm (KMNH IvR500912), obtained from the female (KMNH IvR 500909), 0.5 mm (KMNH IvR500913), obtained from the female (KMNH IvR 500910), data same as holotype; 2 ovigerous $\bigcirc \bigcirc \bigcirc$, 1.5 mm (KMNH IvR 500914), 1.5 mm (KMNH IvR 500915), 2 $\bigcirc \bigcirc \bigcirc$, 0.5 mm (KMNH IvR500916), obtained from the female (KMNH IvR 500914), 0.5 mm (KMNH IvR500917), obtained from the female (KMNH IvR 500915), Akino-hama, Izu-Oshima Island, Sagami Sea, Japan, 9 August 2014, 35 m; 1 non-ovigerous \bigcirc , 0.8 mm (KMNH IvR 500918), Akino-hama, Izu-Oshima Island, Sagami Sea, Japan, 19 August 2014, 35 m; 1 ovigerous \bigcirc , 0.5 mm (KMNH IvR 500919), 1 \bigcirc , 0.5 mm (KMNH IvR 500920), obtained from the female (KMNH IvR 500919), 1 \bigcirc , 0.5 mm (KMNH IvR 500920), obtained from the female (KMNH IvR 500919), 1 \bigcirc , 0.5 mm (KMNH IvR 500920), obtained from the female (KMNH IvR 500919), 1 \bigcirc , 0.5 mm (KMNH IvR 500920), obtained from the female (KMNH IvR 500919), 1 \bigcirc , 0.5 mm (KMNH IvR 500920), obtained from the female (KMNH IvR 500919), 1 \bigcirc , 0.5 mm (KMNH IvR 500920), obtained from the female (KMNH IvR 500919), 1 \bigcirc , 0.5 mm (KMNH IvR 500920), obtained from the female (KMNH IvR 500919), 1 \bigcirc , 0.5 mm (KMNH IvR 500920), obtained from the female (KMNH IvR 500919), 1 \bigcirc , 0.5 mm (KMNH IvR 500920), obtained from the female (KMNH IvR 500919), 1 \bigcirc , 0.5 mm (KMNH IvR 500920), obtained from the female (KMNH IvR 500919), 1 \bigcirc , 0.5 mm (KMNH IvR 500920), obtained from the female (KMNH IvR 500919), 0.5 mm (KMNH IvR 500920), 0.5 mm (KMNH IvR 500919), 0.5 mm (KMNH IvR 500920), 0.5 mm (KMNH IvR 500919), 0.5 mm (KMNH IvR 500920), 0.5 mm (KMNH IvR 500919), 0.5 mm (KMNH IvR 500920), 0.5 mm (KMNH IvR 500919), 0.5 mm (KMNH IvR 500920), 0.5 mm (KMNH IvR 500919), 0.5 mm (KMNH IvR 500920), 0.5 mm (KMNH IvR 500919), 0.5 mm (KMNH IvR 500920), 0.5 mm (KMNH IvR 500919), 0.5 mm (KMNH IvR 500920), 0.5 mm (KMNH IvR 500919), 0.5 mm (KMNH IvR 500920), 0.5 mm (KMNH IvR 500910), 0.5 mm (KMNH IvR 500910

Diagnosis. Female: body length and width subequal, anteriorly widest; frontal margin of cephalon exceeding anterior margins of lateral lamellae; frontal part of cephalon half as long as wide; pleon unsegmented, vermiform, elongate half as long as total body length. Male: cephalon fused with first pereomere; uropod composed of protopod and inner and outer ramus.

Description of female. Body (Figs 2A, B, 5A) semicircular, anteriorly widest, 1.1 times as long as maximum width (including lateral lamellae), moderately vaulted dorsally, with pair of broad lateral lamellae filled with 145 eggs; lateral lamellae not reaching beyond frontal margin of cephalon. Egg diameter ranged from 72.8 to 88.4 µm (N = 20; average = 81.8±3.9). Cephalon (Fig. 2B; see Fig. 5A, B) oriented ventrally, without eyes; frontal part long, half as long as wide; anterior margin rounded; posterior margin not visible in dorsal view. Pereon (Fig. 2A) without transverse folds. Medioventral edge of lateral lamellae produced into two digitiform extensions anterior to insertion of pleon (Figs 2B, 5C, E); posterior extension with many scale-like wrinkles. Pleon (Figs 2B, 5A, D-F) segments fused, vermiform, very long, reaching beyond posterior margin of lateral lamellae, with many pits, without lateral plates or pleopods. Pleotelson fused with pleon, without uropods. Antennule and antenna (Figs 3A, 5B) composed of one article each with three setae distally. Oral cone (Figs 3A, 5B) conical, extending beyond surface of cephalon. First to fifth pereopods (Figs 4A, 5B) similar in shape, first pair slightly smaller than others: basis longest; ischium approximately 0.7 times as long as basis; merus fused with carpus; propodus ovate, without setae or spines; dactylus with curved claw.

Description of male. Body (Figs 3B, 5D) curved ventrally; scattered setae present dorsally. Cephalon (Fig. 3B, C) without eyes, fused with first percomere; anterior margin



Figure 1. A female and male of *Aspidophryxus izuensis* sp. n. on the carapace of the mysid *Mysidella ho-shinoi*, Akino-hama, Izu-Oshima Island, Sagami Sea, Japan, 1 January 2015, 35 m depth, habitus in situ, photographed by O. Hoshino.

convex. Second to seventh percomeres (Fig. 3B) separated, subequal in width. Pleon (Fig. 3B, D) unsegmented, slit-like anal cone between uropods. Uropods (Fig. 3B, D) well developed, long, composed of protopod and inner and outer ramus: protopod cylindrical, without setae; inner and outer ramus shorter than protopod, each with two setae distally. Antennule (Fig. 3C) composed of single triangular article, with two distal and two lateral setae. Antenna (Fig. 3C, D) composed of eight articles: first article largest; second article as long as first article; third article shorter than second article; fourth to seventh articles each with one or two setae distally; eighth article with one short and one long setae and one aesthetasc apically. Oral cone (Fig. 3C): pair of mandibular gnathobases protruding from mouth opening. First percopod (Fig. 4B) smaller than all other percopods, basis longest; ischium 0.7 times as long as basis; merus trapezoidal; carpus smallest; propodus ovate, without setae; dactylus short, curved inward. Second to fifth pereopods (Fig. 4C, D) similar in shape: basis longest; ischium shorter than basis; merus trapezoidal; carpus smallest, with one seta distally; propodus ovate, with one projection proximoventrally; dactylus long, slightly curved inward, with one seta ventrally. Sixth pereopod (Fig. 4E) propodus slightly smaller than those of second to fifth pereopods. Seventh pereopod (Fig. 4F) longer than all other pereopods: propodus smaller than propodus of sixth pereopod; dactylus short, curved inward, without setae.



Figure 2. *Aspidophryxus izuensis* sp. n., holotype female: **A** habitus, dorsal **B** habitus, ventral. Scale bar 500 µm. Abbreviation: pl, pleon.



Figure 3. *Aspidophryxus izuensis* sp. n., **A** holotype female **B–D** allotype male (KMNH IvR 500911): **A** cephalon, ventral **B** habitus, lateral **C** cephalon and first and second pereomeres, ventral **D** pleotelson, dorsal. Scale bars 100 μm. Abbreviations: ant-1, antennule; ant-2, antenna; o. c, coral cone; md, mandible; u. p, uropod.

Color in life. Female (Figs 1; see Fig. 2A) whitish and translucent, with six transverse translucent light orange bands dorsally. Male (Fig. 1) whitish and translucent.

Remarks. *Aspidophryxus izuensis* sp. n. can be identified by the following combination of characters: body length and width subequal, anteriorly widest in female; frontal



Figure 4. *Aspidophryxus izuensis* sp. n., **A** holotype female **B–F** allotype male (KMNH IvR 500911): **A** left fifth pereopod, dorsal **B** left first pereopod, lateral; **C** left second pereopod, lateral **D** left fifth pereopod, lateral **F** left seventh pereopod, medial. Scale bar 100 μm.

margin of the cephalon exceeding anterior margins of lateral lamellae in female; pleon unsegmented, vermiform, very long in female; uropod composed of protopod and inner and outer ramus in male.

Aspidophryxus izuensis is most similar to A. discoformis Boyko & Williams, 2012, from Caribbean waters (Boyko and Williams 2012) in having the frontal margin of cephalon exceeding the anterior margins of the lateral lamellae and body length and width being subequal. Aspidophryxus izuensis, however, differs from A. discoformis by the following characters (those of A. discoformis in parentheses): body widest at anterior



Figure 5. *Aspidophryxus izuensis* sp. n., **A** paratype female (KMNH IvR 500909) and male (KMNH IvR 500912) **B, C, E, F** paratype female (KMNH IvR 500909) **D** paratype male (KMNH IvR 500912). **A** habitus, female, ventral, male, dorsal; **B** cephalon and pereopods, ventral **C** pleon and digitate extensions of oostegites, ventral **D** habitus (clinging to female pleon by seventh pereopods), lateral **E** pleon and digitate extensions of oostegites, ventral; **F** female pleon, ventral. Scale bars **A**, 500 μm; **B–D**, 100 μm. Abbreviations: ant-1, antennule; ant-2, antenna; o. c, oral cone; pl, pleon.

part in female (widest at middle); pleon very long, reaching beyond posterior margin of lateral lamellae in female (moderately short, not reaching beyond posterior margin of lateral lamellae); frontal part of cephalon long, half as long as wide in female (short, 0.12 times as long as wide); uropods well developed, long, composed of protopod and inner and outer ramus in male (rudimentary, short, uniramous).

Dajid males are found attached to the pleon, lateral plate, or pleopods of the females by the pereopods (Giard and Bonnier 1889; Shimomura et al. 2005). In *A. izuensis*, the

males cling to near the end of the pleon of females by seventh percopods. The pleon of the female has scale-like wrinkles and many pits on its surface; these features might enable males to more easily cling to the surface. This is one of the first reports on how males attach to the pleon of females in the Dajidae.

Etymology. The new species is named after the type locality.

Key to the females of Aspidophryxus species (modified from Boyko and Williams 2012)

| 1 | Frontal margin of cephalon exceeding anterior margins of lateral lamellae2 |
|---|--|
| _ | Frontal margin of cephalon not exceeding anterior margin of lateral lamellae 3 |
| 2 | Body length and width subequal, antenna a single lobe, pleon unsegmented, |
| | vermiform |
| _ | Body longer than wide, antenna segmented, pleon segmentedA. japonicus |
| 3 | Frontal margin of cephalon rectangular and subequal to mouth/pereopod |
| | region in size, body longer than wide |
| _ | Frontal margin of cephalon irregular shaped, much smaller than mouth/ |
| | pereopod region, body length and width subequal |
| 4 | Body widest at middle part, pleon moderately short, not reaching beyond |
| | posterior margin of lateral lamellae |
| _ | Body widest at anterior part, pleon elongate, reaching beyond posterior mar- |
| | gin of lateral lamellae |
| | |

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RESEARCH ARTICLE



Revision of the genus *Tarema* Schaus, 1896 (Lepidoptera, Mimallonoidea, Mimallonidae) with the description of a new species from southeastern Brazil

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Abstract

The genus *Tarema* Schaus, 1896 is revised. The species *T. fuscosa* Jones, 1908 and *T. rivara* Schaus, 1896 are redescribed, the female of the former is described and figured for the first time, and the genitalia of both sexes for each species are figured for the first time. The lectotype of *Tarema macarina* Schaus, 1928, **syn. n.** is determined to be the female of *T. rivara*. *Tarema bruna* **sp. n.** is described from Sáo Paulo, Brazil. Lectotypes for *T. fuscosa*, *T. rivara*, and *T. macarina* are here designated.

