

Two new species and a new subgenus of toothed Brachyhypopomus electric knifefishes (Gymnotiformes, Hypopomidae) from the central Amazon and considerations pertaining to the evolution of a monophasic electric organ discharge

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Abstract

We describe two new, closely related species of toothed *Brachyhypopomus* (Hypopomidae: Gymnotiformes: Teleostei) from the central Amazon basin and create a new subgenus for them. *Odontohypopomus*, new subgenus of *Brachyhypopomus*, is diagnosed by (1) small teeth present on premaxillae; (2) medialmost two branchiostegal rays thin with blades oriented more vertically than remaining three rays; (3) background color in life (and to lesser extent in preservation) distinctly yellowish with head and sides peppered with small, widely spaced, very dark brown stellate chromatophores that greatly contrast with light background coloration; (4) a dark blotch or bar of subcutaneous pigment below the eye; (5) electric organ discharge waveform of very long duration (head-positive phase approx. 2 milliseconds or longer, head-negative phase shorter or absent) and slow pulse repetition rate (3–16 Hz). The type species of the new subgenus, *Brachyhypopomus (Odontohypopomus) walteri* sp. n., is diagnosed by the following additional character

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states: (1) subcutaneous dark pigment at base of orbit particularly prominent, (2) body semi-translucent and nearly bright yellow background coloration in life, (3) a biphasic electric organ discharge (EOD) waveform of very long duration (between 3.5 and 4 milliseconds at 25° C) with head-positive first phase significantly longer than second head-negative phase in both sexes. *Brachyhypopomus* (*Odontohypopomus*) *bennetti* sp. n. is diagnosed by two character states in addition to those used to diagnose the subgenus Od*ontohypopomus*: (1) a deep electric organ, visible as large semi-transparent area, occupying approximately 14–17% body depth directly posterior to the abdominal cavity in combination with a short, but deep, caudal filament, and (2) a monophasic, head-positive EOD waveform, approximately 2.1 milliseconds in duration in both sexes. These are the only described rhamphichthyoid gymnotiforms with oral teeth, and *B. bennetti* is the first *Brachyhypopomus* reported to have a monophasic (head-positive) EOD waveform. Unlike biphasic species, the waveform of its EOD is largely unaffected by tail damage from predators. Such injuries are common among specimens in our collections. This species' preference for floating meadow habitat along the major channels of the Amazon River basin may put it at particularly high risk of predation and "tail grazing."

Resumo

Nós descrevemos duas novas espécies proximamente relacionadas de Brachyhypopomus (Hypopomidae: Gymnotiformes: Teleostei) da porção central da bacia Amazônica e criamos um novo subgênero para elas. Odontohypopomus, novo subgênero de Brachyhypopomus, é diagnosticado por (1) apresentar dentes pequenos no pré-maxilar; (2) pela forma dos dois raios branquiostegais mais internos, com expansão laminar fina orientada mais verticalmente do que nos três raios remanescentes; (3) coloração de fundo em vida (e, em menor grau, após preservação) distintamente amarelada, com a cabeça e flancos marcados por pequenos cromatóforos marrom escuro de formato estelar e bem espaçados entre si, contrastando fortemente com a tonalidade clara de fundo; (4) uma mancha ou barra escura de pigmento subcutâneo abaixo do olho; (5) forma da onda de descarga do órgão elétrico (DOE) de duração muito longa (fase positiva com aproximadamente 2 milisegundos ou mais, fase negativa mais curta ou ausente) e uma baixa taxa de repetição de pulsos (3-16 Hz). A espécie-tipo do novo subgênero, Brachyhypopomus (Odontohypopomus) walteri sp. nov., é adicionalmente diagnosticada pelos seguintes estados de caráter: (1) pigmentação subcutânea na base da órbita particularmente conspícua; (2) corpo semi-translúcido e com coloração geral em vida amarelo forte, (3) DOE com onda bifásica e de duração muito longa (entre 3,5 e 4 milisegundos a 25° C), com a fase inicial positiva significativamente mais longa do que a segunda fase (negativa) em ambos os sexos. Brachyhypopomus (Odontohypopopmus) bennetti sp. nov. é diagnosticada por dois estados de caráter, além daqueles utilizados para diagnosticar o subgênero Odontohypopomus: (1) órgão elétrico largo em vista lateral, visível como uma grande área semitransparente ocupando aproximadamente 14-17% da altura do corpo, medida imediatamente posterior à cavidade abdominal, combinada com um filamento caudal curto e alto; e (2) DOE monofásica positiva, com duração de aproximadamente 2,1 milisegundos em ambos os sexos. Esses são os únicos Gymnotiformes Rhamphichthyoidea com dentes orais e B. bennetti é a primeira espécie de Brachyhypopomus conhecida por apresentar uma DOE monofásica positiva. Diferentemente das espécies com DOE bifásica, a forma de onda/pulso dessa espécie não é significantemente afetada por danos ao filamento caudal decorrentes de predação. Esse tipo de dano é comum entre os espécimes examinados em nossas coleções. A ocorrência predominante dessa espécie em bancos flutuantes de macrófitas ao longo de alguns dos principais rios formadores da Bacia Amazônica pode representar um risco particularmente alto de predação e mutilação do filamento caudal.

Keywords

Gymnotiform, weakly electric fish, electric organ, electric organ discharge, EOD, Neotropical freshwater fishes, evolution

Introduction

Hypopomid knifefishes are nocturnally active, invertivorous inhabitants of lentic and slowly flowing freshwater habitats from Panama to Uruguay. While infrequently exploited for human consumption because of their small size, hypopomids are often abundant and ecologically important components of Neotropical freshwater environments (Hagedorn 1988, Westby 1988, Crampton 1996, 1998, 2011). The family Hypopomidae is one of six nominal families within the Order Gymnotiformes, all of which detect nearby objects and communicate by means of an active electrosensory system in which weak autogenic electric fields are monitored by frequency-matched dermal electroreceptors. Only the gymnotiform electric eel, *Electrophorus electricus*, has the additional capacity to produce strong electric potentials for prey capture and defense (Zupanc and Bullock 2005). The pulsatile electric organ discharges (EODs) of hypopomids often have species-specific characteristics that are useful for their taxonomy and even identification in the field. Such is particularly the case for the two new species of hypopomid gymnotiform we describe here that frequently co-occur in "floating meadow" habitat common along marginal lagoons and channels of the central Amazon basin.

Brachyhypopomus was created by Mago-Leccia (1994) to distinguish Hypopomus brevirostris (Steindachner, 1868) and other species with short snouts from the longersnouted Hypopomus artedi (Kaup, 1856) and is one of seven genera recognized within the family Hypopomidae (Albert and Crampton 2003). Mago-Leccia (1994) designated Brachyhypopomus brevirostris (Steindachner, 1868), described from the Río Guaporé (Amazon basin) of Bolivia, as the type species of the genus and recognized an additional five species: B. occidentalis (Regan, 1914) from the Río Condoto (Pacific slope) of Colombia, B. beebei (Schultz, 1944) from the Río San Juan (Caribbean drainage) of Venezuela, B. diazi (Fernández Yépez, 1972) from the Río Alpargatón (Caribbean drainage) of Venezuela, B. pinnicaudatus (Hopkins, 1991) from the coastal swamps of French Guiana, and B. janeiroensis (Costa & Campos da Paz, 1992) from the Rio São João near Rio de Janeiro, Brazil. Since then, five additional Brachyhypopomus species have been described. Brachyhypopomus bullocki Sullivan & Hopkins (2009) is from the Llanos (Orinoco basin) of Colombia and Venezuela; the other four species are from the southernmost part of the range of gymnotiforms in southeastern Brazil and Uruguay: B. jureiae Triques & Khamis (2003), B. bombilla Loureiro & Silva (2006), B. draco Gioria et al. (2008), and B. gauderio Gioria & Malabarba (2009). The two Brachyhypopomus species treated here are the first to be described from the central Amazon, although B. brevirostris, B. beebei, B. pinnicaudatus, Microsternarchus bilineatus and other undescribed hypopomids co-occur with them in this region (Sullivan 1997, Albert and Crampton 2003).

Morphological characters that unequivocally support the monophyly of *Brachyhypopomus* are few. Sullivan (1997) listed only a single possible synapomorphy for *Brachyhypopopmus*: the anterior portion of the maxilla is curved such that sides of the upper jaw descend at a distinct angle from the medial (premaxillary) portion of the upper jaw. In most rhamphichthyoids, the maxilla is straight to slightly curved, and the medial and lateral portions of the upper jaw form a continuous curve with little to no inflection point, viewed externally. However, this form of maxilla also occurs in the short-snouted rhamphichthyoid genus Steatogenys and in the Family Sternopygidae and may just be a concomitant feature of short (as opposed to more tubular) snouts. Albert (2001) recognized a monophyletic group consisting of the Brachyhypopmus species recognized by Mago-Leccia (1994) and several undescribed forms on the basis of four synapomorphies: (1) premaxilla gracile with a curved anterior margin and forming a distinct angle with the maxilla in lateral view, (2) dentary gracile, (3) body cavity with 16 or 17 precaudal vertebrae, and (4) a single transitional vertebrae. We regard these characters in combination with those enumerated by Mago-Leccia (1994) as provisionally sufficient to diagnose *Brachyhypopomus*, with the exception that pre-caudal vertebrae may be fewer than indicated by Albert: B. bullocki Sullivan & Hopkins (2009) has a short abdominal cavity with only 11–13 precaudal vertebrae. An unpublished phylogenetic analysis of mitochondrial DNA sequences in Sullivan (1997) indicated monophyly of eleven species, seven of which are now treated as valid Brachyhypopomus, with four additional undescribed forms, two of which are those treated here. This group of eleven species is monophyletic with respect to Hypopomus artedi, Microsternarchus bilineatus, and species of Hypopygus, Steatogenys, Rhamphichthys and Gymnorhamphichthys (Sullivan 1997).

Within gymnotiforms the complete absence of oral teeth is a character state unique to the Hypopomidae and Rhamphichthyidae and is among those used to unite these two families into the superfamily Rhamphichthyoidea (Mago–Leccia 1976, 1978, 1994, Triques 1993, Sullivan 1997, Albert 2001, Albert and Crampton 2003). The two species described here are remarkable for being the only rhamphichthyoids known to bear premaxillary teeth.

Materials and methods

Fishes were collected during day trips from Manaus, Brazil in a motorboat between March and May 1993; others were collected during the Calhamazon Project (Cox Fernandes et al. 2004) in November and December of the same year. The primary collection site for the type material is a few kilometers due south of Manaus in a series of channels, shallow lakes and islands that lie between the blackwater Rio Negro and the whitewater Rio Solimões, close to their confluence, as well as the Ilha da Marchantaria, a large, seasonally flooded island in the Solimões itself. We transported freshly captured individuals to a laboratory at the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus with water from their capture locality. We recorded their EODs in a 10 cm x 40 cm x 12 cm aquarium with silver/silver–chloride electrodes positioned at the head (positive electrode) and tail (negative electrode) of the fish and a reference electrode in the center. EODs were amplified using a CWE Corporation bio–amplifier with filters set to 0.1 Hz to 50,000 Hz using low gain and captured with a Tektronix 222 digital storage oscilloscope (512 point/8-bit resolution). Longer recordings of EOD

trains from the specimens here designated as holotypes were recorded on a Sony Walkman Pro cassette tape recorder, later digitized at 48 kHz on an Edirol FA-66 (Roland Corporation, Los Angeles, CA) and written to wav files with Audacity 2.0 software. Specimens were overanesthetized in MS-222, photographed in a photo aquarium, tagged, and fixed in 10% buffered formalin. Procedures for handling, euthanizing and preserving fishes followed guidelines for the use of fishes in research (AFS/ASIH/AI-FRB 1987).

We examined the type material for all described *Brachyhypopomus* species with the exception of those recently described from southern Brazil and Uruguay (*B. jureiae, B. bombilla, B. draco,* and *B. guaderio*) for which we consulted the published descriptions. We also examined a large quantity of non-type material of both described and undescribed forms (see Comparative Material Examined, below). Measurements were taken with a digital, needle-point caliper to within 0.1 mm under low power magnification. All measurements were taken point-to-point, i.e. not orthogonal to the main body axis. Counts of anal-fin rays and vertebrae were made from film radiographs of the specimens, observed under magnification. All vertebral counts began with C5, the first vertebra to bear a neural spine. "Precaudal vertebrae" include all anterior vertebrae bearing neural spines up to the first vertebra to bear a hemal spine. Vertebrae bearing hemal spines are termed "caudal vertebrae." Counts of pectoral-fin rays, made with the aid of dissecting microscope and strong transmitted light, include all elements. Measurements were taken on the left side unless otherwise specified.

Anatomical measurements and abbreviations follow Hubbs and Lagler (1958). Three measurements require explanation. (1) LEA is the length from the tip of the snout to the posterior end of the anal-fin base. This measurement is generally used as standard length in descriptions of gymnotiforms, since most lack caudal fins and often have regenerated a portion of their caudal filament after injury from predators. Specimens that had suffered such damage anterior to the terminus of the anal fin were identified from radiographs, and excluded from measurements involving the length of the body reported for the type series. LEAs reported on damaged individuals are noted as such. (2) Head length (HL) is measured from the tip of the snout to the end of the opercle bone, not to the uppermost limit of the branchial membrane. (3) Interorbital width is the distance between the upper margins of the eyes. The term "branched" pectoral-fin rays refers to all rays posterior to the anterior unbranched rays, even if the posterior terminal ray is unbranched. The abbreviation "alc" is used to indicate specimens that are preserved in alcohol, "cs" for those that have been cleared and stained. Institutional abbreviations follow Sabaj Pérez (2012).

Because measuring body depth is problematic due to lack of external landmarks on these fishes, distance from the tip of the snout to the 1st, 20th and 40th caudal vertebrae were obtained from film radiographs of these specimens. These distances were then measured off on the specimens themselves and the depth of the body at each of these three points was obtained with digital needle point calipers. Measurements are presented as percentages of LEA except for those within the head that are presented as percentages of HL. Staining protocols for bone and cartilage followed Potthoff (1984). In order to count columns of electrocytes in preserved specimens, skin was peeled back from caudal filaments and electrocytes were observed with strong transmitted light. "Electrocyte columns" refers to the number of bilateral bands of electrocytes along the longitudinal axis of the fish that begin under the head and continue to the tip of the caudal filament. These bands are most visible just above the posterior anal–fin base and on the caudal filament. These columns can often be counted without special preparation by viewing the area with strong transmitted light.

Systematics

Family Hypopomidae Mago-Leccia, 1978 Genus *Brachyhypopomus* Mago-Leccia, 1994

Subgenus Odontohypopomus subgen. n.

http://zoobank.org/7AFCDABC-A141-4E89-B72E-964D17137C5D http://species-id.net/wiki/Odontohypopomus

Type species. Brachyhypopomus (Odontohypopomus) walteri sp. n.

Included species. *Brachyhypopomus (Odontohypopomus) walteri* sp. n., *Brachyhypopomus (Odontohypopomus) bennetti* sp. n.

Diagnosis. This subgenus of *Brachyhypopomus* is diagnosed by (1) teeth present on premaxillae: usually one to five small, needle-like teeth on ventral surface of each (Fig. 1); (2) medialmost two branchiostegal rays thin with blades oriented more vertically than remaining three rays; (3) background color in life and to lesser extent in alcohol distinctly yellowish, head and sides peppered with small, widely spaced, dark brown stellate chromatophores that greatly contrast with background color of skin; bands along sides poorly defined, saddles of pigment mostly incomplete over dorsum; (4) a diffuse blotch of subcutaneous pigment directly beneath orbit, suggestive of a teardrop; (5) EOD pulse waveform of very long duration (head-positive phase approx. 2 milliseconds or longer, head-negative phase shorter or absent; Fig. 2) and slow repetition rate (3–16 Hz).