Keywords

Distribution, Neotropical, Paraguay, *Tarema bruna* sp. n., *Tarema fuscosa, Tarema macarina* syn. n., *Tarema rivara*, taxonomy

Introduction

The genus *Tarema* Schaus, 1896 has been mostly overlooked in the literature since Schaus (1928), save for its mention in two published species lists of Mimallonidae (Gaede 1931, Becker 1996). Recently, however, Herbin and Mielke (2014) reported new collecting data for *T. rivara* Schaus, 1896 quite distant from its type locality,

displaying the broad distribution of this species. Additionally, Diniz et al. (2013) reported the first life history information for the genus in reference to *T. rivara*, including images of the larva and larval sack, as well as host plant data and the first figures accurately depicting both sexes of this species.

Since Schaus (1928), three species have been included in the genus *Tarema: T. rivara*, *T. fuscosa* Jones, 1908, and *T. macarina* Schaus, 1928. Diniz et al. (2013), in figuring both sexes of *T. rivara*, unknowingly revealed the conspecifity of *T. rivara* and *T. macarina*, names applied to the opposite sexes of a single species. We were previously aware of this taxonomic issue, therefore we revise the synonymy and provide accurate figures attributed to the species for aid in future identification. We also provide a distribution map and genitalia figures of both sexes of both species for the first time. Furthermore, a new species is described and figured.

Methods

Dissections were performed as in Lafontaine (2004). Morphological, including genitalia, terminology follows Kristensen (2003). Not all genitalia were prepared on slides to allow for three-dimensional analysis of the complex male genitalia. Genitalia and abdomens, when not slide mounted, are preserved in glycerol filled microvials.

The primary types (when abdomen was present) and at least one specimen from most localities were dissected.

Specimens from the following collections were examined:

| CDH | Coll. Daniel Herbin, Garidech, France |
|-------|---|
| CGCM | Coll. Carlos G. C. Mielke, Curitiba, Paraná, Brazil |
| CNC | Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, |
| | Ontario, Canada |
| CPAC | Coll. Embrapa Cerrados, Planaltina, Distrito Federal, Brazil |
| CUIC | Cornell University Insect Collection, Ithaca, New York, USA |
| DZUP | Coll. Pe. Jesus S. Moure, Departamento de Zoologia, Universidade Fed- |
| | eral do Paraná, Curitiba, Paraná, Brazil |
| MNHU | Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany |
| NHMUK | Natural History Museum, London, U.K. |
| USNM | National Museum of Natural History [formerly United States National |
| | Museum], Washington D.C., USA |

Figures were manipulated with Adobe Photoshop CS4 (Adobe 2008). Male genitalia are figured in natural color with CS4 "auto color" used to improve white backgrounds. Female genitalia were treated with "auto tone" in CS4 to darken characters. The map was created with SimpleMappr (Shorthouse 2010) and edited with CS4. All geographical coordinates are approximate, and are based on the localities provided on specimen labels. GPS data were acquired with Google Earth.

Results and discussion

Tarema Schaus, 1896: 55

Type species. Tarema rivara Schaus, 1896: 55, by original designation.

Diagnosis. The genus *Tarema* is recognized among the family Mimallonidae by generous amounts of light gray scales present over the entirety of the dorsum and ventrum of the wings, as well as on the thorax and abdomen, giving the species of this genus a hoary appearance. The genitalia of *Tarema* are unique in the family. Male genitalia have short, ovoid valves and spike-covered projections emanating from near the base of the valves that may be associated with the transtilla and/or the gnathos. The gnathos itself is reduced to a flat, movable plate that covers the base of the uncus. Long setae emanate from above the phallus in paired, horsetail-like bunches. The phallus is thick and broad, and has two lengthwise processes terminating in a sharp tip and a curved tip respectively. Female genitalia are robust structures with a medium to large coiled ductus-corpus bursae complex. The sclerotized portion of abdominal segment VIII is broad; appearing wrinkled ventrally, and is covered in thick, branched setae. The genus *Alheita* Schaus, 1928 is somewhat similar to *Tarema* in overall small size, wing shape, and minor resemblance of male genitalia, namely the ovoid valves and odd shape of the uncus which is usually more deeply bifid in *Alheita*.

Description. Male. Head: Eyes large, more than two thirds area of head; antenna bipectinate to tip, though pectination reduced along distal fifth of antennal length; labial palpus reduced, three segmented, palpus usually not extending beyond frons, scales generally darker brown dorsally. *Thorax*: Appearing hoary due to banded gray or pale khaki scales interspersed amongst darker ones, prothorax with more heavily concentrated light gray or khaki scales. Legs: Coloration as for thorax, though lighter gray, vestiture finer, bushier. Tibial spurs narrow, sharp, mostly clothed in scales. Forewing dorsum: Forewing length: 9-16 mm, wingspan: 21.5-32.0 mm. Short, triangular, outer margin nearly straight but slightly convex mesally. Ground color ranging from brown or pale clay-orange to nearly black, overall generously shaded by cream or gray scales giving the wing a hoary, layered appearance. Antemedial line absent or nearly so, faint dark band may be present. Postmedial line nearly straight but may be somewhat inwardly or outwardly bent, line preapical such that submarginal area mostly uniform in width from tornus to apex. Apical half of submarginal area with postmedial lunule. Costa appearing lighter than most of wing due to high concentration of gray or khaki scales. Discal spot a thick streak spanning width of discal cell. Forewing ventrum: Antemedial line absent, postmedial line never straight, bulging outward toward wing margin mesally. Hindwing dorsum: Submarginal area with orange to reddish patch of scales mesally, discal mark present but smaller. Hindwing ventrum: Following same pattern as forewing ventrum. Frenulum as single bristle. Venation: Rather typical for Mimallonidae, discal cell quite broad, distal edge sharply slanted (see Schaus 1896). Abdomen: Short, barely or not extending beyond anal angle of hindwing. Genitalia: Complex; vinculum somewhat ovoid or almost circular, ventrally with reduced saccus. Uncus robust, sharp, parrot beak-like and dorsolaterally flattened or reduced to slightly triangular stump with slight bidentation terminally. Gnathos a flattened or curved plate concealing fingerlike sclerotization of anal tube. Valves short, rounded, weakly sclerotized mesally. Base of valves with pair of fingerlike projections, weakly sclerotized knobby area may be present above fingerlike projections. Valves with or without more heavily sclerotized, spined accessory arms that may or may not be attached basally to valves. Diaphragm with pair of horsetail-like seatal patches consisting of setae of variable length that extend outward over phallus below gnathos plate. Juxta partially fused to phallus, encircling it, lightly sclerotized, with ventral lip connecting phallus to base of vinculum (severed to excise phallus). Phallus broad, large, with two elongated accessory projections. Vesica balloon-like, slightly scobinate, separated into fairly distinct diverticula. Female. Head: Similar to male, but broader, antennae and labial palpi smaller. Thorax: As in male. Legs: As in male, though tibial spurs thicker. Forewing dorsum: Forewing length: 10.0-18.5 mm, wingspan: 22.0-34.5 mm. As in male but slightly broader, postmedial line usually more noticeably bent. Forewing ventrum: Similar to forewing ventrum of male, but veins usually lined with contrasting yellow scales. Hindwing dorsum: Coloration and markings as for forewing dorsum. Hindwing ventrum: Follows same pattern as forewing ventrum. Frenulum absent. Abdomen: As in male but slightly more robust. Tergite VIII as three posteriorly directed lobes or as single broad plate, sternite VIII as wrinkled mass consisting of one or two pieces, covered in thick, branched setae. Genitalia: Stout, robust or quite narrow overall; apophyses anteriores highly reduced, apophyses posteriores elongate, spanning length of segment IX. Lamella indistinct due to large sclerotization of sternite VIII. Corpus bursae large, bag-like, coiled, broadly connected beneath sternite VIII /ostium complex, no clear ductus bursae present, occasionally with large, snake-like spermatophore present within corpus bursae. Papillae anales typical of Mimallonidae, appearing rectangular laterally; papillae anales covered with fine setae.

Key to species of Tarema*

*The female of *T. bruna* sp. n. is unknown.

Tarema rivara Schaus, 1896

Figs 1–6, 11, 14, 16

Tarema rivara Schaus, 1896: 55 *Tarema rivara*; Schaus 1928: 670, fig. 88i ♂ *Tarema rivara*; Gaede 1931 *Tarema rivara*; Becker 1996 *Tarema rivara*; Diniz et al. 2013: 88, figs ♂, ♀, larva, larval sack *Tarema macarina* Schaus, 1928: 670, fig. 88i ♀ **syn. n.** *Tarema macarina*; Gaede 1931 *Tarema macarina*; Becker 1996

Type material. *Tarema rivara* **Schaus: lectotype [here designated],** *C*. **BRAZIL: Sáo Paulo:** São Paulo, S.E. Brazil./ Collection, WmSchaus/ Type No. 12566 U.S.N.M/ USNM-Mimal: 1120/ *Tarema rivara* Type. Schaus./ LECTOTYPE male *Tarema rivara* designated by St Laurent, Herbin, and C. Mielke, 2017 [handwritten red label]/ St Laurent diss.: 8-22-16:3/ (USNM, examined). Type locality: Brazil: São Paulo.

Tarema macarina Schaus: lectotype [here designated], \bigcirc . BRAZIL: São Paulo: 1 \bigcirc , São Paulo, S.E. Brazil./ Collection, WmSchaus/ Type No. 33596 U.S.N.M/ USNM-Mimal: 1121/ *Tarema macarina* Type Schaus/ LECTOTYPE female *Tarema macarina* designated by St Laurent, Herbin, and C. Mielke, 2017/ *Tarema rivara* det. St Laurent 2016/ St Laurent diss.: 8-22-16:2/ (USNM, examined). **Paralectotypes**, 2 \bigcirc . BRAZIL: São Paulo: 1 \bigcirc , Brasil. m., S. Paulo 96/ Typus/ Coll. Staudinger/ *Tarema macarina* Schaus, co-type/ (MNHU, photograph examined). Unknown state: 1 \bigcirc , Brasil [illegible]/ *Tarema macarina* co-type Schaus/ 8582/ (MNHU, photograph examined). Type locality: Brazil: São Paulo. – All paralectotypes with the following yellow label: PARALECTOTYPE \bigcirc *Tarema macarina* designated by St Laurent, Herbin, and C. Mielke, 2017.