Teeth are absent from the premaxillae in all other rhamphichthyoid species, but present in all other gymnotiform lineages. (The teeth in preserved *Odontohypopomus* tend to be obscured by overlying tissue and are only easily visible in cleared and stained specimens.) In other *Brachyhypopomus*, the first (more medial) one or two branchiostegal rays are wide and oriented nearly horizontally, EODs are of shorter duration and faster repetition rates with second head–negative phases nearly equal in amplitude or of greater duration than the head–positive first phase, teardrop-like pigment below the orbit is absent, background color is less yellowish and chromatophores not as dark. In several other *Brachyhypopomus* species the pigment on the anterior flanks is arranged into distinct bands.

Etymology. A combination of the Greek word for tooth, *odontos*, and *Hypopomus*, type genus of Hypopomidae.



Figure 1. Upper jaw in ventral view of cleared and stained specimen of *Brachyhypopomus* (*Odontohypopomus*) *walteri* sp. n. (ANSP 194025) showing teeth present on the premaxillae. **PMX**=premaxilla, **MX**=maxilla, **MET**=mesethmoid, **PAL**=ossified element within palatine cartilage (not stained), **VET**=ventral ethmoid.



Figure 2. Electric organ discharge (EOD) waveforms of *Brachyhypopomus walteri* sp. n. and *Brachyhypopomus bennetti* sp. n. **A** EOD of holotype specimen of *Brachyhypopomus walteri* sp. n. **B** EODs of nine paratypes of *Brachyhypopomus walteri* sp. n. **C** EOD of holotype of *Brachyhypopomus bennetti* sp. n. **D** EODs of six paratypes of *Brachyhypopomus bennetti* sp. n. All are five millisecond traces with head positivity recorded upwards; water temperature between 21 and 23°C. Scale bars = 1 millisecond.

Brachybypopomus (Odontobypopomus) walteri sp. n.

http://zoobank.org/81560B78-B663-4446-B0E8-C03CE4FE1279 http://species-id.net/wiki/Brachyhypopomus_walteri Figs 3, 4, Appendix I; Tables 1, 3

Holotype. INPA 8941, tag no. 93-219, 163 mm TL, 126 mm LEA, sex undetermined, Amazonas, Brazil: floating meadow alongside of lake in the Paraná do Paracuúba, near mouth of Rio Negro and entrance to Lago Janauari, approx. 15 km due south of Manaus, 03°12.6'S, 059°59.4'W, J.P. Sullivan and J. Zuanon. 23 April 1993.

Paratypes (20). Brazil: Amazonas: INPA 8926 (3 cs, tag nos. 93-58, 93-140, 93-156), collection data same as for holotype, 24 March-18 April 1993; INPA 8896 (4 alc, tag nos. 93-18, 93-19, 93-22, 93-23, 102-122 mm LEA), Ilha da Marchantaria, Rio Solimões, emergent grasses on shore of island, approx. 15 km upstream from confluence with Rio Negro, near Manaus, approx. 03°14'S, 059°59'W, J.P. Sullivan and J. Zuanon, 9 March 1993; INPA 8880 (3 alc, tag nos. 93-55, 93-56, 93-57, 108-116 mm LEA), locality same as for holotype, 24 March 1993; INPA 8939 (1 alc, specimen number 93-114, 125 mm LEA), locality same as for holotype, 10 April 1993; ANSP 194031 (1 alc, tag no. JPS11-1-93/13, 84 mm LEA), channel between Rio Solimões and Lago Tefé, approx. 03°21'S, 064°40'W, J.P. Sullivan et al., 1 November 1993; ANSP 194032 (1 alc, 110 mm LEA, tag no. JPS11-20-93/1), Rio Içá in roots of water hyacinth along margin of inlet,15 km upstream of the mouth of the Icá, approx. 03°06'S, 068°05'W, J.P. Sullivan et al., 20 November 1993; ANSP 194033 (1 alc, tag no. CALH-11-20-93/2, 97 mm LEA), near Santo Antonio do Icá and mouth of Rio Icá in floating vegetation, approx. 03°07'S, 067°57'W, J.P. Sullivan et al., 20 November 1993; CUMV 97641 (1 alc, damaged, 80 mm TL, tag no. JPF-93-187/1), Rio Negro above Manaus, 03°05.38'S, 060°27.02'W, J.P. Sullivan and J.P. Friel, 14 December 1993; CUMV 97642 (5 alc, 2 damaged: tag nos. JPF-93-188/3, 188/4, 104, 100 mm LEA, 3 intact: tag nos. JPF-93-188/2, 188/5, 188/6, 95-102 mm LEA), Rio Negro above Manaus, 03°05.59'S, 60°26.83'W, J.P. Sullivan and J.P. Friel, 14 December 1993.

Non-types. Brazil: Amazonas: Rio Solimões drainage: INHS 70542 (4 of 10, alc, 71–162 mm LEA), Ilha da Marchantaria, approx. 03°14'S, 059°59'W, P. Bayley, 14 March 1978; MZUSP 30061 (1 alc, 70 mm LEA), Rio Tefé, Lago Mucura, M. Goulding, 5 August 1979; USNM 306874 (2 alc, 91 & 100 mm LEA), Paraná da Ilha da Marchantaria, approx. 03°14'S, 059°59'W, depth 0–1.3 meters P. Bayley, 25 April 1978; USNM 306919 (1 alc, 75 mm LEA), Lago Camaleão, Ilha da Marchantaria, approx. 03°14'S, 059°59' W, P. Bayley, 29 March 1977; INPA 33268 (3 alc), Coari, 03°51.17'S, 063°28.12'W, L. Rapp Py-Daniel et al., 13 September 2013; INPA 33253 (3 alc), Manacapuru, Canaboca III, 03°35.55'S, 060°50.15'W, L. Rapp Py-Daniel et al., 17 September 2003; INPA 30241 (8 alc, 63.65–113.62 mm LEA), São Paulo de Olivença, Rio Camatiã, comunidade Monte Sinai, approx. 03°27.57'S, 068°56.00'W, L. Rapp Py-Daniel et al., 4 April 2008; ANSP 194025 (5 alc, 59.9–126.2 mm LEA, 1 cs, 117.4 mm), same data previous. Rio Uatumã: INPA 39074 (1 alc), São Sebastião do Uatumã, right bank in front of São José do Jabote, 01°56.20'S, 058°17.78'W, L.



Figure 3. Holotype of *Brachyhypopomus walteri*, INPA 8941 (TL 163 mm, LEA 126 mm), sex undetermined, Paraná do Paracuúba, Amazonas, Brazil. Preserved whole specimen shown above close-up view of specimen immediately post-mortem. Scale bars equal 1 cm.

Rapp Py-Daniel et al., 1 October 2011. Rio Japurá: INPA 9945 (30 alc), Lago Caetano (várzea lake) 1 km N of Jarauá, 02°50.97'S, 064°55.70'W, W.G.R. Crampton, 8 January 1995. Rio Purus: INPA 17112 (20 alc), Paraná do Seixo, Lago Jari, 04°54.67'S, 062°21.42'W, L. Rapp Py-Daniel et al., 8 June 2001; INPA 29259 (12 alc), Beruri, Lago Ayapuá, Igarapé Ajará, 04°25.12'S, 062°15.60'W, L. Rapp Py-Daniel et al., 15 November 2007; INPA 17192 (27 alc), Igarapé das duas bocas, Paraná do Jari, 04°53.12'S, 062°20.18'W, L. Rapp Py-Daniel et al., 7 June 2001. Pará: Rio Tapajós drainage: INPA 32703 (1 alc) Rio Crepori, Jacareacanga, Igarapé do Cocho, 06°44.90'S, 056°54.72'W, W.S. Pedroza, 31 July 2008. Rio Amazonas drainage: INPA 33192 (1 alc), Almeirim, Paranaguara, 01°44.48'S, 053°10.25'W, J. Zuanon et al., 5 October 2003. Rondônia: Rio Guaporé-Madeira drainage: INPA 9721 (19 alc), 15 km above Guajará-Mirim on Rio Pacaás Novos, approx. 10°56.8'S, 065°14.3'W, G.M. dos Santos, 26 November 1983; INPA 9727 (78 alc), mouth of Rio Pacaás Novos into Rio Guaporé, G.M. dos Santos, 26 November 1983. Roraima: Rio Branco drainage: INPA 30748 (11 alc), near Boa Vista, 02°47.51'N, 060°40.15'W, L.N. Carvalho, 29 September 2006; INPA 30749 (8 alc), near Boa Vista, 02°47.51'N, 060°40.15'W, L.N. Carvalho, 29 September 2006. Ecuador: Río Napo drainage: FMNH 102276 (8 alc, 69–107 mm LEA), Río Napo, along edge of Lago Anangucocha, approx. 01°28.48'S, 077°33.73'W, D. Stewart et al., 13 October 1981.

Diagnosis. *Brachyhypopomus (Odontohypopomus) walteri* sp. n. is diagnosed by the following three character states in combination with the character states listed above for *Odontohypopomus*: (1) patch of brown pigment below skin at base of orbit distinct; (2) body yellow and semi-translucent in living specimens; (3) caudal filament long and fine, greater than 20% of LEA in intact specimens; (4) EOD pulse duration very long (between 3.5 and 4 milliseconds at 25° C) with head-positive first phase of longer duration than second head-negative phase in both sexes (Fig. 2 A, B).

In all other *Brachyhypopomus* with biphasic EODs, the second, head-negative phase of the EOD is nearly equal in amplitude or of greater duration than the head-positive first phase. *Microsternarchus bilineatus* has an EOD waveform of similar duration, but the second phase is roughly equal or longer than the first (and the repetition rate is far faster). No other species of *Brachyhypopomus* is as distinctly yellow in color, particularly in life.

This species can be distinguished from the similar *B. bennetti* sp. n. by a shorter body (depth quickly tapers posteriorly: depth of body at 40th post-abdominal vertebra 36–41% of depth at first abdominal vertebra vs. 46–57% in *B. bennetti*), fewer anal fin rays (198–216 rays vs. 227–255 rays in *B. bennetti*), a shallower electric organ, and a long, fine caudal filament (length 20–32% of LEA vs. 10–19% of LEA in *B. bennetti*) with three or four bilateral columns of electrocytes at base of caudal filament (vs. six columns in *B. bennetti* sp. n.). Subcutaneous pigment below eye is absent in other hypopomids and usually less conspicuous in the sister species *B. bennetti* sp. n. The EOD waveform of *B. walteri* sp. n. is biphasic in contrast to *B. bennetti*'s monophasic EOD waveform. *Brachyhypopomus bennetti* sp. n. tends to be more darkly pigmented and less yellow and translucent.

Description. Morphometric and meristic data are presented in Tables 1, 3 and 4. A Brachyhypopomus of moderate to small adult size for a hypopomid; largest specimen examined measures 175 mm TL, 125 mm LEA. Body very compressed, depth at posterior end of abdominal cavity 2.7-3.1 times body width. Body more compressed posteriorly, sides of body with only slight curvature posterior to abdominal cavity. Dorsal profile gently convex. Depth quickly tapers posteriorly: depth of body at 40th post-abdominal vertebra 36-41% depth at first abdominal vertebra. Head short in comparison to body length, deep and wide: HL 11.2-12.6% LEA, head depth at occiput 72-81% HL, head width at opercle 54-63% HL. Head triangular in lateral view, dorsal profile of head straight from occiput to point of downturn of snout, ventral profile of head straight from lower jaw to opercular area with little if any concavity between opercular area and tip of lower jaw. Eye moderate in size, 12.4-14.5% HL. Mouth small, terminal, jaws equal, gape 20-23% HL. Closed lips meet ventral to a horizontal through ventral margin of eye. One to five small needle-like conical teeth present on each premaxilla (Fig. 1), lower jaw edentate. Maxilla moderate in length, thin, with slight curvature. Snout moderate in length, 26–29% HL, edge of upper lip close to farthest anterior extent of snout. Posterior naris close to eye, posterior nariseye 1.8-3.7% HL. Lateral ethmoid present. Round ossification present in anterior portion of palatine cartilage (Fig. 1). Infraorbital portion of cephalic lateralis system



Figure 4. Paratypes of *Brachyhypopomus walteri*. **A** Paratype tag no. 93-55 from INPA 8880 (TL 164 mm, LEA 118 mm), sex undetermined, Ilha da Marchantaria, Rio Solimões, Amazonas, Brazil **B** Paratype tag no. 93-114 from INPA 8939 (TL 155 mm, LEA 125 mm), female, collected with holotype. Preserved whole specimens shown above close-up views of specimens immediately post-mortem. Scale bars equal 1 cm.

incomplete, lacking recurrent anterodorsal segment and associated pores beneath and anterior to the posterior nares that are present in most other *Brachyhypopomus* (see fig. 53 in Sullivan 1997); fourth supraorbital pore lying near vertical through posterior

nostril, pores inconspicuous. Preopercular lateral-line canal embedded in preopercle, canals radiating out to pores. Pores of lateral-line canal immediately behind head without downward pointing tubes. Discernible lateral scales terminate along caudal filament. Five branchiostegal rays, medialmost two thin with blades oriented nearly vertically compared to outer three (see diagnosis of Odontohypopomus). Gill rakers robust for genus, some with weakly ossified cores, on anterior faces of first four gill arches. Rakers subtended on ceratohyals one to four by small trough-shaped ossicles. Approximately 40 gill filaments on arch one. Three pectoral radials, all partially fused together at proximal end. Mesocoracoid bridge absent. Pectoral fin broad, 12–15 branched plus unbranched rays, length 5.3-7.0% LEA. 198-216 anal fin rays, longest rays 4.0-4.9% LEA. Precaudal vertebrae 13-16, up to 75 caudal vertebrae in advance of regenerated portion of caudal filament. Body excluding head and fins covered with thin cycloid scales, small dorsally, larger posterolaterally, partially obscured by skin. Twelve scale rows above, 13 scale rows below lateral line at farthest extent of pectoral fin. Anal-fin origin slightly posterior to vertical at midpoint of extended pectoral fin. Caudal filaments long and fine in intact mature specimens, 20-32% of TL. Sexual dimorphism of caudal filaments not observed. Three or four bilateral columns of electrocytes along caudal filament, number often alternating along length of caudal filament; 38-63 rows of electrocytes. Electrocytes do not extend farther anteriorly than base of urogenital pore. No accessory electric organs on head or humeral region.

Electric organ discharge. The EOD is biphasic and 3.2–4.5 milliseconds in total duration at 25°C; the first head-positive phase is 1.7–1.9 times duration of second head-negative phase (Fig. 2). Resting EOD repetition rate is slow (3.1–16.3 Hz, mean 9.4 Hz, median 9.8, at 21–25°C, n=23). See Appendix II.

Coloration. Background color yellow in life, yellowish-tan in preservation. In life, body semi-translucent, with gill filaments appearing cherry red through opercle, gut dark, and swim bladder whitish through abdominal wall. Pigmentation variable: poorly to moderately developed irregular bands along sides, darker and wide above lateral line, often with a spot of darker intensity on lateral line itself. Bands either restricted to anterior portion of body above lateral line or connected to fainter bands below. Some bands connect to eight to 12 irregular saddles across dorsum. Saddles more regular in smaller individuals. Dorsal rami of the anterior lateral line nerve visible when viewed from above as two thin, dark parallel lines running along upper back beginning a short distance behind head and continuing to mid-point of the back. Cheeks, underside of head and sides of body below lateral line peppered with prominent dark brown stellate chromatophores that greatly contrast with background color of skin and that do not form part of a larger pattern. Diffuse pigment below eye resembling a teardrop is more prominent in live specimens as overlying tissue becomes opaque upon preservation. Pectoral and anal fin with irregular brown pigment along rays; interradial membranes hyaline.