Additional specimens examined. (28 3, 14 9) BRAZIL: Maranhão: 1 3, Feira Nova do Maranhão, Retiro, 07°00'31"S, 46°26'41"W, 480 m: 16–17.II.2013, C. Miel-ke leg., Coll. C. Mielke 26.333 (CGCM). **Bahia:** 1 3, Barreiras, 12°9'S, 45°00'W, 700 m: 4.II.1994, Coleção EMBRAPA-CPAC No. 15.987, [Camargo leg.] (CPAC). **Mato**

Grosso: 1 Q, Chapada [dos] Guimarães: 25.V.1989, V.O. Becker leg., Coll. Becker 75031, USNM-Mimal: 2320 (USNM). 1 Å, No specific locality: XII.1929, Coll. R. Spitz, Rothschild Bequest 1939–1 (NHMUK). Goiás: 1 3, Ponte Funda, Vianópolis: 24.X.1987, Tangerini leg., genitalia prep. D. Herbin ref H. 1010 (CDH). 19, Ipameri: 10.X.1988, V.O. Becker leg., Coll. Becker 59419, USNM-Mimal: 2323, St Laurent diss.: 8-22-16:8 (USNM). Distrito Federal: 1 3, 1 9, Estação Florestal, Cabeça do Veado, 1100 m: 17.X.1971, 23.X.1971, E.G., I. & E.A. Munroe leg., St Laurent diss.: 3-14-16:7, 3-14-16:8 (CNC). 5 ♂, 2 ♀, Planaltina, 15°35'S, 47°42'W, 1000 m: 1-10.XI.1994, Tangerini leg. (1 3, CDH); 25.IX.1985, 5.XI.1988, V.O. Becker leg., Coll. Becker 57771, 58871, 58872, USNM-Mimal: 2301-2304, 2321, 2322 $(4 \ 3, 2 \ 9, \text{USNM})$. 1 $\ 3, \text{Planaltina: } 15.X.1995 (MWM)$. Minas Gerais: 1 $\ 3, \text{Serra}$ do Cipó à Conceição do Mato Dentro, km 126.3, 19°14'51"S, 43°30'38"W, 1270 m: 18.XI.2012, genitalia prep. D. Herbin ref H. 1012 (CDH). 1 3, Malacacheta, 500 m: I.1998, H. Thöny leg., genital prep. 29.234 (MWM). 1 Å, Sete Lagoas, 720 m: 15.III.1974, V.O. Becker leg., Coll. Becker 411, USNM-Mimal: 2300 (USNM). 1 ∂, Paracatu, 17°13'S, 46°52'W, 920 m: 5.II.1994, Colecão EMBRAPA-CPAC No. 14.664 (CPAC). 1 Å, Iraí de Minas, 18°43'S, 47°30'W, 950 m: 9.II.1994, Coleção EMBRAPA-CPAC No. 14.145 (CPAC). 1 &, São Roque de Minas, São José do Barreiro, 870 m, 3.XII.2016, C. Mielke leg., Coll. C. Mielke 32.162 [point not on map] (CGCM). São Paulo: 2 3, Ribeirão Preto, Fazenda da Pedra, Rio Tamanduá: Travassos & Pearson leg., 12-15.X.1953 (NHMUK); HRP 643, USNM-Mimal.: 2425 (USNM). 1 ♂, Locality as for previous but 500 m: 2–5.III.1954, Pearson & Oiticica leg., Brit. Mus. 1962–112 (NHMUK). 1 3, Alto da Serra [Paranapiacaba]: I.1926, R. Spitz leg., Rothschild Bequest 1939-1, St Laurent diss.: 7-7-16:4 (NHMUK). 1 ♂, Miracatu, 700 m: 20.XI.1997, H. Thöny leg., genital prep. 29.233 (MWM). 2 ♂, 2 ♀, No additional locality data: E.D. Jones Coll., Brit. Mus. 1919–295 (NHMUK); Rothschild Bequest 1939-1 (NHMUK). 1 3, No specific locality, 750 m: E.D. Jones Coll., Brit. Mus. 1919–295, NHMUK010354581, St Laurent diss.: 8-29-16:5 (NHMUK). Paraná: 1 Å, Campo do Tenente, 850 m: 17.X.1985, [O.] Mielke leg., DZ 15.496 (DZUP). 1 Å, Ponta Grossa: II.1957, at light, No. 1780, Coll. F. Justus Jor (DZUP). 1 2, Castro, 950 m: E.D. Jones leg., E.D. Jones Coll., Brit. Mus. 1919-295 (NHMUK). 1 ♀, Tucunduva [Sengés], 650 m: 17.II.1913, E.D. Jones leg., E.D. Jones Coll., Brit. Mus. 1919–295 (NHMUK). Santa Catarina: 1 3, No additional locality data: F. Hoffmann leg., USNM-Mimal: 2681, St Laurent diss.: 8-22-16:7 (USNM). No state: 1 ♀, "Bresil", Joicey Coll. Brit. Mus. 1925–157 (NHMUK). **PARAGUAY: Cordillera:** 1 ^Q, Pirareta, 25°29'S, 56°56'W, 200 m: 26–31.VIII.2012, [U. Drechsel] leg., genitalia prep. D. Herbin ref H. 1014 (CDH). Amambay: 1 Estancia Oliva, 22°10'S, 56°26'W, 225 m: 23–25.I.2013, [U. Drechsel leg.], (CDH). **Guairá:** 1 9, Villarica: 2.X.1925, F. Schade leg., J.J. Joicey Esq., B.M. 1929–458, St Laurent diss.: 7-7-16:5 (NHMUK). **Paraguarí**: 1 \bigcirc , Sapucay [*recte* Sapucai]: 12.VIII.1904, W. Foster leg., Rothschild Bequest 1939–1 (NHMUK).

Diagnosis. *Tarema rivara* can be differentiated from others in the genus by the pervasive orange to orange-red coloration on the wings in males, and by the faint orange



Figures 1–6. *Tarema rivara* adults, **a** dorsal **b** ventral. I ♂, Lectotype, Brazil, São Paulo (USNM) **2** ♂, Brazil, Maranhão, Feira Nova do Maranhão, Retiro, 480 m [image originally published by Antenor, reused with permision] (CGCM) **3** ♂, Brazil, Minas Gerais, Serra do Cipó à Conceição do Mato Dentro, km 126.3, 1270 m (CDH) **4** ♀, Lectotype of *Tarema macarina* syn. n., Brazil, São Paulo (USNM) **5** ♀, Paraguay, Amambay, Estancia Oliva, 225 m (CDH) **6** ♀, Brazil, Distrito Federal, Estação Florestal, Cabeça do Veado, 1100 m (CNC). Scale bar: 1 cm.

hue on the wings of the females which is concentrated antemedially and/or submarginally. The more similar T. bruna sp. n. is more earthen brown in color than T. rivara, with a longer postmedial lunule that reaches the wing margin without becoming diffuse. In both sexes, T. rivara has a smaller wingspan than T. fuscosa and lacks a distinct dark brown patch of scales at the apex of the forewings. This patch of scales is distinct in T. fuscosa due to the contrast with the light cream color of the postmedial lunule that borders it. Genitalia are quite different between these species, in T. rivara the valves are reduced to small lobes connected to a flattened, spiny accessory, while the valves of T. fuscosa and T. bruna sp. n. are larger and not connected to, or lack the accessory arms. The gnathos of T. rivara is a rectangular plate rather than ovoid as in T. fuscosa, or tapered hexagonal as in T. bruna sp. n., the fingerlike projections at the base of the valves are smaller in T. rivara, and finally the phallus of T. rivara (and T. bruna sp. n.) bears a smooth dorsal projection whereas the same projection is short and spined in T. fuscosa. The key differences in female genitalia are the larger corpus bursae in T. rivara and the trilobed tergite VIII, which is a broad, singular plate in T. fuscosa. The female tergite can usually be examined under a microscrope after brushing off scales, without dissecting the specimen.

Description. Male. Head: As for genus, gray with orange undertone, antenna coloration as for head. Thorax: Coloration similar to that of head, but more orange, appearing hoary due to banded gray scales interspersed amongst orange hued ones, prothorax covered almost entirely in light gray scales. Legs: As for genus but tibia mostly orange. Forewing dorsum: Forewing length: 9–13 mm, avg.: 11.5 mm, wingspan: 21.5-29.0 mm, n=16. Ground color ranging from clay-orange to almost brick red, overall generously shaded by gray scales giving the wing a hoary, layered appearance, especially medially. Postmedial line as for genus but coloration light cream and bordered externally with black scaling continuously along length. Antemedial area with salmon orange hue, medial area always lighter gray compared to orange or reddish submarginal area. Apical half of submarginal area with postmedial lunule, the latter never parallel with margin or postmedial line, either smoothly curved toward margin or angled acutely from postmedial line, becoming diffuse before reaching wing margin, basal half of submarginal area with bright orange or red patch along postmedial line. Discal spot as for genus. Fringe light gray to khaki with lighter and darker patches, including salmon colored scales. Forewing ventrum: Similar to dorsum but usually lighter due to more extensive covering of gray scales; antemedial line absent, postmedial line very faint, bulging outward toward wing margin mesally. Postmedial lunule present as on dorsum, more distinct than postmedial line. Hindwing dorsum: Coloration as for forewing dorsum, following similar patterning but antemedial line absent, postmedial line slightly concave, and submarginal area always orange to more reddish, postmedial lunule absent or just a faint suffusion, coloration usually concentrated somewhat mesally. Hindwing ventrum: Following same pattern as forewing ventrum. Abdomen: As for genus, concolorous with thorax. Genitalia: (Fig. 11) n=12. Vinculum almost circular. Uncus robust, sharp, parrot beak-like when viewed laterally, uncus dorsolaterally flattened. Gnathos a rectangular, elongated plate with slight curvature mesally. Valve short, rounded, weakly sclerotized mesally, strongly affixed to vinculum such that they



Figures 7–10. *Tarema* adults, **a** dorsal **b** ventral. **7** *T. bruna* holotype ♂, Brazil, São Paulo, Alto da Serra [Paranapiacaba] (NHMUK) **8** *T. fuscosa* lectotype ♂, Brazil, Paraná, Castro (NHMUK) **9** *T. fuscosa* ♂, Brazil, São Paulo, Guapiara, Paivinha, 800 m (CGCM) **10** *T. fuscosa* ♀, Brazil, São Paulo, Guapiara, Paivinha, 800 m (CGCM). Scale bar: 1 cm.

do not open fully. Base of valves with pair of small, fingerlike projections, weakly sclerotized knobby area present above fingerlike projections. Valve with more heavily sclerotized, spined accessory arms attached basally to valves, arms originate from transtilla or base of valve (unclear), connected along length of valve. Accessory arms flattened and ventrally spined. Diaphragm with pair of horsetail-like seatal patches consisting of setae of variable length that extend outward over phallus for about three-quarters length of gnathos plate, setae mostly straight. Phallus broad, large, with two elongated accessory projections of variable length, projection superior to phallus smooth, straight, sharply pointed; other projection shorter, narrower, running laterally along phallus originating from within phallus, tip of second projection sharp, but variously bent, size of phallus relative to projections somewhat variable. Vesica balloon-like, slightly scobinate. Female. Head: Similar to male, but broader, antennae and labial palpi smaller. Thorax: As in male, but usually grayer or occasionally more salmon colored. Legs: As in male, though tibial spurs thicker. Forewing dorsum: Forewing length: 10-15 mm, avg.: 12.1 mm, wingspan: 22-30 mm, n=13. Sexual dimorphism strong, wing shape and markings similar to male, but wing broader, coloration usually much more subdued gray and brown, if salmon hue present, generally restricted to antemedial area, though rarely some specimens with salmon hue more pervasive, especially submarginally, otherwise submarginal area solid brown, postmedial lunule usually fainter than in male, sometimes almost absent except for small streak. Fringe with distinctly black portion apically. Forewing ventrum: Similar to forewing ventrum of male, but salmon hue generally absent, veins usually lined with contrasting yellow scales, wing grayer overall but apical region more distinctly solid brown than in male. *Hindwing dorsum*: Coloration and markings as for forewing dorsum, though postmedial lunule absent. Hindwing ventrum: Follows same pattern as forewing ventrum. Abdomen: As in male but slightly more robust, coloration subdued. Tergite VIII as three posteriorly directed lobes, sternite VIII as large, curved, wrinkled mass, covered in thick, branched setae. Genitalia: (Fig. 14) n=5. As for genus, two dissections with large, snake-like structure, apparently a spermatophore based on presence in one dissected male, present within corpus bursae. Papillae anales narrow.

Distribution (Fig. 16). This species has a wide distribution in South America, and although most records come from Brazilian Cerrado in Bahia, Maranhão, Mato Grosso, Goiás, Minas Gerais, and Distrito Federal, *T. rivara* is also known from Brazilian Atlantic Forest in São Paulo, mixed ombrophilous forest in the state of Paraná, and inland forests of Paraguay. We are also aware of one specimen from Santa Catarina, though unfortunately it lacks more detailed data that would allow us to understand the habitat in which it inhabits in this state.

Natural history. Diniz et al. (2013) report *T. rivara* larvae feeding on Vochysiaceae, including the species *Qualea grandiflora*, *Q. multiflora*, and *Q. parviflora*. The same authors describe the larval sack as being constructed from leaves, silk, and feces. These larval sacks are of the less uniformly constructed variety in Mimallonidae, and are thus more similar to those of *Lacosoma* Grote, 1864 and *Cicinnus melsheimeri* (Harris, 1841) rather than highly compacted, rigid structures as seen in *Menevia* Schaus, 1928, *C. packardii* (Grote, 1865), or *C. bahamensis* St Laurent & McCabe, 2016, among others (R. A. St. Laurent pers. obs.).

Remarks. In the original description of *T. rivara*, Schaus (1896) stated: "What I believe to be the Q of this species has the reddish shades replaced by dark brown." Apparently Schaus was well aware of the dimorphism of *T. rivara* at the time of its original description, thus it is somewhat surprising that he described the female of *T. rivara* as a new species, *T. macarina*, over 30 years later (Schaus 1928). We are also

aware of a *T. rivara* female specimen determined as this species and not *T. macarina* at the NHMUK. However, we infer that Schaus changed this earlier determination due to the fact that he had located what he believed to be the male of *T. macarina* in the MNHU as per the following statement from Schaus (1928) in his treatment of *T. macarina* are present in the MNHU with Schaus's handwriting on the "type" labels; however, both specimens are female, as is the lectotype (here designated) in the USNM.

The complete lack of any male specimens correctly determined as *T. macarina* and the unusual disparity of female *T. rivara* led us to believe that these names are synonyms. Many records of *T. rivara* and *T. macarina* are sympatric, and thus support this hypothesis. A close analysis of *T. rivara* females reveals hints of orange coloration antemedially, a coloration abundant in the male specimens, but not in *T. fuscosa*. Given that *T. fuscosa* females can be easily determined as such due to the lack of sexual dimorphism in this species, the disparity of opposite sexes for *T. rivara* and *T. macarina* provides clear evidence that they represent a single, dimorphic species. Furthermore, a dissection of *T. rivara* females reveal the long, snake-like spermatophore seen in male *T. rivara*, unlike the smaller spermatophore of *T. fuscosa*.

Diniz et al. (2013) figure a larva and adults of both sexes of *T. rivara*, correctly figuring the female of *T. rivara*, which again, matches the type specimens of *T. macarina*.

Compared to *T. fuscosa* below, this species seems to primarily be an inhabitant of drier Cerrado but is also present in the more humid Atlantic forest in the states of São Paulo (type locality) and Paraná where it is sympatric with *T. fuscosa*, but apparently not synchronic. In these regions of sympatry, *T. rivara* flies during the summer (October through February), while *T. fuscosa* flies in the winter, though exceptions to these flight times are present in regions where both species are not found together.

Tarema fuscosa Jones, 1908

Figs 8–10, 12, 15, 16

Tarema fuscosa Jones, 1908: 173–174 *Tarema fuscosa*; Schaus 1928: 670, fig. 88i ♂ *Tarema fuscosa*; Gaede 1931 *Tarema fuscosa*; Becker 1996

Type material. Lectotype [here designated], ♂. **BRAZIL: Paraná:** Castro, Paraná, 950 m, E.D. Jones / *Tarema fuscosa* Type D. Jones/ E.D. Jones Coll., Brit. Mus., 1919–295/ BMNH(E) #805428/ SYN-TYPE/ NHMUK010354542/ [genitalia] VIAL NHMUK010402134/ LECTOTYPE male *Tarema fuscosa* designated by St Laurent, Herbin, and C. Mielke, 2017 [handwritten red label]/ (NHMUK, examined). Type locality: Brazil: Paraná: Castro.

Additional specimens examined. (114 3, 4 \bigcirc) BRAZIL: Distrito Federal: 1 3, Estação Florestal, Cabeça do Veado, 1100 m: 17.X.1971, E.G., I. & E.A. Mun-

roe leg., St Laurent diss.: 3-14-16:10 (CNC). 2 3, Parque do Gama: 10.X.1971, E.G. Munroe & K.S. Brown leg., St Laurent diss.: 3-14-16:9 (CNC). Bahia: 35 3, 1 ^Q, env. Camacan (SB), 15°25'S, 39°34'W, 800m: X.2011, XI.2011, XII.2011, H. Thöny leg., genital prep. 29.217 (MWM). 1 Å, env. Camacan (SB), 750 m: IV.2011, H. Thöny leg. (MWM). 1 ♂, 1 ♀, env. Camacan, ca. 750 m: 10–14.XI.2010, Th. Greifenstein leg. (MWM). 2 d, Camacan, 15°24'S, 39°30'W: III.2011, H. Thöny leg. (MWM). 1 Å, Maraú, Fazenda Água Boa, 14°13'S, 39°29'W, 150 m: IV.2011, H. Thöny leg. (MWM). 2 Å, env. Camacan, 15°25'S, 39°34'W, 800 m: X.2012, H. Thöny leg. (MWM). Espírito Santo: 10 3, Santa Leopoldina, Village Tirol, 24°75'S, 40°50'W, 700 m: 22-31.X.1996, 20.II-30.III.1997, V.1997, 15.V.1997, VIII.1997, 15.IX.1997, VI.1998, X.1999, H. Thöny leg. (MWM). 5 Å, Santa Leopoldina, Village Tirol, 700 m: III.1999, VI.1999, X.1999, III.2000, H. Thöny leg. (MWM). 1 Å, Santa Leopoldina, Village Tirol, 20°10'S, 40°33'W, 700 m: XI.2000, H. Thöny leg. (MWM). 9 3, Santa Leopoldina, Boqueirão, 600 m: 15.II.1997, VI.1997, 15.IX.1997, H. Thöny leg. (MWM). 2 👌 No additional locality data: USNM-Mimal: 2729, 2730 (USNM). **Rio de Janeiro** 1 \mathcal{E} , Barreira, Teresópolis: 18.X.1955, Coll. Gagarin (DZUP). 1 &, Petrópolis: 19.XI.1928, Gagarin leg., Coll. Gagarin (DZUP). 4 \mathcal{O} , Parque Nacional do Itatiaia, Lago Azul, 800 m: 20–22. VI.1955, R. Barros, D. Albuquerque, & Pearson leg. (NHMUK). 1 3, Itatiaia, Horto Florestal (=horticultural garden), 800 m: 10.VIII.1953, Travassos & Pearson leg., Brit. Mus. 1962-112 (NHMUK). 1 3, No additional locality data: Coll. Thalenhorst, Coll. Staudinger (MNHU). São Paulo: 9 3, 1 2, Guapiara, Paivinha, 800 m: 5–6.XI.2004 (1 Å), 24–27.VII.2005 (2 Å), 18.VII.2007 (1 Å), 11.VIII.2007 (3 ♂, 1 ♀), 12.IX.2007 (2 ♂), C. Mielke leg., Coll. C. Mielke 25.772, 26.433, 26.535, 26.537, 26.680, 26.955, 26.977, 27.060, 28.074, 28.106 (CGCM). 1 d, Embu-Guaçu: Sitío, L. Travassos F. leg. (CDH). 4 ♂, Apiaí, 750 m: 8.VIII.2006 (2 ♂), 7.IX.2007 (2 Å), C. Mielke leg. (CDH). 1 Å, Ypiranga [recte Ipiranga, São Paulo]: V.1924, R. Spitz, Rothschild Bequest, BM 1939-1 (NHMUK). 2 3, Alto da Serra [Paranapiacaba]: VI.1926, VII.1928, R. Spitz leg., Rothschild Bequest, BM 1939-1 (NHMUK). 2 3, Salesópolis, Boracea [Boracéia], 850 m: 26.VIII.1949, Travassos, Travassos Filho, Pearson, & Rabello leg., Brit. Mus. 1962-112 (NHMUK); 23–26.V.1952, Pearson leg., 528, USNM-Mimal: 2424 (USNM). Paraná: 2 3, Ponta Grossa: IV.1948, No. 1552, Coll. F. Justus Jor (DZUP). 1 3, Tijucas do Sul [recte Guaratuba], Castelhanos, 20°26'S, 54°39'W [coordinates likely incorrect], 500 m: 1.VI.1999, H. Thöny leg. (MWM). Santa Catarina: 1 3, São Bento do Sul, Rio Vermelho, Road to Rio Natal, 26°20'00.77"S, 49°18'28.25"W, 503 m: no date, Rank leg., genitalia prep. D. Herbin ref H. 1013 (CDH). 8 ♂, São Bento do Sul, Rio Natal, 850 m: VI.1998, VII.1998, VIII.1998, IX.1998, X.1998, VII.1999, H. Thöny leg. (MWM). 1 Å, Blumenau: E. Wenzel S.G. leg. (MNHU). 1 Å, No additional locality data: St Laurent diss.: 2-26-16:7 (CUIC). 1 🖧, No additional locality data/illegible: Dognin Coll., 269, USNM-Mimal: 2678 (USNM). No state: 1 9, "Brasil", Mssn. G. (MNHU).

Diagnosis. Compared to the other two species in the genus, *T. fuscosa* is easily recognized by the very dark brown to nearly black ground color, with a dark patch at



Figures 11–13. *Tarema* male genitalia, **a** ventral **b** lateral **c** phallus lateral. 11 *T. rivara*, Brazil, Distrito Federal, Estação Florestal, Cabeça do Veado, 1100 m, St Laurent diss.: 3-14-16:7 (CNC) 12 *T. fuscosa*, Brazil, Santa Catarina, St Laurent diss.: 2-26-16:7 (CUIC) 13 *T. bruna* holotype, Brazil, São Paulo, Alto da Serra [Paranapiacaba], NHMUK010402168 genitalia prep. [13b horizontally flipped] (NHMUK). Scale bar: 1 mm.

the apex of the forewings surrounded by pale cream markings. The male genitalia is unique in having heavily sclerotized, spiny, club-like vincular arms that are not connected lengthwise to the valves. This is also the only species in the genus with an ovoid gnathos plate. Additionally, the dorsal projection of the phallus is short and spiny, not smooth as in the other two species. The female genitalia have a smaller corpus bursae than in *T. rivara* and a broad singular tergite VIII, as opposed to the trilobed corresponding tergite of *T. rivara*.