Distribution and ecology. See distribution map (Fig. 5). *Brachyhypopomus walteri* sp. n. is known only from the Amazon basin where it appears to be common in

Measurement	holotype	range	mean	S.D.	N
Total length (TL) (mm)	163.0	116–175	153.2	15.3	11
Length to end of anal fin (LEA) (mm)	126.0	85-127	111	13	11
Head length (HL) (mm)	14.4	10.3–14.5	13	1.4	11
Caudal filament length (% TL)	22.7	19.6–31.8	27.3	3.5	11
Proportion of LEA (%)					
Head length	11.4	11.2-12.6	11.7	0.5	11
Snout to occiput	8.5	7.9–9.6	8.9	0.5	11
Snout to anal fin origin	19.9	18.4–21.2	19.6	0.9	11
Depth at 1st post-abdominal vertebra	12.2	10.5-13.2	12	0.8	11
Depth at 20th post-abdominal vertebra	9.4	8.5-10.0	9.4	0.5	11
Depth at 40th post-abdominal vertebra	4.7	4.4–5.2	4.7	0.3	11
Caudal filament base depth	1.9	1.6-2.1	1.8	0.2	11
Longest anal fin ray	4.6	4.0-4.9	4.5	0.2	11
Longest pectoral fin ray	5.4	5.3–7.0	6.1	0.6	11
Proportion of HL (%)					
Snout length	28.5	25.7-29.0	27.4	1.2	11
Gape	22.9	19.8–23.2	21.5	1.4	11
Orbital diameter	12.5	12.4–14.5	13.5	0.7	11
Interorbital distance	23.9	21.7-26.5	24	1.6	11
Posterior naris-eye	3.4	1.8–3.7	2.8	0.7	11
Branchial aperture	29.7	23.8-30.6	26.9	2.6	11
Head width at opercle	63.3	54.4-63.3	58.8	3.2	11
Head width at eye	42.2	40.1-43.8	41.9	1.3	11
Head depth at occiput	79.0	72.1-80.9	76.4	3.1	11

Table 1. Summary of morphometric measurements for *Brachyhypopomus walteri* sp. n. (included are holotype and ten paratypes identified from radiographs as undamaged at anal-fin terminus).

floating meadow habitats, (mostly composed of the grass *Paspalum repens*, Poaceae), on the margins of the Amazonas/Solimões and its tributaries. It has been collected predominantly in white water, but also in areas near the confluence of black water rivers with the Amazonas/Solimões ranging from low to medium conductivity. Apart from one collection very near Manaus and the white water Rio Branco, it is absent from collections in the Rio Negro system. It is frequently taken with *B. bennetti* sp. n. and sometimes with *B. brevirostris*. Species of *Eigenmannia*, *Gymnotus*, the apteronotid *Parapteronotus hasemani* and the electric eel, *Electrophorus electricus*, frequently co-occur in the floating meadow habitats preferred by this species.

Etymology. This species is named for Walter Heiligenberg (1938–1994) in honor of his discoveries in electric fish neurophysiology and behavior made at the Scripps Institute of Oceanography. These notably include the "jamming avoidance response" in *Eigenmannia*, often described as the best-understood vertebrate behavior.



Figure 5. Distribution of examined specimens of *Brachyhypopomus walteri* sp. n. (blue circles) and *B. bennetti* sp. n. (red diamonds). Common holotype locality for both species indicated by yellow star.

Brachyhypopomus (*Odontohypopomus*) *bennetti* sp. n. http://zoobank.org/20BDF5D2-49FD-4B21-819B-54C4684B9772 http://species-id.net/wiki/Brachyhypopomus_bennetti Figs 6, 7, Appendix I; Tables 2, 3

Holotype. INPA 39560 (ex-8941), tag no. 93-220, 215 mm TL, 176 mm LEA, female, Amazonas, Brazil: floating meadow along side of lake in the Paraná do Paracuúba, near mouth of Rio Negro and entrance to Lago Janauari, approx. 15 km due south of Manaus, 03°12.6'S, 059°59.40'W, J.P. Sullivan and J. Zuanon, 23 April 1993.

Paratypes (18). Brazil: Amazonas: INPA 39561 (1 cs, tag no. 93-221, 95 mm LEA, damaged), same data as holotype; INPA 39579 (1 alc, tag no. 93-26, 152 mm LEA, damaged), Ilha da Marchantaria, approx. 03°14'S, 059°59'W, J.P. Sullivan & J. Zuanon, 5 March 1993; INPA 8862 (2 alc, tag nos. 93-139, 93-163, 152 mm & 162 mm LEA, respectively, damaged), Paraná do Paracuúba near holotype locality, J.P. Sullivan & J. Zuanon, 14 April 1993; INPA 8863 (1 alc, tag no. 93-222, 145 mm LEA, damaged), Lago Janauari & Paraná do Paracuúba near holotype locality, J.P. Sullivan & J. Zuanon, 24 April 1993; INPA 39578 (1 alc, tag no. 93-54, 153 mm LEA, damaged), Paraná do Paracuúba near holotype locality, J.P. Sullivan & J. Zuanon, 24 April 1993; INPA 39578 (1 alc, tag no. 93-54, 153 mm LEA, damaged), Paraná do Paracuúba near holotype locality, J.P. Sullivan & J. Zuanon, 24 April 1993; INPA 39578 (1 alc, tag no. 93-54, 153 mm LEA, damaged), Paraná do Paracuúba near holotype locality, J.P. Sullivan & J. Zuanon, 24 March 1993; INPA 39580 (3 alc, 2 damaged: tag nos. 93-112, 93-113, 160 &170 mm LEA



Figure 6. Holotype of *Brachyhypopomus bennetti*, INPA 39560 (TL 215 mm, LEA 171 mm), female, Paraná do Paracuúba, Amazonas, Brazil. Preserved whole specimen shown above close-up view of specimen immediately post-mortem. Scale bars equals 1 cm.

respectively, 1 intact: tag no. 93-116, 161 mm LEA), same data as for holotype; INPA 8940 (3 alc, all intact, tag nos. 93-137, 93-141, 93-165, 167–171 mm LEA), lake between Janauari and Solimões, approx. 03°12.6'S, 060°01.9'W, J.P. Sullivan & J. Zuanon, 14 April 1993; INPA 39581 (1 alc, tag no. 93-214, 150 mm LEA, intact), same data as previous; ANSP 194034 (1 alc, tag no. JPS-93-44/1, 125 mm LEA, intact), floating grasses directly in front of town of Fonte Boa, 02°30.57'S, 066°05.72'W, J.P. Sullivan, 11 November 1993; ANSP 194035 (1 alc, tag no. JPS-93-57/1, 89 mm LEA, intact), Rio Jutaí near mouth into Solimões, floating grasses and water hyacinth, approx. 02°40'S, 066°40'W, J.P. Sullivan, 16 November 1993; CUMV 97640 (3 alc, 1 intact: tag no. JPS-93-37/1, 98 mm LEA, 2 damaged: tag nos. JPS-93-37/2, JPS-93-37/3, 118 & 75 mm LEA, respectively), Rio Juruá near mouth into Solimões, approx. 02°40'S, 065°45'W, floating vegetation, J.P. Sullivan, 8 November 1993.

Non-types. Bolivia: Beni: Río Beni drainage: CAS 72216 (1 alc, 126 mm LEA), Reyes, 24 mi. NE of Rurrenabaque on the pampas, approx. 14°17'S, 067°20' W, N.E. Pearson, Mulford Expedition, 15 November 1921; CAS 81631 (1 alc, size n.a.), data same as for previous. Brazil: Amazonas: Rio Solimões drainage: INHS 70542 (5 of 10, alc, 71–162 mm LEA), Ilha da Marchantaria south of Manaus, approx. 03°14'S, 059°58' W, P. Bayley, 14 March 1978; MCZ 78163 (1 of 8, alc, 98 mm LEA,) Lago Jacaretinga near Manaus, T.J. Zaret et al., 5 November 1979; USNM 306841 (1 alc, 147 mm LEA), Paraná do Lago Januauacá, entrance to Lago do Castanho, 0–2.1 meters depth, P. Bayley, 30 March 1977; USNM 306859 (1 alc, 72 mm LEA), Lago Terra Preta, Janauari, depth 0-1 meter, P. Bayley, 3 August 1977; USNM 306875 (1 alc, 131 mm LEA), Lago Janauari, near its outflow, depth 0.6-1 meters; USNM 306929 (10 alc, 71-139 mm LEA), Lago Camaleão, near Manaus within Ilha da Marchantaria, P. Bayley, 28 March 1977; USNM 306947 (1 alc, 96 mm LEA), collection locality same as for previous, P. Bayley, 29 March 1977; INPA 13569 (2 alc), Iranduba, Ilha da Marchantaria, Lago Camaleão, P. Petry & R. Sotero, 3 April 1993; INPA 33255 (3 alc), Manaus, Ilha da Paciência, 03°16.68'S, 060°16.58'W, L. Rapp Py-Daniel et al., 18 September 2003; INPA 32091 (3 alc), Manaus, Lago do Rei, J.I.S. Botero, 30 June 1998; INPA 6403 (5 alc), Iranduba, Lago Janauacá, INPA staff, 12 September 1979; INPA 39563 (4 alc), Coari, 03°51.17'S, 063°28.12'W, L. Rapp Py-Daniel et al., 13 September 2003; INPA 33270 (3 alc), Fonte Boa, Lago "Ressaca Grande", 02°28.43'S, 066°09.28'W, J. Zuanon et al., 8 September 2003; INPA 39562 (5 alc, 54.9-144.1 LEA), São Paulo de Olivença, Rio Camatiã, comunidade Monte Sinai, approx. 03°27.57'S, 068°56.00'W, L. Rapp Py-Daniel et al., 4 April 2008; ANSP 194026 (4 alc, 65.1–132.6 mm LEA), same data as previous; INPA 18244 (6 alc) Alvarães, Lago Geraldo, Reserva Mamirauá, W.G.R. Crampton, 29 May 1998; INPA 18245 (4 alc), Alvarães, Lago Curuçá Aberto, Reserva Mamirauá, W.G.R. Crampton, 1 June 1998; INPA 18246 (3 alc), Alvaráes, Lago Curúça Comprido, Reserva Mamirauá, W.G.R. Crampton, 2 June 1998; INPA 15816 (34), INPA 18241 (1 alc), INPA 18242 (1 alc), INPA 18243 (1 alc), INPA 18348 (1 alc), INPA 18349 (1 alc), INPA 18350 (1 alc), 18351 (2 alc), INPA 18352 (1 alc), INPA 18354 (3 alc), Alvarães, Lago Mamirauá system, W.G.R. Crampton, 1 April 1997–18 May 1998; INPA 18355 (3 alc), Alvaráes, Lago Mamirauá, Lago Promessa, W.G.R. Crampton, 19 May 1998; INPA 18357 (3 alc), Alvarães, Lago Curuçá, Lago Mamirauá system, W.G.R. Crampton, 30 May 1998; INPA 18358 (2 alc), Alvarães, Lago Miratinin, Lago Mamirauá system, W.G.R. Crampton, 4 June 1998; INPA 18361 (2 alc), Lago Apolônio, Lago Mamirauá system, W.G.R. Crampton, 1 July 1999; INPA 18362 (1 alc), Lago Secretária, Lago Mamirauá system, W.G.R. Crampton, 9 June 2000; INPA 33196 (1 alc), Tabatinga, Comunidade Palmares, 03°57.89'S, 069°20.19'W, J. Zuanon et al., 2 September 2003. Rio Jutaí drainage: INPA 33187 (3 alc), Ressaca do Luizinho, 02°42.98'S, 066°48.22'W, J. Zuanon et al., 6 September 2003. Pará: Rio Amazonas drainage: INPA 39564 (1 alc), Almeirim, Comunidade Paranaguara, 01°44.48'S, 053°10.25'W, J. Zuanon et al., 5 October 2003. Rio Tapajós drainage: INPA 39518 (1 alc), Belterra, Igarapé do Índio near mouth to Rio Tapajós, 02°40'S, 054°58'W, F.R. Ribeiro, 26 December 2008. Colombia: Amazonas: Río Amazonas drainage: FMNH 85363 (38 alc, 67-153 mm LEA), Río Amazonas 2–3 miles upstream of Leticia, approx. 04°05'S, 070°03'W, Na-



Figure 7. Paratypes of *Brachyhypopomus bennetti*. **A** Paratype tag no. 93-214 from INPA 39581 (TL 175 mm, LEA 150 mm), female, Lago Janauari, Amazonas, Brazil **B** Paratype tag no. 93-137, INPA 8940 (TL 190 mm, LEA 167 mm), Lago Janauari. Preserved whole specimens shown above close-up views of specimens immediately post-mortem. Scale bars equal 1 cm.

varro, Thomerson et al., 13 November 1973; USNM 216870 (1 alc, 110 mm LEA), Leticia, D. Kramer, 4 December 1974. **Ecuador**: Napo: Río Napo drainage: FMNH 102270 (2 alc, 56 & 110 mm LEA), Laguna de Limoncocha, D. Stewart et al., 4 Oc-

tober 1981. **Peru**: Loreto: Río Ucayali drainage: AMNH 78060 (7 of 14, alc, 81–101 mm LEA), several sites along 10 km stretch, Ferraris, Montrevil et al., 7 July 1987.

Diagnosis. Brachyhypopomus (Odontohypopomus) bennetti sp. n. is diagnosed by two character states in addition to those used to diagnose the subgenus Odontohypopomus above: (1) electric organ along caudal filament and along body above anal fin exceedingly deep and visible as large semi-translucent area, occupying approximately 14–17% body depth directly posterior to abdominal cavity; (2) monophasic, headpositive EOD, approximately 2.1 milliseconds in duration in both sexes at 25°C. The appearance of the electric organ in this species when backlit (Fig. 8) is significantly larger than in any other species of Brachyhypopomus. No other described Brachyhypopomus has a monophasic EOD waveform.

This species can be distinguished from the similar *B. walteri* sp. n. by a longer body (depth gradually tapers posteriorly: depth of body at 40th post-abdominal vertebra 46–57% vs. 36–41% of depth at first abdominal vertebra vs. in *B. walteri*), more numerous anal fin rays (227–255 vs. 198–216 in *B. walteri*), a deeper electric organ along the body and a short, deep caudal filament (10–19% of LEA vs. 20–32% of LEA in *B. bennetti*) with six bilateral columns of electrocytes at its base (vs. three or four columns in *B. bennetti* sp. n.). Subcutaneous pigment suggestive of a teardrop below eye is usually less conspicuous than in the sister species *B. walteri* sp. n., although often present. The EOD waveform of *B bennetti* sp. n. is monophasic in contrast to *B. walteri* s biphasic EOD waveform. *B. walteri* sp. n. tends to be less darkly pigmented and more translucent and yellowish in life than *B. bennetti* sp. n.