Description. Male. Head: As for genus, gravish brown; antenna coloration usually as for head, though pectination darker brown than flagellum; labial palpus reduced, apparently three segmented, but third segment much reduced. Thorax: Coloration similar to that of head, though appearing hoary due to banded brown and pale khaki to cream colored scales, prothorax with more heavily concentrated khaki or cream colored scales. Legs: Coloration as for thorax, though femur and tibia darker brown, tarsus lighter, cream colored. Forewing dorsum: Forewing length: 11-16 mm, avg.: 13.8 mm, wingspan: 22-31 mm, n=17. Ground color ranging from pale reddish brown to nearly black, overall generously shaded by cream colored scales giving the wing a hoary, layered appearance. Postmedial line as for genus, but coloration light cream not bordered externally with black except for darkened region concentrated near to tornus. Ante- and median areas usually concolorous, submarginal area with reduced cream colored scales, appearing much darker red-brown, brown, to nearly black. Apical half of submarginal area with postmedial lunule, the latter either slightly curved toward wing margin, or nearly parallel with margin, especially along apical half of lunule, basal half of submarginal area with darker red-brown or black patch along postmedial line, apex with darker brown patch outlined by white lunule and cream colored patch immediately beneath darker apical patch. Costa appearing lighter than most of wing due to heavy concentration of cream or khaki colored scales. Discal spot as for genus. Fringe light gray to khaki with lighter and darker patches. Forewing ventrum: Similar to dorsum but usually lighter due to more extensive covering of cream and khaki scales, some of which appear yellowish, apical half of submarginal area darker than that of dorsum, except where interrupted by lighter band below apical patch; antemedial line always absent, postmedial line never straight, angled outward toward wing margin mesally. Hindwing dorsum: Coloration as for forewing dorsum, following similar patterning but antemedial line absent, postmedial line slightly concave, and submarginal area more uniformly dark reddish brown, dark brown, or black, always with contrasting orange patch of scales mesally. *Hindwing ventrum*: Following same pattern as forewing ventrum, postmedial lunule reduced to straight, faint streak. Abdomen: As for genus, concolorous with thorax. Genitalia: (Fig. 12) n=7. Vinculum somewhat ovoid, ventrally with reduced saccus. Uncus robust but reduced to slightly triangular stump with slight bidentation terminally. Gnathos an ovoid, elongated, mesally indented plate. Valves short, rounded, weakly sclerotized mesally. Base of valves with pair of long, fingerlike projections. Valves with more heavily sclerotized, spined accessory arms connected to vinculum. Accessory arms narrow and tube-like, terminating in enlarged club end with spines concentrated terminally or present along entire length of arm. Diaphragm with pair of horsetail-like setal patches consisting of very



Figures 14, 15. *Tarema* female genitalia, **a** ventral **b** dorsal. **14** *T. rivara*, Brazil, Distrito Federal, Estação Florestal, Cabeça do Veado, 1100 m, St Laurent diss.: 3-14-16:8 (CNC) **15** *T. fuscosa*, Brazil, São Paulo, Guapiara, Paivinha, 800 m, C. Mielke genitalia prep. CGCM 26.955 (CGCM). Scale bar: 1 mm.

long setae that extend outward over phallus below gnathos plate, setae curled backward at end. Phallus broad, large, widened distally, with two elongated accessory projections, one projection more variable in length, superior to phallus, irregular, pointed, spined; other projection longer, narrower, running laterally along phallus originating from within phallus, tip of second projection sharp, angled backward. Vesica balloonlike, slightly scobinate, separated into fairly distinct diverticula. **Female.** *Head*: Similar to male, but broader, antennae and labial palpi smaller. *Thorax*: As in male, though cream colored scales may be a bit yellower. *Legs*: As in male. *Forewing dorsum*: Forewing length: 17.0–18.5 mm, avg.: 17.5 mm, wingspan: 31.0–34.5 mm, n=3. Sexual dimorphism reduced, as in male but slightly broader, postmedial line usually more noticeably bent. *Forewing ventrum*: Similar to forewing ventrum of male, but veins usually lined with yellow scales. *Hindwing dorsum*: Coloration and markings as for forewing dorsum, orange mesal patch present in male very faint in female. *Hindwing ventrum*: Follows same pattern as forewing ventrum. *Abdomen*: As in male but slightly more robust. Tergite VIII as single broad plate, sternite VIII as wrinkled mass consisting of two pieces, covered in thick, branched setae. *Genitalia*: (Fig. 15) n=1. As for genus but particularly stout, robust. Corpus bursae somewhat reduced in size.

Distribution (Fig. 16). Although we report a few records from central Brazil (Distrito Federal), most records of this species are restricted to the Brazilian Atlantic Forest in the states of Bahia, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, and Santa Catarina. See remarks for potential issues pertaining to the Cerrado records.

Remarks. As mentioned in the remarks of *T. rivara*, *T. fuscosa* shows a trend in distribution where it is more commonly encountered in humid Atlantic Forest than elsewhere in Brazil. Although we do have some records of *T. fuscosa* from Distrito Federal, there is a possibility that they were mislabeled. Out of over 100 examined specimens of *T. fuscosa*, the only Cerrado material was from the same collector, who also collected in regions where *T. fuscosa* would be more expected, such as the Brazilian states of Paraná and São Paulo. We could not locate any *T. fuscosa* specimens from the Cerrado among the Mimallonidae specimens collected there in the USNM, NHMUK, or CPAC.

Prior to this work, the female of *T. fuscosa* was not reported in the literature; therefore we describe and figure it here for the first time.

Tarema bruna sp. n.

http://zoobank.org/F649B060-A03F-4CD2-BF63-F35071A6B9A1 Figs 7, 13, 16

Type material. Holotype, *A*. **BRAZIL: São Paulo:** Alto de [*recte* da] Serra, [Paranapiacaba, Santo André], São Paulo, November, 1922. (R. Spitz [leg.])./ Rothschild Bequest BM 1939-1/ [genitalia] VIAL NHMUK010402168 / NHMUK010318286/ HOLOTYPE male *Tarema bruna* St Laurent, Herbin, & C. Mielke, 2017 [handwritten red label]/ (NHMUK). Type locality: Brazil: São Paulo: Paranapiacaba.

Diagnosis. Externally this species is most similar to *T. rivara*, but can be easily distinguished by the earthen brown and clay brown coloration rather than orange or red-orange in *T. rivara*. Additionally, in *T. bruna* sp. n. the postmedial lunule reaches the wing margin without becoming highly diffuse, and is parallel to the wing margin for its entire length until bending outward. The male genitalia is unique in the extreme reduction of the heavily sclerotized vincular/valve arms, present as a small extension at



Figure 16. Known distribution of *Tarema*. Numbers superimposed on the map refer to the following annotations: I Outlier data point for *T. fuscosa* in Brazil, Distrito Federal may be erroneous (see remarks for that species). **2** The point where all three symbols are found on top of each other is a single locality, that being Brazil, São Paulo, Paranapiacaba. **3** Data point for *T. rivara* in Brazil, Santa Catarina is placed at the center of the state because no detailed locality data is available for this species from Santa Catarina.

the base of the valves. The phallus is also unique in the thinness of the dorsal projection, which is smooth as in *T. rivara*, not spined as in *T. fuscosa*.

Description. Male. *Head*: As for genus, coloration earthen brown. *Thorax*: Coloration similar to that of head, appearing hoary due to banded gray and cream colored scales interspersed amongst brown ones, prothorax covered almost entirely in these lighter scales. *Legs*: As for genus. *Forewing dorsum*: Forewing length: 13 mm, wingspan: 26 mm, n=1. Ground color a mixture of earthen brown tones and clay-brown, overall generously shaded by cream colored scales giving the wing a hoary, layered appearance, especially medially. Antemedial line faint, brown, wavy. Postmedial line as for genus but wavier, coloration light cream, not bordered by darker scales except for a small external portion above the tornus. Antemedial area with salmon orange hue, medial area with postmedial lunule, the latter parallel with margin, then smoothly curved toward margin reaching wing margin without becoming diffuse, basal half of submarginal area darkest brown, apical portion external to lunule lighter brown. Discal spot as for genus. Fringe light cream with lighter and darker patches. *Forewing ventrum*: Similar

to dorsum but lighter due to more extensive covering of gray and cream colored scales; antemedial line absent, postmedial line faint, bulging outward toward wing margin mesally. Postmedial lunule present as on dorsum, more distinct than postmedial line. Hindwing dorsum: Coloration as for forewing dorsum, following similar patterning but antemedial line absent, postmedial line straight and faintly outlined by black scales, postmedial lunule very faint. Hindwing ventrum: Following same pattern as forewing ventrum, though discal mark very dark, well defined as black oval. Abdomen: As for genus, concolorous with thorax. Genitalia: (Fig. 13) n=1. Vinculum somewhat ovoid, ventrally with reduced saccus. Uncus robust but reduced to slightly triangular stump. Gnathos a tapered, elongated, hexagonal plate. Valves short, rounded. Base of valves with pair of long, fingerlike projections. Slightly more strongly sclerotized, small projections emanate from base of valves. Diaphragm with pair of horsetail-like setal patches consisting of very long setae that extend outward over phallus below gnathos plate, setae curled backward at end. Phallus broad, large, widened distally, with two elongated accessory projections, one projection superior to phallus, smooth, narrow, pointed, other projection longer, narrower, running laterally along phallus originating from within phallus, tip of second projection sharp, angled forward. Vesica balloonlike. Female. Unknown.

Distribution (Fig. 16). This new species is so far known only from the type locality at Paranapiacaba (previously known as Alto da Serra, a train station), São Paulo, Brazil. According to GoogleEarth, the elevation at this locality is approximately 700 m.

Etymology. This species is named for its brown (*bruna* Latin) coloration, which largely distinguishes it from the red or orange *T. rivara* and the black, gray, and cream-colored *T. fuscosa*.

Remarks. The discovery of a unique new species of *Tarema* from eastern São Paulo is surprising because this is a relatively well-surveyed region of Brazil (R. A. St. Laurent pers. obs.). Both *T. rivara* and *T. fuscosa* have been collected from the type locality of *T. bruna* (NHMUK), though at different times of the year. As previously mentioned in the remarks of *T. rivara*, that species is primarily a summer species, with records from Paranapiacaba in January, while *T. fuscosa* has only been collected there in the winter (June and July). More material of *T. bruna* will be needed to verify its voltinism.

An issue is presented by the fact that the type localities of *T. rivara, T. macarina,* and *T. bruna* are all from São Paulo, Brazil with specific type locality information from within the state only available for *T. bruna*. Therefore, the possibility arose that the name *T. macarina* could be wrongfully synonymized with *T. rivara* if indeed it is conspecific with the new species described herein. However, we consider the apparent rarity of *T. bruna* combined with the genitalia similarities between the lectotype of *T. macarina* and other *T. rivara* females dissected from São Paulo and elsewhere, including Cerrado regions, more suggestive that the name *T. macarina* does in fact represent the female of *T. rivara*, a much more commonly collected and widespread species. If future evidence were found to contradict our hypothesis, *T. bruna* would then be a junior and subjective synonym of *T. macarina*. It is therefore necessary that more material of *T. bruna* be found or collected, particularly in aim to locate the female of this species.

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RESEARCH ARTICLE



Discovery of a new species of hermit crab of the genus Pylopaguropsis Alcock, 1905 from the Caribbean: "den commensal" or "cleaner"? (Crustacea, Anomura, Paguridae)

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Abstract

A new secretive, yet brightly colored hermit crab species of the family Paguridae, Pylopaguropsis mollymullerae sp. n., is fully described based on specimens from the reefs of Bonaire, Lesser Antilles, southern Caribbean Sea. Populations of this new species were discovered and photographed in the Bonaire National Marine Park under a large coral ledge, at a depth of 13.7 m, living in crevices known by scuba divers to serve as den to a pair of "flaming reef lobsters" Enoplometopus antillensis, or a "broad banded moray" Channomuraena vittata. This new species is only the second species of Pylopaguropsis Alcock, 1905 known from the western Atlantic, the 20th named worldwide, and belongs in the teevana group of species of the genus. It is remarkably similar, and herein considered geminate, to the tropical eastern Pacific congener, P. teevana (Boone, 1932), the two being characterized and uniquely different from all other species of the genus, by the striking and deeply excavated, scoop-like ventral surface of the chela of the right cheliped. Minor differences separate this new species from *P. teevana* in the relative length of the antennal acicles (exceeding the corneas versus not exceeding the corneas in *P. teevana*); dorsal armature of the right chela (smooth or with scattered minute tubercles versus with numerous small tubercles in P. teevana); surface shape of the lateral face of the dactyl of right percopod 3 (evenly convex versus flattened in P. teevana); and coloration (red bright red stripes versus brown stripes in P. teevana). The highly visible color pattern of bright red stripes on white background typical of decapods known to have cleaning symbioses with fish, dense setation on the flagella of the antennae, and preference for a crevicular habitat, combined with brief

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in situ nocturnal observations, suggests the possibility that *P. mollymullerae* sp. n. engages in "cleaner" activities or functions as a "den commensal" with moray eels. The morphology and possible meaning of the observed behavior is discussed. A tabular summary of the distribution, habitat, and published information on all species of *Pylopaguropsis* is presented. Supplemental photographs and a video of live *P. mollymullerae* **sp. n.** are included.

Keywords

Bonaire, Caribbean, "cleaner", "den commensal", hermit crab, new species, Paguridae, Pylopaguropsis

Introduction

The genus Pylopaguropsis Alcock, 1905, currently includes a group of 19 morphologically striking species that typically live in hard bottoms on or near coral reefs, and at depths ranging from the subtidal to the upper continental slope (0–610 m). One additional species remains undescribed (Arima 2014, Komai pers. comm.). Most species are distributed in the Indo-West Pacific region to Central and South Pacific as far east as Easter Island, with only two species known so far from elsewhere: P. teevana (Boone, 1932), from the eastern tropical Pacific, and *P. atlantica* Wass, 1963, from the tropical western Atlantic. In addition to their distinctive coloration patterns that typically consist of dark stripes or brightly colored appendages (Asakura 2000, Asakura and Paulay 2003, Komai and Osawa 2004, Osawa and Okuno 2007, McLaughlin et al. 2010, Asakura 2010, Rahayu and Komai 2013, Arima 2014), species of this genus stand out by having a characteristically massive right cheliped, with a large operculate or semioperculate chela, and a dactyl that articulates obliquely with the palm. Other defining diagnostic characters include 13 pairs of biserial phyllobranchiate gills; crista dentata of third maxilliped with accessory tooth; male with unpaired left pleopods 3-5; and females with paired pleopods 1 modified as gonopods, and unpaired left pleopods 2-5 (for full diagnosis see Asakura 2000: 72, and McLaughlin 2003: 126).

The taxonomic history of *Pylopaguropsis* was discussed by McLaughlin and Haig (1989) in a review of this genus which they divided into the *magnimanus* group (species with dactyls of left and right pereopods 3 dissimilar), and the *teevana* group (species with dactyls of left and right pereopods 3 similar). Briefly, this genus was originally described by Alcock (1905) as monotypic, to accommodate *P. magnimanus* Henderson, 1896, a species that Alcock found to be related to, but that differed significantly from species of *Pylopagurus* A. Milne Edwards & Bouvier, 1891. A second species was added to this genus by Forest (1955), who concluded that *Eupagurus* (= *Pagurus*) *zebra* Henderson, 1896 belonged in *Pylopaguropsis*. Subsequently, a third species and first from the Atlantic, was added, *P. atlantica* Wass, 1963. McLaughlin and Haig (1989) found that the monotypic *Galapagurus* Boone, 1932 agreed with the more senior *Pylopaguropsis*, proceeded to synonymize the two genera, and thus changed the genus of its single eastern Pacific species, *G. teevanus* Boone, 1932, as well as the spelling of Boone's species name to *teevana* in order to agree with the feminine *Pylopaguropsis*. McLaughlin and Haig also added seven new species, all from the Indo-West to the

Central or South Pacific islands, bringing to 11 the total number of species of *Pylop-aguropsis* known at the time. In a review of Japanese species of *Pylopaguropsis*, Asakura (2000) described two more new species from Japan, and later Asakura and Paulay (2003) added yet another new species from French Polynesia. Komai and Osawa (2004), and Osawa and Okuno (2007) each added one more new species from Japanese waters. Finally, three more new species were described from the Philippines, one by Asakura (2010), two by Rahayu and Komai (2013), and as previously mentioned, yet another one remains undescribed (Arima 2014). Although all known species of *Pylopaguropsis* are now well documented from a taxonomic and morphological point of view, their biology and ecology is at best poorly known.

Recent underwater photographs and video obtained using scuba by Ms Ellen Muller at several dive sites in the National Marine Park of the southern Caribbean island of Bonaire, Lesser Antilles, revealed the presence of a small (a few millimeters in size), intriguing and brightly colored red-striped pagurid hermit crab that appeared to belong to Pylopaguropsis. The specimens in the photographs, however, could not be matched using images alone, to any of the known species of the genus from the western tropical Atlantic, and seemed to represent and undescribed species. A specimen of this hermit crab was first photographed inadvertently alongside an individual of the "flaming reef lobster", Enoplometopus antillensis (Lütken, 1865), sighted while observing reef invertebrates that aggregate in crevices under a large coral ledge, and subsequently additional specimens of this hermit crab were again photographed in a nearby crevice inhabited by a "broad banded moray" Channomuraena vittata (Richardson, 1845). In order to study in detail and determine the identity of this unusual hermit crab, permits were obtained from the Government of the Island Territory of Bonaire to collect a few specimens and ship them for study to the National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM). Close examination of the specimens collected confirmed not only that indeed they are of a new species of *Pylopaguropsis*, but also that this new species is remarkably similar and undoubtedly more closely related, to the single eastern tropical Pacific member of this genus, P. teevana. Furthermore, the morphological characteristics, color pattern, and observed reclusive behavior in proximity to the moray eel, suggest the possibility that this new species might function in some capacity as a "cleaner", or perhaps is ecologically associated as a commensal with the moray eel. This new species is herein fully described and illustrated, including color photographs, and video of live specimens in the habitat where it was found. A list of all known species of Pylopaguropsis from the world is included, with a summary of their geographic distributions, depth ranges, and recorded habitats (Table 1).

Materials and methods

The holotype and paratypes of the new species described herein are deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington DC (USNM). The specimens were collected by hand, using scuba, and

| orld, with their general geographic and bathymetric distribution. CNP: Central North Pacific; EP: | d Sea; SEP: southeastern Pacific; WA: western Atlantic; WP: western Pacific. |
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| e world, with their β | : Red Sea; SEP: sou |
| Alcock, 1905 from th | Indo-West Pacific; R |
| ies of Pylopaguropsis 1 | ndian Ocean; IWP: I |
| Table 1. List of spec | eastern Pacific; IO: I |

| Genus/species | Geographic distribution | Depth range (m) | Habitat | References |
|---|--|--------------------|--|---|
| Pylopaguropsis atlantica Wass, 1963 | WA: southeast Florida, USA; Straits of Florida; Colombia; Suriname | 84–200 | coral, rock | Wass 1963, Bullis and Thompson 1965, McLaughlin and Haig 1989, Campos et al. 2005 |
| Pylopaguropsis bellula Osawa & Okuno, 2007 | WP: Ryukyus Islands, Japan | 18–30 | submarine caves or dark crevices on fore reef slopes | Osawa and Okuno 2007, Arima 2014 |
| Pylopaguropsis fimbriata McLaughlin & Haig, 1989 | IWP: Okinawa, Japan; Guam; east Malaysia; Indonesia | 10–15 | hard bottom, coral, dark crevices on rocky walls | McLaughlin and Haig 1989, Asakura 2000, Arima 2014 |
| Pylopaguropsis furusei Asakura, 2000 | WP: Ogasawara Islands, Japan | 3–30 | hard bottom, coral, crevices on rocky walls | Asakura 2000, Arima 2014 |
| Pylopaguropsis garciai McLaughlin & Haig, 1989 | SEP: Easter Island, Chile | 40 | probably coral or hard bottom | McLaughlin and Haig 1989 |
| Pylopaguropsis granulata Asakura, 2000 | WP: Okinawa, Japan | 10 | coral, hard bottom, crevices | Asakura 2000, Arima 2014 |
| Pylopaguropsis keijii McLaughlin & Haig, 1989 | CNP; IWP: Hawaii; Okinawa, Japan; Guam and West Caroline Islands; Maldives; Zanzibar | 10-17 | coral (<i>Pocillopora</i> <i>meandrina</i>), crevices on rocky walls | McLaughlin and Haig 1989, Asakura 2000, Arima 2014 |
| Pylopaguropsis laevispinosa McLaughlin & Haig, 1989 | WP: Okinawa, Ryukyus Islands, Japan | 3-70.1 | probably coral or hard bottom | McLaughlin and Haig 1989, Komai and Osawa 2004 |
| Pylopaguropsis lemaitrei Asakura & Paulay, 2003 | SP: Marquesas and Tuamotu Archipelago, French Polynesia | 4.6–12.2 | under rocks on outer reef slope | Asakura and Paulay 2003 |
| Pylopaguropsis lewinsohni McLaughlin & Haig, 1989 | RS: Gulf Aqaba | 0-10 | coral, dark crevices on rocky walls | McLaughlin and Haig 1989, Arima 2014 |
| Pylopaguropsis magnimanus (Henderson, 1896) | IO: Bay of Bengal to Sri Lanka; northern Arabian Sea | 119–397 | soft bottom (mud) | Alcock 1902, McLaughlin and Haig 1989 |
| Pylopaguropsis mollymullerae sp. n. | WA: Bonaire, southern Caribbean | 11.6–13.7 | in crevices under coral ledges | This report |
| Pylopaguropsis pustulosa McLaughlin & Haig, 1989 | IO: Somalia | 90 | unknown | McLaughlin and Haig 1989 |
| Pylopaguropsis pygmaeus Rahayu & Komai, 2013 | WP: Philippines | 80-128 | sand on echinoderms bed | Rahayu and Komai 2013 |
| Pylopaguropsis rahayuae Asakura, 2010 | WP: Philippines | 4–30 | reef wall with cave, reef platform and slope | Asakura 2010 |
| Pylopaguropsis similis Rahayu & Komai, 2013 | WP: Philippines | 100 | unknown | Rahayu and Komai 2013 |

| Genus/species | Geographic distribution | Depth range (m) | Habitat | References |
|---|---|--------------------|---|---|
| Pylopaguropsis speciosa McLaughlin & Haig, 1989 | WP: Okinawa, Japan | 10-610 | coral or hard bottom, crevices | McLaughlin and Haig 1989, Asakura 2000, Arima 2014 |
| Pylopaguropsis teevana (Boone, 1932) | EP: Colombia; Ecuador; Galapagos Islands | 0.3–9.7 | probably coral or hard bottom | Boone 1932, McLaughlin and Haig 1989 |
| Pylepaguropsis vicina Komai & Osawa, 2004 | IWP: Kii Peninsula and Nansei Islands, Japan; Banda Sea, Indonesia | 50-167 | sponge and coral bottom, seamount | McLaughlin and Haig 1989, Komai and Osawa 2004 |
| Pylopaguropsis zebra (Henderson, 1893) | IWP: Japan; Korea Strait; East China Sea; Indonesia; Australia; South Africa | 50-180 | coral or hard bottom, dark crevices on rocky walls | McLaughlin and Haig 1989, Asakura 2000, Arima 2014 |
| Pylopaguropsis sp. (undescribed) | IWP: Japan | 72 | coral, rocky substrate | Arima 2014 |

during late afternoon or night dives, by E Muller. General terminology follows that used by McLaughlin and Haig (1989), Lemaitre (1995), and McLaughlin (2003). Pereopods and pleopods are indicated with a number, except for the chelipeds, which correspond to pereopods 1. Measurement indicated for the specimens are of shield length, measured in millimeters (mm), taken from the midpoint of rostral lobe to midpoint of posterior margin of shield.