Description. Morphometric and meristic data are presented in Tables 2-4. A Brachyhypopomus of moderate adult size for a hypopomid; largest specimen examined measures 232 mm TL, 189 mm LEA. Body very long and compressed, depth at posterior end of abdominal cavity 2.6 to 2.9 times body width. Body more compressed posteriorly, but sides of body with only slight curvature posterior to abdominal cavity. Dorsal profile gently convex. Depth gradually tapers posteriorly: depth of body at 40th post-abdominal vertebra 46-57% of depth at first abdominal vertebra. Head short in comparison to body length, deep and wide: HL 10.3-12.3% LEA, head depth at occiput 76–80% HL, head width at opercle 58–65% HL. Head triangular in lateral view: dorsal profile of head straight from occiput to point of downturn of snout, ventral profile of head straight from lower jaw to opercular area with little if any concavity between opercular area and tip of lower jaw. Eye moderate in size, 11–14% HL. Mouth small, terminal, jaws equal, gape 21–26% HL. Closed lips meet ventral to a horizontal through ventral margin of eye. One or more small needle-like conical teeth present on each premaxilla. This feature is variable, in one case observed only unilaterally. Lower jaw edentate. Maxilla moderate in length, thin, with slight curvature. Snout length moderate, 26-30% HL, edge of upper lip close to farthest anterior extent of snout. Posterior nostril particularly small and close to eye: posterior naris-eye 2.3-4.3% HL. Lateral ethmoids present. Round ossification present in anterior of palatine cartilage. Infraorbital portion of cephalic lateralis system incomplete, lacking recurrent anterodorsal segment and associated pores beneath and anterior to the posterior nares present

Measurement	holotype	range	mean	S.D.	N
Total length (TL) (mm)	215.0	98-215	173	44.2	10
Length to end of anal fin (LEA) (mm)	176.0	89–176	149.9	32.4	10
Head length (HL) (mm)	18.5	10.8–19.6	16.7	3.2	10
Caudal filament length (% TL)	18.1	1.4-18.9	12.1	5.6	10
Proportion of LEA (%)					
Head length	10.5	10.3-12.3	11.2	0.7	10
Snout to occiput	8.2	7.7–9.9	8.6	0.7	10
Snout to anal fin origin	17.0	16.7–19.0	17.5	0.8	10
Depth at 1st post-abdominal vertebra	10.8	10.6-12.9	11.6	0.7	10
Depth at 20th post-abdominal vertebra	8.7	8.5–10.1	9.1	0.5	10
Depth at 40th post-abdominal vertebra	5.3	5.1-6.2	5.6	0.3	10
Caudal filament base depth	2.4	1.3–3.2	2.1	0.6	10
Longest anal fin ray	4.0	4.0-4.5	4.3	0.2	10
Longest pectoral fin ray	5.7	5.4–7.5	6.0	0.7	10
Proportion of HL (%)					
Snout length	27.7	25.7–29.5	27.6	1.3	10
Gape	21.8	21.2–25.5	22.6	1.6	10
Orbital diameter	13.4	11.6–14.1	12.7	0.9	10
Interorbital distance	28.4	22.4–28.4	25.1	1.9	10
Posterior naris-eye	0.4	2.3-4.3	3.3	0.7	10
Branchial aperture	29.3	26.4-33.6	30.3	2	10
Head width at opercle	64.2	58.4-64.8	62.0	2.1	10
Head width at eye	44.9	39.9-44.9	42.4	1.7	10
Head depth at occiput	80.3	76.3-80.3	78.3	1.5	10

Table 2. Summary of morphometric measurements for *Brachyhypopomus bennetti* sp. n. (included are holotype and nine paratypes, identified from radiographs as undamaged at anal-fin terminus).

Table 3. Anal-fin ray counts of *Brachyhypopomus walteri* sp. n. and *B. bennetti* sp. n. (holotypes and paratypes) compared to seven other *Brachyhypopomus* species; modal values **highlighted**.

Species	170-179	180–189	190–199	200–209	210-219	220-229	230–239	240-249	250-259	260–269	270-279
B. walteri sp. n.			2	5	2						
B. bennetti sp. n.						1	4	3	2		
B. brevirostris							2	5	4	3	2
B. bullocki			4	5	13	4	3				
B. beebei					4	5	2				
B. pinnicaudatus	2	5	2	2	1						
B. occidentalis (types)				2							
<i>B. occidentalis</i> (Maracaibo Basin)			2	6	2						
B. diazi			3	16	9	4					
B. janeiroensis			3	7							

in most other *Brachyhypopomus* (see fig. 53 in Sullivan 1997); fourth supraorbital pore lying near vertical through posterior nostril, pores inconspicuous. Preopercular lateralline canal embedded in preopercle, canals radiating out to pores. Pores of lateral-line canal immediately behind head without downward pointing tubes. Discernible lateral scales terminate along caudal filament. Five branchiostegal rays, medialmost two thin compared to outer three, blades oriented nearly vertically. Gill rakers robust for genus, some with weakly ossified cores, on anterior faces of first four gill arches. Rakers subtended on ceratohyals 1–4 by small trough-shaped ossicles. Approximately 50 gill filaments on arch one. Three pectoral radials, with partial fusion of all three at proximal end. Mesocoracoid bridge absent. Pectoral fin broad, robust, 14–17 branched plus unbranched rays, length 5.4-7.5% LEA. Anal-fin rays 227-255, length 4.0-4.5% LEA. Precaudal vertebrae 13-15, a high proportion of specimens show signs of damage and regeneration above anal fin terminus. As many as 72 caudal vertebrae in advance of regenerated portion of caudal filament. Body excluding head and fins covered with thin cycloid scales, small dorsally, larger posterolaterally, partially obscured by skin. Twelve scale rows above, 16 scale rows below lateral line at farthest extent of pectoral fin. Anal-fin origin near vertical through midpoint of extended pectoral fin. Caudal filaments short in intact mature specimens: 10-19% TL. Sexual dimorphism of caudal filaments not noted. Six columns of electrocytes at base of caudal filament, number of columns reduce to three or two along length of filament; 22-35 rows of electrocytes. Electrocytes do not extend anterior to base of urogenital pore. No accessory electric organs on head or humeral region.

Electric organ discharge. The EOD has a simple, head-positive monophasic waveform with a total duration 1.9–2.4 milliseconds at 25°C (Fig. 2). No sexual dimorphism has been observed. Resting EOD rate is very slow (2.0–8.9 Hz, mean 4.7 Hz, median 4.9 Hz, at 21–25° C, n=31). See Appendix III.

Coloration. Background color yellowish-tan in life, brownish-tan in preservation. Pigmentation variable: poorly to moderately developed irregular bands along sides, darker and wide above lateral line, often with a spot of darker intensity on lateral line itself. Bands either restricted to anterior portion of body above lateral line or connected to fainter bands below. Some bands connect to 8–12 irregular saddles across dorsum. Saddles more regular in smaller individuals. Dorsal rami of the anterior lateral line nerve visible when viewed from above as two thin, dark parallel lines running along upper back beginning a short distance behind head and continuing to mid-point of the back. Cheeks, underside of head and sides of body below lateral line peppered with prominent dark brown stellate chromatophores that greatly contrast with background color of skin and that do not form part of a larger pattern. Pectoral and anal fins with irregular brown pigment along rays, interradial membranes hyaline.

Distribution and ecology. See distribution map, Fig. 5. *Brachyhypopomus bennetti* sp. n. is known only from Amazon Basin where it appears to be common in floating meadow habitats on the margins of the Amazonas/Solimões River and its tributaries. Its distribution and habitat preference seems very similar to that of its sister species, *Brachyhypopomus walteri* sp. n., with which it is often collected.



Figure 8. Paratypes of *Brachyhypopomus bennetti* sp. n. (top 3) and *B. walteri* sp. n. (bottom 3) showing transparency of electric organ to transmitted light and comparative depth of the electric organ in the two species.

Table 4. Prec	audal vertebrae	counts of <i>Brack</i>	hyhypopomus	<i>walteri</i> sp. n	. and <i>B</i> .	<i>bennetti</i> sp. n.	(holotypes
and paratypes)	compared to se	ven other Brack	hyhypopomus :	species; mod	al values	highlighted.	

Species	11	12	13	14	15	16	17	18
<i>B. walteri</i> sp. n.			4	5	1	1		
<i>B. bennetti</i> sp. n.			2	5	3			
B. brevirostris				5	11	4		
B. bullocki	2	21	6					
B. beebei							11	4
B. pinnicaudatus				2	13	20	1	
B. occidentalis (types)				1	4	2		
<i>B.</i> cf. <i>occidentalis</i> (Maracaibo Basin)			1	8	1			
B. diazi			7	31	2			
B. janeiroensis					2	8		

Etymology. This species is named for Michael V.L. Bennett of the Albert Einstein College of Medicine of Yeshiva University, Bronx, New York, in honor of his pioneering work on electric fish neurophysiology. Bennett (1961, 1971) reported studying a *Brachyhypopomus* (therein *Hypopomus*) with a monophasic EOD likely to have been this species.

Key to the species of subgenus Odontohypopomus

Discussion

Affinities of the new subgenus

Together, several shared character states unobserved in other Hypopomidae and so presumably derived (teeth on the premaxillae, branchiostegal-ray orientation, similar pigmentation and long duration EODs with slow repetition rates) are strong evidence that these two new species are closest relatives among the described *Brachyhypopomus*. An unpublished analysis of mitochondrial DNA sequences in Sullivan (1997) further supports this conclusion. We take the step of erecting the new subgenus Odontohypopomus to provide a name to this distinctive, toothed subgroup of Brachyhypopomus that will serve to unite them should the genus be reorganized in the future. Other subgroups of *Brachyhypopomus* have already been recognized, although this one is the first to be formerly named. (Until others are, all other Brachyhypopomus species belong to the nominotypical subgenus Brachyhypopomus by default.) While phylogenetic relationships among all the described species of hypopomids remain to be determined, the available morphological and molecular data in Sullivan (1997) in combination with the subsequent descriptions of Brachyhypopomus species suggest the following natural subgroups withing the genus: (1) the "beebei-group" (unnamed Clade E in Sullivan 1997): including B. beebei, B. pinnicaudatus, B. gauderio, and B. draco; (2) the "occidentalis group" (unnamed Clade F in Sullivan 1997) including B. occidentalis, and B. diazi; and (3) the "brevirostris group" (unnamed Clade B in Sullivan 1997) including B. brevirostris and B. bullocki. Affinities of other species to these groups are less certain. Brachyhypopomus janeiroensis Costa & Campos da Paz, 1992 shares at least one derived

condition with *B. beebei* and *B. pinnicaudatus*: a free preopercular lateralis canal (Sullivan 1997). From its description and photo, *B. jureiae* Triques & Khamis, 2003 would appear to be a close relative of *B. janeiroensis* while the position of *B. bombilla* Loureiro & Silva, 2006 within *Brachyhypopomus* is difficult to assess from its description alone. We leave the task of recognizing additional subgenera of *Brachyhypopomus* to other authors currently revising the group.

Distinguishing between B. walteri sp. n. and B. bennetti sp. n.

When first collected, we considered whether these two morphotypes represented sexual dimorphism within a single species (indeed the two are frequently lumped in existing museum lots), but the observation of unambiguous males and females within each type dispelled this possibility. The two species are most easily distinguished from each other by differences in the thickness of the electric organ, the length of the caudal filament and their EOD, as well as by anal-fin ray counts. Brachyhypopomus bennetti sp. n. has a short but very deep caudal filament (length less than 20% TL) and a monophasic EOD waveform. By contrast, caudal filaments of *B. walteri* sp. n. measure 20-30% TL in individuals with sufficiently regenerated caudal filaments and this species has a very long, biphasic EOD waveform. Damage to the caudal portion of the body is common in both species and many specimens show incomplete regeneration. The electric organ of *B. bennetti* has six columns of electrocytes at the base of the caudal filament, that of B. walteri only three or four, and B. bennetti's organ viewed with transmitted light appears to occupy much more tissue above the anal fin musculature, along length of the body, than in B. walteri (Fig. 8). The EODs of B. bennetti are monophasic, while those of B. walteri are biphasic (Fig. 2). Brachyhypopomus bennetti have 227-255 anal fin rays while *B. walteri* have considerably fewer, 198–216. Furthermore, the teardrop-like pigment below the eye is usually more prominent in *B. walteri*, although also present to varying degrees in individuals of both species. We have examined an insufficient sample of cleared and stained specimens to judge if there are differences in the number of premaxillary teeth between the species, although in a sample of three cleared and stained specimens we found no more than two teeth per premaxilla in B. bennetti while up to five teeth per premaxilla in a sample of four cleared and stained B. walteri. In both species, the number of teeth is variable. Unfortunately, it is difficult to see these teeth in alcoholic specimens as they are obscured by thick, opaque tissue lining the roof of the mouth.

Ecological and evolutionary considerations

The probable sister-species status of *B. walteri* and *B. bennetti* is especially interesting given that they are frequently collected together (including at their common type locality) and have a broadly overlapping geographic distribution. Both species are known

exclusively from the Amazonas/Solimões basin and seem to prefer the root tangle of large, floating grass meadows that are common along the margins of the Amazon's river-floodplain system (Fig. 9). Why the ancestor of these two species would have regained oral teeth remains an interesting question, one that could perhaps be addressed by future studies of the diet and feeding behavior of these two species relative to their congeners.

Brachyhypopomus bennetti is unusual both for its remarkably large electric organ (as proportion of body depth occupied, depth of the caudal filament and a high number of horizontal columns of electrocytes) and an unusual EOD waveform that consists of a simple, head-positive pulse of long duration. Hopkins (1999) suggested that the differences in electric organ structure among species of Brachyhypopomus may often be adaptations to the conductivity of water in a species' preferred environment. Other species with five or six parallel columns of electrocytes and short caudal filaments such as B. diazi and B. occidentalis tend to be found in high conductivity environments (above 150 µS/cm), while species with three columns and extended caudal filaments such as B. brevirostris and B. bullocki are most commonly found in lower conductivity environments (often well below 100 μ S/cm). The first type of organ, with more electrocytes in parallel, but fewer in series, has low internal resistance and is adapted to generating current in water with low resistivity (high conductivity). The latter type, with more electrocytes in series, but fewer in parallel, has higher internal resistance and is capable of generating the higher voltages necessary for passing current through highly resistive (low conductivity) water. Thus, species-specific differences in electric organ structure may often reflect impedance-matching to water conductivity regimes (Hopkins 1999).

Conductivity in the white water floating meadow habitat where *B. bennetti* and *B. walteri* were collected is intermediate for Neotropical freshwater habitats: between 60 and 100 μ S/cm (pers. obs.). The characteristics of *B. walteri*'s electric organ (3 or 4 columns, intermediate length caudal filament) are similar to those seen in the probable sister clade to *Odontohypopomus*, *B. pinnicaudatus* + *B. beebei*. (Although these latter two species similarly occupy intermediate resistivity environments and are sometimes collected within floating meadows, they are primarily found farther from large river channels in "terra firme" creeks and lagoons.) Given this phylogenetic assumption, it seems probable that *B. bennetti*'s enlarged electric organ with five or six horizontal electrocyte columns evolved from an ancestor with an electric organ similar to that seen in *B. walteri*, *B. pinnicaudatus* and *B. beebei*, but as an adaptation to something other than high water conductivity.

In a study that considered selective pressures on gymnotiform EOD waveform evolution, and in which *B. bennetti* and *B. walteri* were identified as "sp. 1" and "sp. 2," respectively, Stoddard (1999) reported that amplitude-calibrated recordings of *B. bennetti*'s monophasic EOD show them to be very much more powerful than those of other, similarly sized *Brachyhypopomus* species and between five and ten times greater amplitude than those of *B. walteri*. The unusual EOD waveform, hypertrophied electric organ and high-amplitude EOD of *Brachyhypopomus bennetti* invites inquiry into the possible adaptive value of these features.



Figure 9. Type locality and habitat for *Brachyhypopomus bennetti* sp. n. and *B. walteri* sp. n. and method of capture with seines pulled underneath floating vegetation (*Paspalum repens* and *Eichhornia crassipes*) from a motorboat. Paraná do Paracuúba, south of Manaus, Brazil, approximately 03°12.6'S, 59°59.4'W.