Results

Systematic account

Family Paguridae Latreille, 1802

Pylopaguropsis mollymullerae sp. n.

http://zoobank.org/329C796C-EC46-4A85-A9EB-3FD21298A4BC Figs 1–6, Table 1, Suppl. materials 1–3 (color photographs, video)

Type material. Holotype: male 2.4 mm, "Something Special", central W coast of Bonaire, 12°09'46.0"N, 68°17'08.6"W, 11.6 m, 17 December 2015, sand/rubble under coral ledge, night dive, coll. E Muller (USNM 1291987).

Paratypes (all same locality, habitat, and collector, as holotype): 1 male 1.8 mm (USNM 1291989), 1 male 2.2 mm (USNM 1291988), 13.7 m; 1 male 0.9 mm, 1 female 1.5 mm, 27 January 2016 (USNM 1292072); 1 ovigerous female 1.9 mm, 28 January 2016 (USNM 1292073).

Non-type specimens (not collected) photographed in situ. 5 sex undertermined (Fig. 6C, E, and Suppl. material 3), "Something Special", 12°09'46.0"N, 68°17'08.6"W, ~10 m, night dive; 1 ovigerous female, 1 sex undetermined (color photos in Suppl. materials 1–2), "Front Porch", E Muller night dives 4125 095a and 4125 156z2, central W coast of Bonaire, 12°09'55.2"N, 68°17'12.0"W, night dive, 12.2 m, 17 September 2016.

Description. Shield (Fig. 1A) about as long as broad, weakly convex, well calcified, smooth except for weak depression behind each lateral projection; naked except for few short rows or tufts of fine setae. Rostrum acutely triangular, ending in small, sharp spine, and extending well beyond distal level of lateral projections. Anterior margins between rostrum and lateral projections concave. Lateral projections broadly triangular, ending in small, sharp spine. Anterolateral margins sloping. Accessory portions narrow, well calcified, fused to shield. Branchiostegite membranous; anterior margin rounded, setose.

Ocular peduncles moderately long, about 0.8 as long as shield, slightly inflated basally and tapering to base of corneas, with dorsodistal row of long setae; corneas weakly dilated. Ocular acicles subtriangular, with strong terminal spine; separated basally by less than basal width of one acicle.


Figure 1. *Pylopaguropsis mollymullerae* sp. n., holotype male 2.4 mm, Bonaire (USNM 1291987). **A** shield, cephalic appendages, dorsal **B** left antennal flagellum, dorsal **C** propodus and dactyl of righ pereopod 4, lateral **D** sternum and coxae of chelipeds and pereopods 2–5, ventral **E** telson, dorsal. Scale bars 1 mm for **A**, **B**, **D**; 0.5 mm for **C**, **E**.

Antennules (Fig. 1A) exceeding distal margins of corneas by 0.5–0.6 length of ultimate segment. Ultimate segment with few long dorsodistal setae. Penultimate and basal segments naked or with scattered short setae. Basal segment with laterodistal spine. Ventral flagellum with five or six articles.

Antennal peduncles (Fig. 1A) exceeding distal margins of corneas by 0.2 length of fifth segment. Fifth and fourth segments unarmed except for sparse setae. Third seg-



Figure 2. *Pylopaguropsis mollymullerae* sp. n., paratype male 1.8 mm, Bonaire (USNM 1291989). Left mouthparts, internal: **A** mandible **B** maxillule **C** maxilla **D** first maxilliped **E** second maxilliped **F** third maxilliped. Scale bar 0.5 mm.

ment with strong ventromesial spine. Second segment naked or with scattered short setae; dorsolateral distal angle strongly produced, ending in small spine at tip; dorsomesial distal angle with small spine. First segment with small spine on lateral face distally. Acicle broadly curved outward, slightly exceeding distal margin of cornea, terminating in strong spine; with dorsomesial row of long setae. Flagellum (Fig. 1B) slightly exceeding extended right cheliped, densely setose, with setae >1 - 8 flagellar articles in length.

Mandible (Fig. 2A) with edge of incisor process armed with three blunt calcareous teeth. Maxillule (Fig. 2B) with endopod slender, internal lobe with one long bristle.



Figure 3. *Pylopaguropsis mollymullerae* sp. n., holotype male 2.4 mm, Bonaire (USNM 1291987). **A** right cheliped, dorsal **B** dactyl and fixed finger of same, ventral **C** left cheliped, dorsal **D** same, lateral **E** same mesial. Scale bar 1 mm.

Maxilla (Fig. 2C) with endopodite slightly exceeding distal end of scaphognathite. First maxilliped (Fig. 2D) with endopodite not exceeding distal endite. Second maxilliped (Fig. 2E) without distinguishing characters. Third maxilliped (Fig. 2F) with merus armed with small blunt, dorsodistal spine; ischium with crista dentata consisting of about 13 small, subequal corneous teeth, two larger basal teeth, and one accessory tooth; basis with two sharp teeth on mesial margin; coxa with small distomesial spine. Sternite IX (of third maxillipeds) with small, sharp spine on each side of midline.

Chelipeds markedly asymmetrical. Right cheliped (Fig. 3A, B, 4A-E) massive, nearly naked, with chela operculate, ovate; fingers curving ventrally, broad basally and terminating in small, inwardly curved, corneous claw; cutting edges (Fig. Fig. 3B) uneven, minutely and sharply denticulate, fixed finger with large subtriangular tooth medially. Dactyl 0.8 times as long as palm, set very obliquely relative to longitudinal axis of chela; dorsoventrally flattened; dorsal surface weakly convex, unarmed except for scattered short setae; dorsomesial margin sharp, plate-like; ventral surface moderately concave, with longitudinal ridge parallel to mesial margin. Palm and fixed finger weakly convex, nearly naked or with scattered short setae; dorsal surfaces with scattered small, low tubercles on lateral half, smooth except for shallow longitudinal groove on mesial half; lateral margin sharply defined by minute denticles; mesial face strongly produced ventrally, ventromesial margin rounded; ventral surface smooth, deeply excavated, mesial face and lateral margin forming distinct, semi-cylindrical scoop-like surface. Carpus subtrapezoidal, naked; dorsal surface with dorsolateral and dorsomesial ridges marked by minute, sharp spines; lateral face sloping; ventrolateral margin unarmed; mesial face strongly sloping, distomesial margin with row of minute spines; ventral surface convex, smooth. Merus subtriangular, smooth; ventromesial margin minutely spinulose proximally except for row of moderately strong spines distally; ventrolateral margin unarmed. Ischium unarmed except for ventromesial row of setae.

Left cheliped (Fig. 3C–E) slender, reaching nearly to base of dactyl of right cheliped. Fingers each terminating in short, inwardly curved corneous claw; dactyl shorter than palm, cutting edge with row of closely set, minute corneous spinules, mesial face with few tufts of long setae; fixed finger with tufts of setae on lateral face, cutting edge with row of small, well-spaced calcareous teeth interspersed with fused corneous spinules. Palm smooth, naked except for tufts of long setae mostly on dorsomesial face. Carpus subtriangular; dorsal margin with row of tufts of setae, lacking spines. Merus nearly naked except for scattered tufts of setae; ventrolateral margin with row of few well-spaced spines usually on distal half; ventromesial margin unarmed. Ischium unarmed except for ventromesial row of setae.

Ambulatory legs or percopods 2 and 3 (Fig. 5A–F) not significantly different left from right; meri to dactyls with lateral faces evenly convex, with long setae or tufts of setae on dorsal margins. Dactyl nearly straight, about 1.8 times as long as propodi, terminating in sharp corneous claw; dorsomesial margin with row of minute corneous spinules on distal half; ventromesial margin with row of 6–8 corneous spinules. Propodus slightly arched. Carpi each with small dorsodistal spine. Merus unarmed. Ischium with row of setae on ventral margins.

Sternite XII (of pereopod 3; Fig. 1D) with anterior lobe weakly rounded, setose.

Pereopod 4 (Fig. 1C) semichelate. Dactyl subtriangular, terminating in sharp, corneous claw, lacking preungual process; with ventrolateral row of minute, fused corneous teeth. Propodal rasp consisting of one distal row of lanceolate scales.

Pereopod 5 chelate. Propodal rasp occupying nearly half of lateral face of propodus.



Figure 4. *Pylopaguropsis mollymullerae* sp. n., right cheliped. **A** ventral, holotype male 2.4 mm, Bonaire (USNM 1291987) **B–E** dorsal (**B**), dorsomesial (**C**), ventral (**D**), ventromesial (**E**), paratype male 1.8 mm, Bonaire (USNM 1291989). Scale bars 1 mm.

Sternite XIV (pereopod 5) subdivided anteriorly into two subrectangular, setose lobes (Fig. 1D).

Uropods strongly asymmetrical. Telson (Fig. 1E) with distinct lateral indentations separating anterior and posterior lobes; posterior lobes subtriangular, nearly symmetrical, separated by deep, narrow median cleft, distal margins armed with row of small, sharp spines and blunt laterodistal angle.

Male with paired gonopores (Fig. 1D), and unpaired left pleopods 2–5. Female with paired pleopods 1 modified as gonopods, and unpaired left pleopods 2–5 (pleopod 5 not ovigerous).

Coloration (Fig. 6A, B, Suppl. materials 1–3). General background color white with bright red stripes. Shield white with two pairs of oblique red stripes on each side of anterior half. Ocular peduncles white with two red stripes uniting across corneas. Corneas transparent, with black colored core. Antennular peduncle white with red dorsal stripe. Antennal peduncles white with red dorsal and ventral red stripe; antennal acicle white with red dorsal stripe; flagellum light red. Right cheliped with dorsal surfaces of chela, carpus and merus light red, and mesial faces with continuous red stripe; lateral faces of carpus and merus white with continuous red stripe. Left cheliped white with dorsal, lateral, and mesial red stripes; merus to propodus with dorsal, lateral and mesial red stripes; ischium white with red dorsal stripe.

Distribution. So far known only from the island of Bonaire, Lesser Antilles, southern Caribbean Sea; depth: 11.6–13.7 m.

Etymology. The name of this new species is given to acknowledge the efforts of the collector, photographer and environmentalist, Ms Ellen Muller, who when informed of the intended honor, preferred that the name of her granddaughter, Ms Molly Muller,



Figure 5. *Pylopaguropsis mollymullerae* sp. n., holotype male 2.4 mm, Bonaire (USNM 1291987). **A** left pereopod 2, lateral **B** left pereopod 3 (dactyl tip missing), lateral **C** right pereopod 2, lateral **D** dactyl of same, mesial **E** right pereopod 3, lateral **F** dactyl of same, mesial. Scale bar 1 mm.

be used, in hopes to inspire her to continue the tradition of protecting the amazing and fragile diversity of marine life in Bonaire.

Common name. "Candy striped hermit crab", in reference to the bright white and red striped color pattern that is similar to that of traditional candy cane.