Biphasic EODs in pulse gymnotiforms may have evolved from primitive monophasic EODs as a means to reduce the low frequency/direct current component of the signal to which electroreceptive predators (other gymnotiforms and catfishes equipped with ampullary-type electroreceptors) are sensitive (Stoddard 1999, Stoddard 2002, Stoddard and Markham 2008). Monophasic EODs are rare among modern adult gymnotiforms with pulse-type EODs: the only species reported to have them apart from *B. bennetti, Electrophorus electricus* (itself an electroreceptive predator) and one species of *Gymnotus* (*G. cylindricus*) from Guatemala. The first is protected from predation by its strong electric discharge and the second is geographically isolated from electric eels and other electroreceptive predators such as pimelodid catfishes. Noting that *B. bennetti*'s monophasic waveform is nearly identical in duration and shape to that of the electric eel, Stoddard (1999) suggested that the convergence may be a form of Batesian mimicry to deter predation by electroreceptive predators that associate monophasic EODs with electric eels.

Our fieldwork confirms that electric eels are common at the *Odontohypopomus* collection localities, as are piscivorous *Gymnotus* species that likely account for some of the tail damage observed in our specimens. Preference for floating meadow habitat near deep water also make these species vulnerable to predation from large pimelodid catfishes, such as *Pseudoplatystoma tigrinum*, a species that may specialize on gymnotiforms (Reid 1983, Zuanon 1990). Exposure to the high predation pressure that

likely characterizes Amazonian floating meadow habitat might favor the evolution of an EOD mimic of *E. electricus* and Stoddard's hypothesis makes predictions with respect to the behavior of electroreceptive predators that should be tested. However, in our collections we note similar proportions (>60%) of both *B. bennetti* and *B. walteri* that exhibit regenerated caudal filaments and posterior anal fin rays from earlier predation. We do not know the identity of these "tail grazers" and what proportion of them are electroreceptive, but the monophasic EOD of *B. bennetti* clearly does not prevent a high proportion of individuals from suffering such injuries.

An alternative (or additional) advantage of EOD monophasy in *Brachyhypopomus bennetti* may be related to the fact that, in contrast to its biphasic relatives, its EOD waveform remains largely unaltered after tail predation (Fig. 10). In a typical biphasic *Brachyhypopomus* EOD, the anterior and caudal portions of the electric organ do not contribute equally to the head-positive and head-negative phases. Only the posterior portion of the electric organ that includes the caudal filament produces the head-negative second phase to the EOD waveform, while the anterior electric organ produces a mostly head-positive, monophasic pulse (Bennett 1961, 1971, Caputi 1999, Stoddard 1999, Stoddard and Markham 2008). For this reason, individuals suffering predation injuries to the caudal filament and caudal portion of the body produce EODs with attenuated head-negative second phases (Fig. 10 A, B). Electrical crypsis by biphasy may be effectively impossible under conditions. EOD monophasy for electric eel mimicry is one interesting possibility, but monophasy for stability of the waveform is another.

Active electroreception and electric communication rely upon "tuberous"-type dermal electroreceptors some populations of which are narrowly tuned to the peak frequency of the fishes' own EOD (Bastian 1976, 1977, Hopkins 1976) and to the EODs of conspecific individuals detected at a distance (Hopkins and Heiligenberg 1978). Any mismatch between a fishes' EOD frequency spectrum and the frequency sensitivity of its own electroreceptors (and those of conspecific individuals) will be deleterious. In species with biphasic EODs, tail predation not only decreases the amplitude of the EOD, but alters its waveform and thus its frequency spectrum (Fig. 10 A, B), whereas such injury in Brachyhypopomus bennetti only affects amplitude (Fig 10 C). Hence it is worth considering that the monophasic EOD of Brachyhypopomus bennetti may have evolved to provide its electrosensory system greater robustness to tail injuries. Likewise, the positioning of more of the electric organ rostrally on the body (as opposed to along an exposed caudal filament) and a high amplitude EOD would increase resiliency of electrosensory function in fish that regularly lose caudal electrocytes to predation. These two hypotheses to account for the distinctive characteristics of B. bennetti's EOD and electric organ are not incompatible: this species could, in theory, enjoy advantages from both electric eel mimicry and EOD waveform stability simultaneously.

Sister species *Brachyhypopomus walteri* lacks these characteristics of the electric organ and EOD despite also persisting in floating meadows. However, differences in behavior or feeding ecology of these two species might result in exposure to different selective pressures, even in the same habitat, and future study may yet indicate differ-



Figure 10. Effect of loss of caudal portion of body by predation on electric organ discharge (EOD) waveform in three species of *Brachyhypopomus*. Undamaged individuals indicated by black dots and black EOD trace, those with regenerating caudal body following substantial injury with red **A** *B. pinnicauda-tus* specimens 93-20 (above) and 93-25 (below) **B** *B. walteri* paratypes 93-188/2 (above) and 93-187-1 (below). Damaged paratype 93-140 (blue trace) not shown **C** *B. bennetti* paratypes 93-37/1 (above) and 93-37/3 (below). EODs shown with head positivity upwards and amplitude-normalized.

ences in niche breadth and distribution between *B. walteri* and *B. bennetti*. The very different EOD waveforms of these two species may mediate reproductive isolation between them and reproductive character displacement may have also played a role in the divergence of these signals, as has been suggested for sympatric *Gymnotus* species (Crampton et al. 2011).

Comparative material examined

Type material: *Brachyhypopomus beebei* (Schultz), holotype USNM 120753 and two paratypes MBUCV 15163 and AMNH 15453, Caripito, Venezuela; *Rhamphichthys artedi* Kaup, syntype, MNHN 3157, La Mana River, French Guyana; *Rhamphichthys mulleri* Kaup, syntype, MNHN 3983 Cayenne, French Guiana; *Rhamphichthys brevirostris* Steindachner, two paralectotypes NMW 650398, Rio Guaporé, Brazil; Parupygus savannensis Hoedeman, holotype, ZMA 102375, Sipaliwini River, Surinam; Parupygus litaniensis Hoedeman, holotype, ZMA 100428, Litany River, Surinam, and paratype, ZMA 100407, La Mana River, French Guiana; Hypopomus occidentalis Regan, 7 syntypes, BMNH 1914.5.18.94-8, Río Condoto, Colombia; Hypopomus pinnicaudatus Hopkins, holotype, ANSP 163463, and paratype CU 71933, coastal French Guiana; Hypopomus janeiroensis Costa & Campos da Paz, holotype and paratypes, MZUSP 43130, tributary of the Rio São Joao near Rio de Janeiro, Brazil; Brachyhypopomus bullocki: holotype ANSP 187477, paratypes (15) ANSP 138024 (Colombia: Meta-Orinoco); Type material for Brachyhypopomus*diazi* is unlocatable. New collections of this species were made at the type locality (CU 94862). Non-type material: Hypopomus artedi: CU 71952 & CU 71953 (French Guiana: La Mana); FMNH 56768 (Brazil: Para: Amazon); USNM 225655 (Suriname: Sipaliwini). Brachyhypopomus beebei: ANSP 130488 (Ecuador: Napo); CAS 67702 (Peru: Amazon); CU 71944, CU 71945, CU 71956 (French Guiana: Sinnamary); FMNH 102272 (Peru: Yasuni-Amazon); FMNH 102281 (Peru: Napo-Amazon); FMNH 102279, 102284 & FMNH 102285 (Peru: Aguarico-Amazon); MCZ 30175 (Guyana: Nicaparoo-Amazon); USNM 301694 (French Guiana: coastal drainage); USNM 302003 (Suriname: Nickerie-Corantijn). Brachyhypopomus brevirostris: AMNH 40086 (Bolivia: Beni-Madeira-Amazon); CU 71942 (French Guiana: Kaw); CU 71957 (Venezuela: Apure–Orinoco); FMNH 54544 (Brazil: Guaporé); INPA 4385 (Brazil: Mato Grosso: Aripuaná); INPA 7358-7363, 7366-7367, 7373, 7377, 7379–7382, 7388, 7392 (Brazil: Roraima: Branco-Amazon); UMMZ 204512, 204743 (Bolivia: Beni-Madeira-Amazon); USNM 198081, 306868 (Brazil, Amazonas: Amazon). Brachyhypopomus bullocki: see list in Sullivan and Hopkins (2009); Brachyhypopomus diazi: MBUCV 16895 (Venezuela: Tocuyo); CU 94862 (Venezuela: Yaracuy); CU 94862 (Venezuela: Portuguesa-Orinoco). Brachyhypopomus occidentalis: ANSP 163176 (Costa Rica: Limon); CU 71936 (Panama: Atlantic slope); CU 71934 (Colombia: Pacific slope); FMNH 56791 (Colombia: San Juan); FMNH 56779, 56788, 56789 (Colombia: Pacific slope); FMNH 79124, 93123 (Ecuador: Palenque); INHS 60283 & USNM 121586 (Venezuela: Lago Maracaibo); USNM 302020 (Panama: Río Santa Maria). Brachyhypopomus pinnicaudatus: ANSP 163465 (French Guyana: coastal); FMNH 54546 (Brazil, Rio Grande do Sul: coastal); FMNH 54550 (Brazil, Amazonas: Amazon); INPA 4389, MCZ 78165 (Brazil, Amazonas: Amazon); UMMZ 207598 (Paraguay: Pilcomayo); USNM 216870 (Colombia: Amazon); USNM 229915 (Brazil, Amazonas: Amazon); USNM 263859 (Peru: Madre de Dios-Amazon); USNM 301966, 301967, 306866, 306694, 306749, 306789 (Brazil, Amazonas: Amazon). Brachyhypopomus sp. (indet. or undescribed): AMNH 39774, 39932 (Bolivia: Itenez-Amazon), AMNH 78060, 78112, 78114 (Peru: Ucayali-Amazon), ANSP 53894 (Brazil, Mato Grosso: Rio Paraguay); CU 71941 (Guyana: Rupununi); FMNH 53325 (Guyana: Nickaparoo); MCZ 2769 (Brazil, Amazonas: Amazon); MCZ 9435 (Brazil, Para: Amazon); MCZ 30175 (Guyana: Nickaparoo); MCZ 52124 (Brazil, Minas Gerais: São Francisco); UMMZ 206285, 206470 (Paraguay: coastal); USNM 199213 (Brazil, Mato Grosso: Juruena-Amazon);

USNM 266718 (Venezuela: Upper Orinoco); USNM 260254 (Venezuela: Apure– Orinoco); USNM 301979 (Brazil, Mato Grosso: Guaporé); USNM 301981 (Brazil, Mato Grosso: Xingu). Additional specimens examined in Sullivan (1997).

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Appendix I

Radiographs of *Brachyhypopomus bennetti* sp. n. holotype (top) and *B. walteri* sp. n. holotype (bottom) (doi: 10.3897/zookeys.327.5427.app1) File format: JPEG image file (jpg).

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Citation: Sullivan JP, Zuanon J, Fernandes CC (2013) Two new species and a new subgenus of toothed *Brachyhypopomus* electric knifefishes (Gymnotiformes, Hypopomidae) from the central Amazon and considerations pertaining to the evolution of a monophasic electric organ discharge. ZooKeys 327: 1–34. doi: 10.3897/zooKeys.327.5427 Radiographs of Brachyhypopomus bennetti sp. n. holotype (top) and B. *walteri* sp. n. holotype (bottom). doi: 10.3897/zooKeys.327.5427.app1

Appendix II

Audio recording of resting electric organ discharge of *Brachyhypopomus walteri* sp. n. (doi: 10.3897/zookeys.327.5427.app2) File format: Waveform Audio File (wav).

Explanation note: Audio recording of resting electric organ discharge of *Brachyhypopomus walteri* sp. n. holotype specimen (93-219) [.wav file, 4.3 MB].

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Citation: Sullivan JP, Zuanon J, Fernandes CC (2013) Two new species and a new subgenus of toothed *Brachyhypopomus* electric knifefishes (Gymnotiformes, Hypopomidae) from the central Amazon and considerations pertaining to the evolution of a monophasic electric organ discharge. ZooKeys 327: 1–34. doi: 10.3897/zookeys.327.5427 Audio recording of resting electric organ discharge of Brachyhypopomus walteri sp. n. doi: 10.3897/zookeys.327.5427.app2

Appendix III

Audio recording of resting electric organ discharge of *Brachyhypopomus bennetti* sp. n. (doi: 10.3897/zookeys.327.5427.app3) File format: Waveform Audio File (wav).

Explanation note: Audio recording of resting electric organ discharge of *Brachyhypopomus bennetti* sp. n. holotype specimen (93-220) [.wav file, 4.2 MB].

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Citation: Sullivan JP, Zuanon J, Fernandes CC (2013) Two new species and a new subgenus of toothed *Brachyhypopomus* electric knifefishes (Gymnotiformes, Hypopomidae) from the central Amazon and considerations pertaining to the evolution of a monophasic electric organ discharge. ZooKeys 327: 1–34. doi: 10.3897/zookeys.327.5427 Audio recording of resting electric organ discharge of Brachyhypopomus bennetti sp. n. doi: 10.3897/zookeys.327.5427.app3

RESEARCH ARTICLE



Intraspecific variation in the turtle barnacle, Cylindrolepas sinica Ren, 1980 (Cirripedia, Thoracica, Coronuloidea), with brief notes on habitat selectivity

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Abstract

Specimens of the turtle barnacle *Cylindrolepas sinica* Ren, 1980 were collected from sea turtles in Japanese waters. The specimens were hexagonal in shape and were found burrowing into the sea turtle plastron. Specimens were dissected and the hard and soft parts were compared with the original description.

Keywords

Turtle barnacle, Cylindrolepas, epibiont, variation, redescription, mitochondrial genes 12S and 16S

Introduction

Ren (1980) described a new species of barnacle, *Cylindrolepas sinica*, collected from green sea turtles, *Chelonia mydas* (Linnaeus, 1758). Hayashi (2009) subsequently recorded *Cylindrolepas sinica* from three species of sea turtle: the green sea turtle, *C. my-das*, loggerhead, *Caretta caretta* (Linnaeus, 1758), and hawksbill, *Eretmochelys imbricata* (Linnaeus, 1766). Subsequently, 13 species of the superfamily Coronuloidea, including *C. sinica*, were recorded during a 10-year (2002–2011) survey of epibionts attached to marine vertebrates from Japanese waters (Hayashi 2012). As shown in previous studies (Hayashi 2009, 2012), *C. sinica* is a common species on Japanese sea turtles.

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This species was described as a cylindrical and rounded barnacle in previous studies (as shown in Fig. 1A and 1B). This study describes the intraspecific variation occurring in *C. sinica* and emphasises the morphological differences between *C. sinica* and related species. Brief comments on host selectivity are also presented.

Materials and methods

Epibiotic barnacles were sampled from sea turtles on breeding beaches, in bycatch, and from strandings in Japanese waters (see Hayashi 2012). Specimens of *C. sinica* were collected from the turtle (skin and plastron) and preserved in 99% ethanol. The specimens were dissected and their soft parts mounted on slides with a drop of glycerine. The specimens examined have been deposited in Fujukan, the Museum of the University of Ryukyus, under accession numbers RUMF-ZC.

Systematics

Class Maxillopoda Dahl, 1956 Subclass Cirripedia Burmeister, 1834 Superorder Thoracica Darwin, 1854 Order Sessilia Lamarck, 1818 Suborder Balanomorpha Pilsbry, 1916 Superfamily Coronuloidea Newman & Ross, 1976 Family Platylepadidae Newman & Ross, 1976 Genus *Cylindrolepas* Pilsbry 1916

Cylindrolepas sinica Ren, 1980 http://species-id.net/wiki/Cylindrolepas_sinica Figs 1, 2

Cylindrolepas sinica Ren, 1980: 194, fig. 6; pl. 2 figs 12–20. Hayashi 2009: 1, fig. 1A, B. Hayashi 2012: 118, figs 10, 15g, pl. 3d. *Platylepas decorata* Zardus & Balazs, 2007: 1303, figs 7–9. Frick and Zardus 2010: 294.

Material examined. From the plastron of a green sea turtle stranded on Ishigaki Island, Okinawa, Japan, November 25, 2001, Ryota Hayashi coll. (RUMF-ZC-02047); from the plastron of a living green sea turtle, April 17, 2004, Hahajima Island, Ogasawara, Tokyo, Japan, Ryota Hayashi coll. (RUMF-ZC-02045); from a plastic tag on a stranded loggerhead sea turtle, September 26, 2010 at Yomitan, Okinawa, Japan, Ryota Hayashi coll. (RUMF-ZC-02048).

Additional description of intraspecific variation in the parietal wall. Wall outline stellate, parietes concave (Fig. 1C); translucent between external ornamentation, external


Figure 1. *Cylindrolepas sinica* Ren, 1980. **A–B** original variant occurring on the soft skin of sea turtles (RUMF-ZC-02030) **C–H** hexagonal variant occurring on the plastron of sea turtles (RUMF-ZC-02045) **A** and **C**, upper, basal, upper oblique and lateral views **B** and **D** parietal plates (surface and back view) **E** sutural elaboration of the parietal wall **F** upper view of radii **G** inner view of basal margin **H** basal margin with parietal ribs **I** hexagonal shell wall of *Xenobalanus globicipitis*.

longitudinal ridges low, broad, poorly defined, growth ridges numerous, fine, closely spaced; (Fig. 1D); sutural elaborations opaque, erect, irregular ridges slightly directed toward apex, not cupped (Fig. 1E); radii very narrow, externally teeth partly concealed



Figure 2. Habitat of *Cylindrolepas sinica* Ren, 1980. **A** the original rounded form aggregated on the tail of a green sea turtle **B** the hexagonal variant burrowing into a green sea turtle plastron **C** an unusual specimen attached to a plastic tag on a loggerhead sea turtle **D** close-up view of the individual attached to the plastic tag.

by sutural elaborations (Fig. 1F); internal midrib broad, short, flaring terminally or clubshaped, directed more downward than medially (Fig. 1G); internal lateral ribs well developed, moderately broad, short, extending below the basal margin, approximately same size and number of ribs on each side of midrib on all plates (Fig. 1G–H); sheath about two-thirds height of wall, basally terminating abruptly, not depending (Fig. 1D). Opercular valves and soft parts as described in Ren (1980) and Hayashi (2012).

Remarks. The original description of *C. sinica* described the rounded, cylindrical form and is accurate for individuals occurring on the soft skin of sea turtles. The general morphology of this species is as described by Ren (1980) and Hayashi (2012) and illustrated in the present work in Figs 1A, 1B, and 2A. Frick and Zardus (2010) and Frick (2013) regarded *C. sinica* as a junior synonym of *Platylepas decorata* Darwin, 1854. However, morphological differences between *C. sinica* and *P. decorata* are clearly detailed by Monroe and Limpus (1979), Ren (1980), Young (1991), and Hayashi (2012). *C. sinica* can be distinguished from other species easily by the morphological

	Labrum	Basal margin of sheath	Ornamentation of suture	Longitudinal ridges on parietes	Radii	Midrib folds	Secondary ribs	Inner surface of parietes
Cylindrolepas sinica	with a few teeth on each crest	continuous with inner laminae	present	absent	not visible	not visible	present	smooth
Cylindrolepas darwiniana	multidentate	continuous with inner laminae	rudimentary	rudimentary	not visible	not visible	present	smooth
Platylepas decorata	multidentate	depending	present	present	not visible	conspicuous	present	smooth
Platylepas hexastylos	with a few teeth on each crest	depending	absent	absent	visible, narrow	conspicuous	absent	with longitu- dinal ridges

Table 1. Comparative features of Cylindrolepas spp. and Platylepas spp.

Table 2. List of the materials examined. The GenBank accession numbers are from Hayashi et al. (2013).

	Host animal	Collected Locality	Materials deposited number	GenBank accession numbers
Cylindrolepas sinica (hexagonal form)	Chelonia mydas	Hahajima I., Ogasawara, Tokyo	RUMF-ZC-02045	AB723955
Cylindrolepas sinica (hexagonal form)	Chelonia mydas	Hahajima I., Ogasawara, Tokyo	RUMF-ZC-02047	AB723954
Cylindrolepas sinica (rounded form)	Chelonia mydas	Kanna, Ginoza, Okinawa	RUMF-ZC-02030	AB723953
Cylindrolepas darwiniana	Caretta caretta	Toya, Yomitan, Okinawa	RUMF-ZC-02029	AB723959
Cylindrolepas darwiniana	Caretta caretta	Toya, Yomitan, Okinawa	RUMF-ZC-02028	AB723960
Platylepas decorata	Chelonia mydas	Kanna, Ginoza, Okinawa	RUMF-ZC-02042	AB723950
Platylepas decorata	Chelonia mydas	Kanna, Ginoza, Okinawa	RUMF-ZC-02046	AB723951
Platylepas decorata	Chelonia mydas	Kanna, Ginoza, Okinawa	RUMF-ZC-02027	AB723952
Platylepas hexastylos	Caretta caretta	Otsuchi, Iwate	RUMF-ZC-02025	AB723956

characteristics listed in Table 1. In addition, the mitochondrial sequence variation of this and related species has been confirmed (the 12S rRNA, tRNA-Val and 16S rRNA regions, Table 2, see Appendix). Therefore, *Cylindrolepas sinica* is a valid species. In the phylogenetic analysis of Hayashi et al. (2013), *C. sinica* clustered with the whale barnacles (*Xenobalanus, Coronula*, and *Cryptolepas*). The pseudo-stalked barnacle *Xenobalanus globicipitis* also has hexagonal and cylindrical shell walls (Fig. 1A–I). Comparing these findings, *C. sinica* is likely ancestral to the whale barnacles (Hayashi et al. 2013).

Discussion

The rounded form (Fig. 1A and 1B) of this species (described by Ren 1980; Hayashi 2012) is found in the soft skin of sea turtles and forms colonies in proximity to other individuals, as well as in aggregations (Fig. 2A). The hexagonal variant of this species burrows into the hard parts of the turtle body (plastron) and is often found as isolated individuals (Fig. 2B). Therefore, the shell morphology of *C. sinica* exhibits phenotypic plasticity through habitat selection.

In a rare case, one individual was collected from a plastic tag attached to a loggerhead sea turtle (Fig. 2C, D). The tagged turtle was captured on June 24, 2010 in a set net at Yomitan, Okinawa, Japan, and recaptured in the same net on August 26, and finally found as a floating stranding nearby on September 26. These records indicate that this turtle was a resident in this coastal area, as reported in Hayashi (2009), and the presence of *C. sinica* is consistent with the previous report. In addition, this is the first record of the occurrence of C. sinica on an artificial object. This case indicates that C. sinica can attach to hard substrates, as well as living soft tissue, and the host selectivity of C. sinica is not the substrate material. Nogata and Matsumura (2006) reported the larval development and settlement of the whale barnacle, Coronula diadema (Linnaeus, 1767), which settled in a polystyrene Petri dish containing a small, isolated piece of skin tissue from the host whale. They suggested the involvement of a chemical cue from the host whale tissue in inducing larval settlement. In light of these findings, our finding of C. sinica settling on a plastic tag, and not directly on the body of the turtle, suggests that this settlement was triggered by a similar chemical cue. More information is necessary to clarify the settlement mechanism of epibiotic barnacles.

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Appendix

Phylogenetic analysis



The consensus trees in the neighbour-joining and maximum-parsimony analyses were inferred from 1000 bootstrap replicates and both analyses were conducted using MEGA ver. 5.0 (Tamura et al. 2011). The sequences were aligned using MUSCLE included in MEGA ver. 5.0. At each node, the numbers separated by the slash indicate the percentage NJ and MP bootstrap support, respectively (1000 replicates).

RESEARCH ARTICLE



Plutella australiana (Lepidoptera, Plutellidae), an overlooked diamondback moth revealed by DNA barcodes

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Abstract

The genus *Plutella* was thought to be represented in Australia by a single introduced species, *P. xylostella* (Linnaeus), the diamondback moth. Its status as a major pest of cruciferous crops, and the difficulty in developing control strategies has motivated broad-ranging studies on its biology. Prior genetic work has generally supported the conclusion that populations of this migratory species are connected by substantial gene flow. However, the present study reveals the presence of two genetically divergent lineages of this taxon in Australia. One shows close genetic and morphological similarity with the nearly cosmopolitan *Plutella xylostella*. The second lineage possesses a similar external morphology, but marked sequence divergence in the barcode region of the cytochrome *c* oxidase I gene, coupled with clear differences in genitalia. As a consequence, members of this lineage are described as a new species, *P. australiana* Landry & Hebert, which is broadly distributed in the eastern half of Australia.

Keywords

Australia, karsholtella, new species, xylostella

Introduction

The diamondback moth, *Plutella xylostella* (Linnaeus), is one of the most damaging insect pests, attacking cruciferous crops, such as cabbage and cauliflower, across its nearly cosmopolitan range. Because biological agents have proven ineffectual (Goodwin 1979), most control programs for this moth have relied on insecticides. Costs for its control are significant; they were estimated at one billion US dollars in 1992 (Talekar and Shelton 1993). Because P. xylostella has rapidly developed resistance to most insecticides (Sun et al. 1986), and was the first insect species to become resistant to Bacillus thuringensis (Talekar and Shelton 1993), work is being directed towards gaining a deeper understanding of its biology. One line of investigation has involved evaluations of gene flow among its populations through the analysis of protein polymorphisms and sequence divergence in mitochondrial genes. Initial studies of allozyme variation (Caprio and Tabashnik 1992, Kim et al. 1999) provided little evidence for geographic shifts in gene frequencies. Subsequent analysis of sequence variation in the mitochondrial cytochrome c oxidase I (COI) gene in P. xylostella from China, Hawaii, Korea, Philippines, and USA showed less than 1% sequence divergence among populations (Chang et al. 1997, Li et al. 2006). These genetic results suggest substantial gene flow among widely separated populations, supporting expectations from observational studies which have indicated that *P. xylostella* is highly migratory with populations in cool temperate regions annually reestablished from southerly locales (Harcourt 1986, Chapman et al. 2002). However, another allozyme study on *P. xylostella* from five continents (Africa, Asia, Australia, Europe, North America) provided a slightly different perspective (Pichon et al. 2006). Populations from most sites had similar allele frequencies, but the population from Japan showed considerable differentiation from those at the other sites, while the Australian populations showed variability. Specimens collected near Sydney possessed allele frequencies similar to populations in other nations (except Japan), but those from four other sites were distinctive. Based on these results, Pichon et al. (2006) concluded that gene flow was sometimes insufficient to prevent regional genetic divergence.

The present study was motivated by a large-scale DNA barcode study of Australian Lepidoptera (Hebert et al. 2013) which indicated that specimens assigned to *P. xylostella* included two lineages with substantial sequence divergence in the barcode region of COI. The present analysis places these results in perspective by comparing levels of sequence divergence among other members of this genus, and by examining the morphology of the two Australian lineages. Because these results provide compelling evidence that the lineages represent different species, a new taxon, apparently endemic to Australia, is described.

Materials and methods

Collections

Most of the Australian specimens of *Plutella* examined in this study were collected at UV light from 2004–2012 as a result of a sampling program to obtain specimens of

Lepidoptera for DNA barcode analysis. The results from Australian specimens were placed in a broader perspective through the inclusion of sequence records from two specimens (when available) for each of five other non-Australian *Plutella* species and one species in the closely allied genus *Eidophasia* possessing coverage on BOLD (Ratnasingham and Hebert 2007). In addition, a barcode record was obtained from the holotype of *Plutella karsholtella* Baraniak, a species which shows close morphological similarity to *P. xylostella*. Described from the Canary Islands, Greece, and Turkey, this species is only known from three females (Baraniak 2003).

DNA sequence analysis

DNA extracts were prepared from a single leg removed from each of 402 specimens of *P. xylostella*. 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). Subsequent analysis focused on the 397 sequence records greater than 500bp in length recovered from these specimens. Sequence divergences were quantified using the Kimura-2-parameter model of nucleotide substitution calculated with the analytical tools on BOLD (www.boldsystems.org). A neighbor-joining (NJ) tree was subsequently constructed with MEGA 5.05 (Tamura et al. 2011).

Specimen and sequence information

Details on the date and site of collection for each specimen, as well as a photograph are available through the following dataset (dx.doi.org/10.5883/DS-PLUT1). The same DOI provides access to the sequence records, trace files, and primer sequences used for PCR amplification, together with GenBank accession numbers.

Morphology

Genitalia dissections and slide mounts followed Landry (2007). Pinned specimens were photographed with a Canon EOS 60D camera 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. Lighting was provided by a ring of 144 LEDs covered with a white diffuser dome (Fisher 2012). 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.

The configuration of the vinculum-saccus in *Plutella* male genitalia makes it difficult to spread the genitalia open in the standard manner for slide mounting without causing significant distortion. As a result, the differences between *P. australiana* and *P. xylostella* are not readily apparent if standard mounts are attempted, even if the unrolling technique is employed. To display them properly, the different parts of the male genitalia were separated and temporarily mounted in lactic acid on slides under cover slips raised with vinyl props as wedges to prevent distortion or flattening. After photography, genitalia parts were permanently embedded in Euparal. Genitalia were photographed with a Nikon DS-Fi1 digital camera mounted on a Nikon Eclipse 800 microscope at magnifications of 100×. Nikon's NIS 2.3 Elements was used to assemble multiple photos of different focal planes into single deep-focus images.

Specimen depositories

AMS	Australian Museum, Sydney, New South Wales, Australia
ANIC	Australian National Insect Collection, CSIRO, Canberra, Australia
ASCU	Agricultural Scientific Collections Unit, Orange Agricultural Institute,
	Orange, New South Wales, Australia
BIOUG	Biodiversity Institute of Ontario, University of Guelph, Guelph, Ontario,
	Canada
BMNH	The Natural History Museum, London, UK
CNC	Canadian National Collection of Insects, Arachnids, and Nematodes,
	Ottawa, Ontario, Canada
USNM	National Museum of Natural History, Smithsonian Institution, Washington,
	D.C., USA
ZMUC	Zoological Museum, University of Copenhagen, Copenhagen, Denmark

Results

Molecular divergences

Analysis revealed that individuals of the five non-Australian species of *Plutella* and the species of *Eidophasia* each formed a distinct sequence cluster in the NJ tree (Figure 1). Interspecific divergences between pairs of these taxa averaged 9.5% and ranged from 2.2%–14.0%. The lowest mean divergence value was between *P. notabilis* Busck and *P. hyperborella* Strand, while the greatest was between *P. xylostella* and *P. geniatella* Zeller (Table 1). Because of their deep divergence, each species was assigned to a different Barcode Index Number (BIN) (Ratnasingham and Hebert 2013). No intraspecific sequence variation was detected in the six species included for comparison, but the 397 specimens originally assigned to *P. xylostella* were separated into two clusters with 8.6% sequence divergence. Members of one cluster derived from Asia, Australia, Europe, and North America, while those in the other cluster were only collected in Australia. Because subsequent morphological studies indicated clear differences in genitalia between



Figure 1. NJ tree based on K2P distances for the barcode region of the cytochrome *c* oxidase I gene among seven species of the genus *Plutella* and one member of the closely allied genus *Eidophasia*. Because of the large number of specimens for both *P. xylostella* and *P. australiana*, the tree nodes have been collapsed and specimen records are plotted by state for Australia and by country of origin in other cases. The bracketed numerals indicate the number of specimens from each site. The type specimen of *P. karsholtella* is reassigned to *P. xylostella* and is the only specimen of this species from Spain (Canary Islands).