Affinities. *Pylopaguropsis mollymullerae* sp. n. is remarkably similar in morphology to *P. teevana*, a species distributed in the tropical eastern Pacific from Colombia



Figure 6. In situ photographs of *Pylopaguropsis mollymullerae* sp. n. and its habitat at Bonaire diving site "Something Special". **A** holotype male 2.4 mm, Bonaire (USNM 1291987) **B** paratype male 1.8 mm, Bonaire (USNM 1291989) **C** three individuals of *P. mollymullerae* sp. n. (foreground, not collected) in den with "broad banded moray" *Channomuraena vittata* **D** coral ledge habitat, with arrow indicating entrance to crevice where five specimens of *P. mollymullerae* sp. n. were collected **E** individual of *P. mollymullerae* sp. n. (expanded and enhanced in oval inset, not collected) on body surface of "broad banded moray" *C. vittata*, with frontal portion of brachyuran *Achelous sebae* visible on lower right.

to Ecuador, including the Galapagos Islands. There is such minimal differentiation between the two species that they can be considered geminate. They are unique among congeners and even among other Paguridae, in the unusual structure of the right chela, with a ventral surface deeply excavated, forming a semi-cylindrical scoop-like surface (Fig. 4A, D, E). Both species also have antennal flagella with long, dense setae. The condition of the antennal flagella was not mentioned by McLaughlin and Haig (1989) in their redescription of *P. teevana*, although in her description Boone (1932: fig. 4, as *Galapagurus teevanus*) did illustrate this setal condition, noting that the flagella have "long radiating setae". The only differences detected between these two species are minor, as follows: the antennal acicles slightly exceed the corneas, whereas the acicles do not reach the distal margin of the cornea in *P. teevana*; the dorsal surfaces of the right chela is smooth (dactyl) or with only scattered minute tubercles on the lateral half (palm), whereas the same surfaces have numerous albeit well-spaced small tubercles in *P. teevana*; and the lateral face of the dactyl of right percopod 3 is evenly convex, whereas the lateral surface is slightly flattened in *P. teevana*. Although coloration was

only briefly described by McLaughlin and Haig (1989: 159, based on AJ Provenzano, Jr's color notes) for *P. teevana*, it appears that at least the striped pattern of that eastern Pacific species is similar to that of the Caribbean *P. mollymullerae* sp. n. In this new species, however, the stripes are bright red over white, whereas in *P. teevana* the stripes are brown over light cream.

Given that the dactyls of the left and right percopods 3 in *Pylopaguropsis mollymullerae* sp. n. are similar, this new species belongs in the *teevana* group of species of this genus as defined by McLaughlin and Haig (1989).

Habitat and behavior. As previously mentioned, P. mollymullerae sp. n. was first photographed fortuitously, but not collected, while observing the "flaming reef lobster" Enoplometopus antillensis. Five of the six specimens collected of Pylopaguropsis mollymullerae sp. n. were found living in gastropod shells, and obtained during dives in late afternoon or at night inside a crevice under a large coral ledge about 3.6 m wide by 1.5 m high at the site "Something Special" (Fig. 6D). The sixth specimen was collected a short distance north of that ledge, at a slightly shallower depth. Specimens were photographed, but not collected, in a crevice where a large "broad banded moray" Channomuraena vittata, has been known to divers to live for many years (Fig. 6C, E). An "ocellate swimming crab", Achelous sebae (H. Milne Edwards, 1834), was also observed at this crevice (Fig. 6E). It appears that this new species is reclusive, and prefers to hide in the deep, dark recesses of crevices under coral ledges where divers (E Muller, pers. comm.) occasionally have also observed two other species of moray eels, the "spotted moray" Gymnothorax moringa (Cuvier, 1829), and the "green moray" G. funebris Ranzani, 1839. After the discovery of specimens of P. mollymullerae sp. n., additional photographs were taken at the site "Front Porch", and a video at the site "Something Special", in order to document any particular behavior (see Suppl. materials 1–3). Frequently, one or more individuals of this this new hermit crab species were seen in close proximity of a moray eel, and in one instance clearly on its body (Fig. 6E).

Discussion

Several aspects of *Pylopaguropsis mollymullerae* sp. n. merit commentary. As previously noted, the morphological similarity of this new species with the eastern Pacific congener, *P. teevana*, is so remarkable that there is little doubt the two are closely related and geminate species that have barely diverged since the complete ocean separation by the central American isthmus. Among the Paguridae that occur in the tropical western Atlantic–tropical eastern Pacific region, very few genera (e.g., *Phimochirus* McLaughlin, 1981, *Spathapagurus* Lemaitre & Felder, 2011) have species that have been declared to contain geminates, although the two regions share a considerable number of genera and have a close geologic history. In addition to the similarity of the deeply excavated, scoop-like ventral surface of the right chela, both species also have the antennal flagella with long setae which in life are set at about 90° angle to the axis of the flagellum (Fig. 6A, B). The function, if any, of the unusual shape of the right chela, and the antennal

flagella, is intriguing. A video of an individual of *P. mollymullerae* sp. n. taken in situ (see Suppl. materials 1–3) shows the hermit crab walking while maintaining the right cheliped partially retracted or bent against the body, so that the chela is positioned in a shield-like manner. When the hermit crab is in motion, the dorsal surface of the chela is facing the substrate, and is clearly used to push itself along the bottom. Despite the scoop-like shape of the ventral surface of the chela which suggests it might be used for gathering materials or maybe digging, no such uses were observed. The long antennal flagella are held straight out on the sides in wing-like fashion, and parallel to the substrate. While these observations of live crabs do not show conclusively any particular function, it seems clear that the odd morphology must represent a specialized adaptation that deserves further study.

Given that Pylopaguropsis mollymullerae sp. n. lives in relatively shallow (scuba depth) habitats in reefs with crystal clear waters, has a conspicuous, bright color pattern, and individuals are of sufficiently large size to be visible to the naked eye, it is surprising that this new species had not been previously discovered. If what we know of the distribution of other pagurids in the western Atlantic is any indication (species are generally broadly distributed), it is unlikely that the occurrence P. mollymullerae sp. n. is geographically restricted to Bonaire. It seems more probable that its presence had not been detected before, in part, because of its secretive, crevicular, nocturnal behavior, apparent association with menacing moray eels that detract collectors, and preference to live in environments such as large coral ledges that are difficult to reach unless using scuba. Based on the few observations that have been made (E Muller, pers. comm.), this new species ventures out of the coral crevices only for short distances during night time. Regrettably, knowledge of the biology or ecology of other species of Pylopaguropsis is fragmentary at best, and thus it is not possible to make significant extrapolations or comparisons except that most species of this genus have, as previously mentioned, bright and often spectacular colorations (Asakura 2000, 2010, Asakura and Paulay 2003, Komai and Osawa 2004, Osawa and Okuno 2007, McLaughlin et al. 2010, Rahayu and Komai 2013, Arima 2014). Based on the information available (Table 1), most congeners except for *P. magnimanus* and *P. pygmaeus*, have been documented to prefer hard bottoms in coral environments. Komai and Osawa (2004: 99) did note that some species usually "inhabit crevices of coral and rocky reefs or among large dead coral plates or blocks"; Osawa and Okuno (2007: 40) found that P. bellula lives in "submarine caves or crevices on fore reef slopes"; and Arima (2014) documented that nine Japanese species (including one undescribed) preferred subtidal reefs and typically dark crevices on coral or rock bottoms and rocky walls.

The behavior of *Pylopaguropsis mollymullerae* sp. n. is also intriguing. Is there an ecological association of this new species with the "broad banded moray" or other moray species? Could this new hermit crab species function as a "cleaner" or a "den commensal"? At least in one instance, an individual was observed crawling on the body of a moray eel (Fig. 6E) with which this new hermit crab species seems to share a den. It is tempting to speculate that this individual of *P. mollymullerae* sp. n. was feeding on mucus or other materials present on the body surface of the moray eel, and thus,

this could be interpreted as a "cleaning" activity or existence of some kind of symbiotic relationship between hermit crab and moray. The brightly colored pattern with red stripes and setose antennae typical of most crustacean "cleaners", tends to support this interpretation. However, as pointed out by Bauer (2004), cleaning symbiosis is a controversial topic, in part because the term "cleaner" has been applied based largely on anecdotal evidence to most of the 43 species of decapods that have been categorized as "cleaners", all of which are caridean or stenopodidean shrimp except for two species of brachyurans (Spotte 1998, Côté 2000, Becker and Grutter 2004, Wicksten 2009). The term "cleaner" in the literature has been used for a wide range of presumed symbiotic associations that are not always clear, although studies have focused much more on "cleaner" fishes (e.g., Losey 1987 and references therein). It would be improbable for a hermit crab that carries a heavy shell as housing, to easily hop on hosts such as fishes that are most often suspended on the water column while "cleaner" activity is to take place. However, moray eels are typically in contact with the bottom inside their dens, and thus it would be possible for a hermit crab to access or climb on the body of the moray eel more easily, as observed for *P. mollymullerae* sp. n. (Fig. 6E). Alternatively, the apparent preference of P. mollymullerae sp. n. to inhabit caves alongside a moray eel, might indicate a case of "den commensalism" (as defined by Wicksten 2009) where the hermit crab can scavenge remains of food eaten by the moray eel. It would be of interest to conduct further, detailed studies on the behavior and ecology of P. *mollymullerae* sp. n. to ascertain if any of the above interpretations are valid.

Acknowledgements

I thank Dr A Anker, who first saw the hermit crab photographs sent to him by Ms E Muller, and suspecting they were of interest, suggested my name as specialist to determine their identity; thus, providing me with the opportunity to describe this beautiful new species. I am most grateful to Ms E. Muller for her environmental awareness, sharp eye and patient efforts to dive, photograph, video, and eventually collect and ship the specimens to my lab for study at the USNM, and allow permission to use her color photographs and videos in this paper. "VIP Diving" in Bonaire is gratefully acknowledged for making possible the diving activities of Ms. E. Muller. I am particularly thankful in Bonaire to the following individuals: Mr F van Slobbe and Mr A Nahr, who as official functionaries of the Bonaire Island Government, kindly and expeditiously processed and approved the permits to collect and export the hermit crab specimens from the Marine Park of Bonaire to the USNM; and Dr RBJ Peachy, Director of the Council of International Education and Exchange Research Station in Bonaire, for her invaluable assistance and guidance to both Ms E Muller and myself, and for arranging the shipping of specimens to USA. Dr DL Felder kindly collaborated by taking the photographs used in Fig. 4B-E, and Drs RT Bauer, C Baldwin, N Chadwick, and MK Wicksten, provided useful comments and references related to "cleaner" organisms. Drs K Baba and T Komai provided valuable information on Japanese publications, and kindly sent very useful translations from the Japanese. Drs T Komai and DL Rahayu provided invaluable comments to the manuscript. Last but not least, Ms R Gulledge is once again profusely acknowledged for her assistance in the preparation of electronic versions of figures.

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Supplementary material I

Photograph of live ovigerous female of *Pylopaguropsis mollymullerae* sp. n. stretching out from gastropod shell

Authors: Rafael Lemaitre

Data type: JPEG file

- Explanation note: Color photograph of *Pylopaguropsis mollymullerae* sp. n. taken by E Muller (dive 4125 095a) at dive site "Front Porch": ovigerous female, not collected.
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Supplementary material 2

Photograph of live specimen of *Pylopaguropsis mollymullerae* sp. n. in gastropod shell Authors: Rafael Lemaitre

Data type: JPEG file

Explanation note: Color photograph of *Pylopaguropsis mollymullerae* sp. n. taken by E Muller (dive 4125 156z2) at dive site "Front Porch": sex not determined, not collected.

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Supplementary material 3

Video of specimen of *Pylopaguropsis mollymullerae* sp. n. in gastropod shell, walking near crevice

Authors: Rafael Lemaitre

Data type: WMV Video file

- Explanation note: In situ video of *Pylopaguropsis mollymullerae* sp. n. taken by E Muller at dive site "Something Special": sex not determined, not collected.
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