	P. armoraciae	P. geniatella	P. hyperboreella	P. xylostella	P. notabilis	P. porrectella	E. vanella
P. geniatella	0.071						
P. hyperboreella	0.050	0.040					
P. xylostella	0.120	0.140	0.126				
P. notabilis	0.066	0.043	0.022	0.138			
P. porrectella	0.079	0.071	0.058	0.138	0.066		
E. vanella	0.098	0.121	0.107	0.115	0.110	0.124	
P. australiana	0.091	0.098	0.085	0.086	0.088	0.096	0.105

Table 1. Mean sequence divergences (K2P) for the barcode region of the COI gene for seven members of the genus *Plutella* and one member of the closely allied genus *Eidophasia*.

specimens in these two groups (see below), the sequence results were reconsidered presuming that the two clusters represented different species. The broadly distributed lineage was undoubtedly true *P. xylostella*, while the other lineage represents an overlooked species that is described below as *P. australiana*. Under this model, intraspecific divergence averaged 0.7% in *P. xylostella*, and 0.1% in *P. australiana*. Sequence analysis also indicated that the holotype female of *P. karsholtella* possessed a barcode sequence that was identical to a prevalent haplotype in *P. xylostella*.

Species description

Plutella australiana Landry & Hebert, sp. n. http://zoobank.org/20416523-A949-4784-BB18-00A8BA208B6D http://species-id.net/wiki/Plutella_australiana Barcode Index Number: BOLD:AAC6876 Figs 3–9, 17, 19, 21, 23, 25, 27, 29, 31

Material examined. Thirty males and 22 females were included in the type series. Five additional specimens were also barcoded but excluded from the type material due to their poor condition.

Type material. Holotype ♂, specimen # BIOUG00844-C06, labelled as follows: [label1] "Subset of: LOT# L#2010AUS-0039 | AUS: New South Wales [sic]: Canberra; Cook | 35.2612°S 149.0591°E 632m asl 15-Oct-10 | coll. Christy Carr, Paul Hebert, Stephanie Kirk, | Jaclyn McCormick, Jayme Sones"; [label2, pale yellow] "Barcode of Life | DNA voucher specimen | Sample ID BIOUG00844-C06 | BOLD Proc. ID: PHLCA1136-11"; [label3, pale green] "genitalia slide | JFL1731 [male symbol]"; [label4, orange] "HOLOTYPE | Plutella | australiana | J.-F. Landry & Hebert". Genitalia slide JFL1731. Condition of specimen: double-mounted, wings partly spread, left antenna missing, right hind and left mid- and hind legs removed for DNA barcoding. Deposited in ANIC.

PARATYPES: 29 males, 22 females. Australian Capital Territory: Canberra, Cook, 8 Moss Street, 35.261°S, 149.059°E, alt. 632 m, UV light, C. Carr, P.D.N.



Figure 2. Sites in Australia where specimens of *Plutella xylostella* (red) and *P. australiana* (blue) have been collected. The pie diagrams show the proportion of the two species at each site. These records only include specimens identified through DNA barcode analysis.

Hebert, S. Kirk, J. McCormick, J. Sones: 13, 1.X.2010, specimen # BIOUG00792-E09 (CNC); 2³, 6.X.2010, specimen # BIOUG00831-A04 (ANIC), BIOUG00831-H06 (BIOUG); 5Å, 7.X.2010–8.X.2010, specimen # BIOUG00788-B01 (ANIC), BIOUG00788-F08 (ANIC), BIOUG00788-F11 (slide JFL1730) (CNC), BI-OUG00788-F12 (ANIC); 1^o, 8.X.2010, specimen # BIOUG00829-H10 (CNC); 1∂, 9.X.2010, specimen # BIOUG00843-C02 (BIOUG); 1∂, 2♀, 15.X.2010, specimen # BIOUG00844-A09 (CNC), BIOUG00844-C03 (AMS), BIOUG00844-G03 (ANIC); 1∂, 2♀, 18.X.2010–20.X.2010, specimen # BIOUG00788-G04, slide JFL1740 (CNC), BIOUG00788-G06, slide JFL1736 (CNC), BIOUG00788-G05 (CNC); 1♂, 25.X.2010, specimen # BIOUG00788-H07 (CNC); 1♀, 27.X.2010, specimen # BIOUG00790-G12 (ANIC). Same locality, collected by P.D.N. Hebert: 23, 22.III.2011, specimen # BIOUG01025-G05 (ZMUC), BIOUG01025-G06 (CNC); 1∂, 1♀, 10.XI.2011, CCDB-12828-G04 (ZMUC), CCDB-12828-F10 (AMS); 1#m 12.XI.2011, specimen # BIOUG02125-G06 (CNC); 3⁽²⁾, 1⁽²⁾, 13.XI.2011, specimen # BIOUG02127-F12 (ANIC), BIOUG02127-G10 (BMNH), BIOUG02127-H01 (ANIC), BIOUG02127-H03 (ANIC); 1∂, 1♀, 16.XI.2011, CCDB-15380-G10 (BI-OUG), CCDB-15380-E08 (AMS); 1♀, 18.XI.2011, BIOUG02123-E08 (USNM);

1♀, 23.X.2011, specimen # BIOUG02109-B09 (BMNH); 1♀, 24.X.2011, specimen # BIOUG02109-C07, slide JFL1741 (ANIC); 19, 5.XI.2011, specimen # BIOUG02112-F11 (AMS); 19, 6.XI.2011, specimen # BIOUG02108-C09, slide JFL1737 (CNC). Same locality, collected by P.D.N. Hebert, R. Labbee, V. Levesque-Beaudin, J. McCormick, J. Sones, J. Webb: 1^Q, 29.III.2011–12.IV.2011, specimen # BIOUG01172-G03, slide JFL1738 (ANIC). Canberra, CSIRO property, 35.275°S, 149.111°E, alt. 588 m: 1^Q, 14.XI.2011–21.XI.2011, Malaise trap, P.D.N. Hebert, specimen # BIOUG02239-A02 (BIOUG). New South Wales: Byron Bay, 28.658°S 153.622°E, alt. 13 m: 1², 30.XII.2007, P.D.N. Hebert, specimen # 07-NSWBB-0046, slide JFL1684 (CNC). 2800 Pinnacle Rd., Lot 58, 33.297°S, 149.075°E, alt. 920 m., 19, 3.III.2005, H. Loecker, specimen # 05-NSW-00731 (ASCU). Orange, 353 Pinnacle Rd., UV light trap, 33.297°S, 149.075°E, 2♂, 1♀, 26.X.2010, H. Loecker, specimen # ww04709–ww04711 (ASCU). Smiths Lake, 32.377°S, 152.504°E, 1∂, 1^Q, 24.XII.2010–24.XII.2010, P.D.N. Hebert, specimen # BIOUG00987-B02 (ANIC), BIOUG00987-E12 (slide JFL1735) (CNC). Weddin Mt. National Park/ Bimbi State Forest, Grenfell, nr. "Seatons Farm", 33.913°S, 147.947°E, at light, 1, 9.XI.2007, H. Loecker, specimen # AM 2272, slide JFL1739 (ASCU). Hat Head, 31.063°S, 153.052°E, alt. 36.58 m., 23, 28.XII.2008, P.D.N. Hebert, specimen # 08-NSWHH-1277 (slide JFL1689) (ANIC), 08-NSWHH-1340 (slide JFL1690) (CNC). South Australia: 1 km N Border Cliffs, near the banks, Renmark, 34.024°S, 140.89°E, 4♂, 25.XI.2011, P.D.N. Hebert, UV light trap, specimen # BIOUG02248-G03 (slide JFL1732) (CNC), BIOUG02248-F12 (ANIC), BIOUG02248-G01 (ANIC), BIOUG02248-G04 (USNM). Lyrup Forest Reserve, 34.274°S, 140.64°E, 1° , 8.XII.2011, P.D.N. Hebert, UV trap by lake, specimen # BIOUG02246-B09 (ANIC). Pike Creek Woolshed, 34.278°S, 140.711°E, 13, 6.XII.2011, P.D.N. Hebert, mercury vapor light, specimen # BIOUG02120-H01 (ANIC).

Additional specimens barcoded, but not included in the type series.

Australian Capital Territory: Canberra, Manuka, 35.278°S, 149.166°E, 1 ex. (abdomen missing), 16.XII.2005, P. Hebert, specimen # 05-ACTC-285 (BIOUG). New South Wales: 2800 Pinnacle Rd., Lot 58, 33.297°S, 149.075°E, 1 \bigcirc , 1 ex. (abdomen missing), 24.II.2005, P.D.N. Hebert, specimen # 05-NSW-00732 (ASCU). Ellenborough, Tom's Creek Retreat, 31.459°S, 152.476°E, 1 ex (abdomen missing), 17.XII.2005, P.D.N. Hebert, specimen # 06-NSWE-00800 (BIOUG). Kosciuszko National Park, Charlottes Pass, 36.26°S, 148.2°E, alt. 1844 m., 1 \bigcirc , 1 \bigcirc , 08–09. III.2009, E.D. Edwards, specimens # am10299, am10372 (ANIC). Queensland: Townsville, Hermit Park, 19.283°S, 146.801°E, 1 ex., 01.X.2010, G. Cocks, specimen # gvc15526-1L (AMS).

Diagnosis. In external appearance *P. australiana* is indistinguishable from *P. xylos-tella*. Both species exhibit significant, overlapping variation in forewing pattern (Figs 3–16). Most specimens of both species have the pale, scalloped band along the hind/ dorsal margin typically used to recognize *P. xylostella*. That band varies from strongly marked to nearly indistinct (the latter particularly so in females) in both species. Here we illustrate only a selection of the variants, but intermediates in amount of dark



Figures 3–16. Dorsal aspect of forewings of *P. australiana* and *P. xylostella*. SpecimenID (sample ID) in parentheses. Scale bar = 2 mm. 3 *P. australiana*, male holotype, Australia: Canberra (BIOUG00844-C06) 4 *P. australiana*, female paratype, Australia: New South Wales, Bimbi State Forest (AM 2272) 5 *P. australiana*, male paratype, Australia: Canberra (BIOUG00788-F11) 6 *P. australiana*, female, Australia: Canberra (BIOUG02123-E08) 7 *P. australiana*, female, Australia: Canberra (BIOUG02108-C09) 9 *P. australiana*, male, Australia: Canberra (CCDB-12828-E05) 11 *P. xylostella*, male, Australia: Canberra (BIOUG02113-F05) 12 *P. xylostella*, female, Australia: Canberra (BIOUG02113-F05) 13 *P. xylostella*, female, Australia: Canberra (CCDB-12828-G07) 14 *P. xylostella*, female, Australia: Canberra (CCDB-12828-H01) 15 *P. xylostella*, female, Canada: Québec (CNCLEP00098486)16 *P. xylostella*, female holotype of *P. karsholtella*, Canary Islands: Tenerife (ZMUC00401145).

specking and spotting, fading of scalloped dorsal band, and intensity of brown colouration, exist among specimens of both examined. No reliable external difference was observed that permits the separation of the two species. Genitalia must be examined and they afford several good characters.

In *P. australiana*, the male genitalia appear overall more slender than in *P. xylostella*, particularly if viewed ventrally (Figs 27–28). The most easily observed difference involves the shape of the vinculum-saccus (Figs 19–22): in *P. australiana* it is slender with a slight medial constriction, a more protruded and inflated anterior apex, and is about $1.5 \times$ as long as wide; in *P. xylostella* it has a broader, more chunky aspect and in profile, is deeply concave, and is about as long as wide. The teguminal processes (Figs 17–18) are more slender and slightly separated medially in *P. australiana*, whereas they are broader and medially contiguous in *P. xylostella*. The valva (Figs 23–24) is evenly rounded with a slight sinuation in the ventral margin, and a zone of spiniform setae that is restricted to the medial area in *P. australiana*; whereas its ventro-distal margin is more or less distinctly angled and the zone of spiniform setae extends all the way to the angled apex in *P. xylostella*.

Female genitalia: In *P. australiana*, abdominal sternum 7 (S7) has a heart-shaped melanized area surrounding the antrum and it has a flat surface; the apex of the tubular projection of the antrum is barely extended beyond the posterior margin of S7 (0.15× length of S7) when viewed ventrally (Fig. 29), and has a constricted, curved apical half when viewed laterally (Fig. 31). In *P. xylostella*, the area of S7 surrounding the antrum is bordered by markedly raised pair of folds of the S7 wall which form two conical projections bracing the tubular projection of the antrum; the apex of the tubular projection of antrum is extended further out beyond posterior margin of S7 (0.5× length of S7) when viewed ventrally (Fig. 30), and is evenly broad and straight when viewed laterally (Fig. 32). The corpus bursae is proportionally smaller and about equal in length to S7 in *P. australiana*, whereas in *P. xylostella* it is proportionally larger and about 1.5× the length of S7.

Description. Male (Figs 3, 5, 9). Head off-white, vertex pale greyish brown, area behind eye and beneath ocellus greyish brown. Labial palpus porrect, segment 2 with forward-directed triangular, pale greyish brown tuft, leading edge white; segment 3 upturned, as long as 2, greyish white to greyish brown. Antenna about two-thirds length of forewing; scape with dense off-white to pale greyish brown pecten; flagel-lum dorsally off-white with a few scattered brown rings in distal half. Mesoscutum off-white. Tegulae greyish brown to brown. Forewing upper surface with costal region brownish grey with sparse, darker speckles; medial and fold region brown to buff-brown; dorsal region off-white to pale buff, sinuous margin with two or three scallops and lined with thin dark brown line, forming a dorsal band of two or three diamonds when wings are folded, in several specimens with dorsal margin lined with a few scattered dark brown dots; apical area paler and mottled with a mix of pale grey, brown, and black suffusion; apical fringe with alternating white and dark brown thin bands.

Female (Figs 4, 6, 7, 8). As male except colouration more variable, with several individuals paler overall and with subdued contrast from brownish buff to pale whitish



Figures 17–22. Male genitalia of *P. australiana* and *P. xylostella*. **17–18** tegumen-gnathos, ventral aspect **17** *P. australiana* (slide JFL1730, specimen BIOUG00788-F11) **18** *P. xylostella* (slide JFL1729, specimen BIOUG02113-A06). 19–20, tegumen-uncus-gnathos-vinculum complex, lateral aspect, valvae and phallus removed **19** *P. australiana* (slide JFL1732, specimen BIOUG02248-G03) **20** *P. xylostella* (slide JFL1733, specimen BIOUG02248-G02). **21–22** vinculum–saccus, ventral aspect **21** *P. australiana* (slide JFL1729). Scale bar = 100µ; all to same scale. at = anal tube; gn = gnathos; sac = saccus; teg = tegumen; tp = teguminal process; vin = vinculum.

grey, tegula off-white, scalloped dorsal region of forewing indistinct, costal and disc area with dark speckles.

Forewing length: males, 5.4mm–6.9mm (mean 6.1mm, n=30); females, 5.6mm–6.9mm (mean 6.1mm, n=22).

Male genitalia (Figs 17, 19, 21, 23, 25, 27) (6 preparations examined). Abdominal tergite 8 (T8) subquadrate, anteriorly with round emargination and protruded antero-lateral corners. Pleural lobes large, about as long as T7+T8, their inner margin edged with thin, ribbon-like sclerotization. Coremata present, 3.5× length of T8. Tegumen a narrow, transverse arch with very narrow dorsal rim, anterior margin laterally notched, pedunculi fused with dorsal arms of vinculum. Uncus absent. Teguminal processes developed as pair of heavily sclerotized, setose lobes projected to one-third of valva length; in profile with dorsal edge broadly rounded and ventral edge straight; in ventral view outline conical with slight outward curvature. Anal tube with lightly sclerotized distal portion about length of teguminal processes. Gnathos a narrow band extended and bent downward at right angle between teguminal processes with apex pointed anteriorly. Vinculum arms dorsally extended and fused with tegumen, ventrally extended into slender, triangular, transversely arched and ventrally concave saccus; in ventral view saccus about $1.5 \times$ as long as wide, middle portion slightly constricted, in profile about 5× as long as high. Valva subelliptical in outline, costa and apex evenly rounded, ventral margin slightly concave, length/width about 2.3; spiniform setae of ventral margin arranged in stretched cluster restricted to medial area; sacculus situated in antero-ventral area, with tight cluster of spiniform setae, which medially abut each other below socii when valvae are closed; outer wall of valva with transparent suboval "window" bearing two tufts of long, fine scales, one in antero-ventral third, the other in dorso-distal third. Phallus thin, sharply pointed, needle-like, with bulbous base braced by pair of posteriorly directed, hook-like processes; bulbus ejaculatorius crescentic in outline, about the size of bulbous base.

Female genitalia (Figs 29, 31) (7 preparations examined). Sternite 7 (S7) with medio-posterior, heart-shaped, sclerotized area that is distinctly delineated from less melanized antero-lateral areas, posterior emargination forming channel surrounding tubular medial projection of antrum bearing apical ostium bursae, sides of channel flat, only medial anteriormost portion of channel slightly raised around base of antrum; tubular projection 0.4× length of S7, in ventral aspect with apex only slightly extended beyond posterior margin of S7 (0.15× length of S7), in lateral view with distal portion constricted and upcurved. Ductus bursae thin, delicate, anterior twothirds membranous, posterior third (section inside antrum) sclerotized. Corpus bursae slightly shorter (0.9) than S7, thinly membranous, delicate, without signa. Posterior apophyses subequal in length to anterior ones. Anterior apophyses with a thin ventral branch extended transversally across S8 to lamella postvaginalis in middle; lamella postvaginalis composed of paired crescentic pads covered with sensilla trichodea and distally setose. Tergite 8 with transversely sclerotized distal third on which base of posterior apophyses are inserted, posterior margin lined with setae. Sternite 8+ovipositor subequal in length to S7.



Figures 23–28. Male genitalia of *P. australiana* and *P. xylostella*. 23–24, valva, inner aspect **23** *P. australiana* (slide JFL1689, specimen 08-NSWHH-1277) **24** *P. xylostella* (slide JFL1733, specimen BIOUG02248-G02). 25–26, phallus, dorsal aspect **25** *P. australiana* (slide JFL1690, specimen 08-NSWHH-1340) **26** *P. xylostella* (slide JFL1688, specimen 06-TASB-01769). 27–28, genitalia with phallus removed, ventral aspect **27** *P. australiana* (slide JFL1735, specimen BIOUG00987-E12) **28** *P. xylostella* (slide JFL1734, specimen 09-NSWHH-1674). Scale bar = 100µ; all to same scale. at = anal tube; scl = sacculus; tp = teguminal process; zss = zone of spiniform setae.

Note about male genitalia. The gnathos of *P. xylostella* has not been described in recent publications (Robinson and Sattler 2001, Baraniak 2003). It is present in both *P. xylostella* and *P. australiana* but difficult to see, especially in standard preparations in which the genitalia is mounted whole and flattened, because it is a narrow band wedged between the two teguminal processes, and it projects inwards (see Figs 17–20). Clarke (1971: 173) stated vaguely "gnathos rather involved, with sclerotized plates on each side", which actually described the teguminal processes more than the gnathos. He went so far as to say that the species was so well known that the description of its genitalia appeared superfluous! The male coremata are tightly associated with the anterior edge of the tegumen-vinculum arch and difficult to keep attached to the pleural lobes during the dissection process.

The term 'teguminal processes' has been used by Kyrki (1984) to designate the paired, setose structures that extend from the posterior margin of the tegumen. These have been termed 'socii' by some authors (e.g. Common 1990). Dugdale et al. (1998) stated that these processes were gnathal rather than teguminal, but did not provide supporting evidence. Kuznetsov and Stekolnikov (1976) called them socii in *P. xylos-tella* but, contrastingly, termed 'gnathos' topographically and functionally similar paired structures in *Eidophasia messingiella* (Fischer von Röslerstamm), a genus often related to *Plutella*. Our own examination revealed only a faint suggestion of suture between those lobes and the transversely narrow tegumen, as well as between the tegumen and the lateral arms of the gnathos. However, all these structures appear to be fused together. What seems clear to us is that the morphology of this region of the male genitalia has not been documented in sufficient detail to interpret these structures unequivocally. Therefore we prefer to use the more morphologically neutral term 'teguminal processes'.

Derivation of specific epithet. This species name reflects the current restriction of this taxon to Australia. It is a noun in apposition.

Distribution. *P. australiana* is so far known only from eastern Australia, in contrast to *P. xylostella* which is cosmopolitan in distribution. *P. australiana* and *P. xylostella* appear to have largely overlapping distributions within Australia as both species were collected in the ACT, NSW, QLD, and SA (Figure 2). They were collected together and on the same dates around Canberra on several occasions (Mar 2011, Apr 2011, Oct 2010 and 2011, Nov 2011), indicating that their adult flight periods and habitat requirements overlap. *P. australiana* may occur in other parts of Australia with the lack of records reflecting gaps in collecting. Although current records suggest that *P. australiana* is absent from Tasmania, further sampling is also required to confirm this fact. The two species appear to be roughly similar in abundance based on current records with 62 *P. xylostella* and 57 *P. australiana* among the haphazardly collected Australian specimens that have been sequenced.

Type locality. Australia, Australian Capital Territory, Cook, 35.2612°S, 149.0591°E.

Host plant. *P. xylostella* is thought to feed on a wide variety of cruciferous plants in Australia, including native and introduced species. However, Australian records are in question because of the past oversight of *P. australiana*. As a result, the host plants of both species are uncertain.



Figures 29–32. Female genitalia. **29** *P. australiana*, ventral aspect (slide JFL1684, specimen 07-NSWBB-0046) **30** *P. xylostella*, ditto (slide JFL1685, specimen 07-NSWBB-0144) **31** *P. australiana*, lateral aspect of antrum projection (slide JFL1736, specimen BIOUG00788-G06) **32** *P. xylostella*, ditto (slide MIC6811, specimen BIOUG02113-D10). Scale: Figs **29–30** = 200µ; Figs **31–32** = 100µ.

Plutella xylostella (Linnaeus, 1758)

http://species-id.net/wiki/Plutella_xylostella Barcode Index Number: BOLD:AAA1513 Figs 10–16, 18, 20, 22, 24, 26, 28, 30, 32

Plutella karsholtella Baraniak, 2003: 31. New synonymy. Type locality: Canary Islands, Tenerife. Holotype in ZMUC. Barcoded.

Remarks. Baraniak (2003) described *P. karsholtella* from three female specimens based on minor differences in genitalia from *P. xylostella*. The main difference (given in his diagnosis) is that the distal portion of the ductus bursae has a curve at the level of the antrum when viewed laterally. There are two drawings of the female genitalia in Baraniak (2003), one showing the ventral aspect, the other in lateral aspect, but it is not indicated what preparations or specimens they are based on, nor whether both were drawn from the same specimen. Considering that the two paratypes are from localities widely distant from the type locality (one is from northwestern Turkey, the other from Greece) and that the difference from *P. xylostella* is slight, it would have been important to indicate the stability of this trait. The similarity of the holotype barcode with a common haplotype of *P. xylostella* and the single minor difference in female genitalia (male genitalia unknown) suggest that it is synonymous with the latter and we consider it so here. We omit the suite of other previously well-established junior synonyms of *P. xylostella*, which can be found in Robinson and Sattler (2001).

The colouration of *P. xylostella* has been characterized as variable, with paler individuals in xeric regions (Robinson and Sattler 2001). Our examination of many specimens from Asia, Australia, Europe, and North America showed that much of the forewing variation appears restricted to females. Males are relatively constant in having the typical forewing pattern with a strongly defined, ochre or cream-coloured, scalloped dorsal fascia contrasting markedly with the brown anterior two-thirds. Females display significant individual variation deviating from this pattern, from a dorsal fascia that is more subdued to one that is indistinct or nearly lacking (Figs 12–16).

In a taxonomic review of Hawaiian *Plutella*, Robinson and Sattler (2001) described two morphologically indistinguishable 'host races' of *P. xylostella*, reared from larvae consuming the fruits (rarely the leaves) of caperbush (*Capparis*, Capparaceae). The recognition of two separate races with the same, albeit unusual, host was geographical, each being restricted to an island: 'host-race 1' found on Oahu was characterized as having a forewing pattern typical of "faded or at best weakly indicated" *P. xylostella*; whereas 'host-race 2' found on the big island of Hawaii was described as "unusual very pale (...) white to cream with faded yellow markings". They did not find significant genitalia differences from typical *P. xylostella*, which also occurs in the Hawaiian archipelago where it has been reared from several Brassicaceae. The colour differences that they describe for the host races appear to fall within the known variation of *P. xylostella* elsewhere and may not be diagnostically significant.

At least one of these Hawaiian races was included in a previous study of mtDNA variation in *P. xylostella* (as undescribed *Plutella* 'UPA' by Chang et al. (1997)). However, the sequenced specimens were without host plant record (not reared) and no vouchers were retained so their identity cannot be verified. Their short sequences (GenBank accession numbers AF019041 for *Plutella* 'UPA' and AF019042 for *Plutella* 'UPB') overlap the 3' half of the barcode region and, when compared to our results, are more than 10% divergent from the *australiana–xylostella* cluster, suggesting no conspecificity with either.

Discussion

Plutella xylostella has long been regarded as a very common and widely distributed species within Australia (Nielsen et al. 1996). The present reevaluation of its taxonomic status was motivated by the results of DNA barcode analysis which revealed that its Australian populations included two lineages showing 8.6% sequence divergence. Because prior studies have indicated that levels of intra-specific variation rarely exceed 2% in Lepidoptera (Hajibabaei et al. 2006, Hebert et al. 2009, Hausmann et al. 2011), this discovery strongly suggested that two species were present. Subsequent morphological examination confirmed the presence of clear differences in genitalia between specimens of the two taxa, motivating recognition of the Australian lineage as a new species. Although this study has led to the discovery of one cryptic species, it has also provided evidence that another species in the genus, *P. karsholtella*, is a junior synonym for *P. xylostella*. We base this conclusion on both its barcode identity with one of the commonest haplotypes in *P. xylostella* and its lack of clear diagnostic morphological features.

The past oversight of the presence of two *Plutella* species in Australia likely explains the regional allozyme variation previously detected in Australian populations of *P. xylostella* (Pichon et al. 2006). For example, the congruence between populations near Sydney and those in other nations could be explained if *P. xylostella* dominated collections from this locality, while those at the other sites were dominated by *P. australiana*. The presence of these two species also has implications for past evaluations of biological control strategies, particularly since both species appear to be abundant and widely distributed in eastern Australia.

There is a need to discover the host plant(s) of *P. australiana* to ascertain if it is also a crop pest. If so, its presence represents a new risk to international trade which should be evaluated. Examining known hosts of *P. xylostella* and other related *Plutella* may provide useful clues. Although *P. xylostella* has been recorded from a wide range of hosts across the world, records from plant families other than Brassicales are uncorroborated, with most being implausible (Robinson and Sattler 2001). However, there are notable exceptions. For example, two 'host races' of *P. xylostella* in Hawaii (Robinson and Sattler (2001)) have been reared from the fruits of caperbush (*Capparis*, Capparaceae, order Brassicales). Löhr and Rossbach (2001)

reported a population of *P. xylostella* from Kenya feeding on sugar snap pea, *Pisum* sativum (Fabaceae). Laboratory tests showed that it was bi-directionally cross-fertile with "normal" crucifer-feeding *P. xylostella* producing viable offspring. Pea-feeding P. xylostella also survived on kale (a crucifer). Their study mentioned that the identity of the species was "not in question", but they did not provide morphological or genetic evidence to support this assertion. It is also noteworthy that *P. armoraciae*, a species from northwestern North America that superficially looks like a very pale xylostella (but is 12% barcode divergent), feeds on horseradish (Armoracia, a perennial Brassicaceae) (Robinson et al. 2000), and Eidophasia dammersi (Busck), originally described in Plutella, from California, feeds on the perennial Cleome isomeris (Cleomaceae), another plant family in the Brassicales. These observations suggest the possibility that the host plant of *P. australiana* is not necessarily a Brassicaceae and that the Brassicales should be searched widely to ascertain the hosts for *P. australiana*. Capparaceae and Cleomaceae are closely related to Brassicaceae with similar phytochemistry (Stevens 2001, Reveal 2011). The single documented occurrence of P. xylostella on a non-Brassicale host might considerably broaden the host possibilities, but the uniqueness of this record and its restricted geographical location in Africa require further study. Restricting the search for *P. australiana* larvae to Brassicales in Australia might be a more fruitful approach to discover its host.

The high genetic distance among taxa analyzed, and the placement of *E. vanella* between the *P. australiana* – *P. xylostella* cluster and other members of *Plutella* suggests that current generic limits need further assessment. Baraniak (2003), studying only the Palearctic fauna and morphology, separated most species formerly in *Plutella* into two separate genera, *Pseudoplutella* Baraniak (monotypic with only *P. porrectella* (Linnaeus), and *Plutelloptera* Baraniak (including *P. geniatella* and *P. hyperboreella* of the present analysis), leaving *Plutella* to comprise only *P. xylostella* – *P. karsholtella*. Despite his arrangement being based on a cladistic analysis, his genera have not been widely adopted or are treated as subgenera of *Plutella* (Fauna Europaea 2013). Further work should combine morphological and genetic data with global taxon coverage to gain a better understanding of generic boundaries.

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RESEARCH ARTICLE



Review of Canadian species of the genus Dinaraea Thomson, with descriptions of six new species (Coleoptera, Staphylinidae, Aleocharinae, Athetini)

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Abstract

Twelve species of the genus *Dinaraea* Thomson are recognized in the Nearctic region, ten of which occur in Canada, all east of the Rocky Mountains. Six species are herein described as new to science: *D. bicornis* Klimaszewski & Webster, **sp. n.**; *D. longipenis* Klimaszewski & Webster, **sp. n.**; *D. quadricornis* Klimaszewski & Webster, **sp. n.**; *D. quadricornis* Klimaszewski & Webster, **sp. n.**; *D. quadricornis* Klimaszewski & Webster, **sp. n.**; *D. worki* Klimaszewski & Jacobs, **sp. n.**; and *D. piceana* Klimaszewski & Jacobs, **sp. n.** Four formerly described species are confirmed in Canada: *D. angustula* (Thomson), *D. backusensis* Klimaszewski & Brunke, *D. borealis* Lohse, and *D. pacei* Klimaszewki & Langor. The previously unknown male of *D. borealis* Lohse and female of *D. backusensis* are described. All species are illustrated with colour habitus images and black and white images of the median lobe of the aedeagus and spermatheca, and tergite VIII and sternite VIII of both sexes. New habitat and distribution data are presented and a key to all Nearctic species of the genus is provided.

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Keywords

Canada, Coleoptera, Dinaraea, Staphylinidae, taxonomy, identification

Introduction

Dinaraea Thomson is a small genus with mainly subcortical species distributed in the Palaearctic and Nearctic regions. There were nine valid species recorded from the Palaearctic region (Lohse 1974, Smetana 2004), and six species recorded from the Nearctic region prior to this publication. The Nearctic species, Dinaraea nomensis Casey, was previously transferred to the genus Boreophilia Benick (Lohse et al. 1990). The remaining six valid Nearctic species previously reported are: D. planaris (Mäklin) from Alaska (Mäklin 1852), D. subdepressa (Bernhauer) from New Hampshire (Bernhauer 1907), D. borealis Lohse described from Quebec (Lohse et al. 1990), D. pacei Klimaszewski & Langor from Newfoundland (Klimaszewski et al. 2011), D. backusensis Klimaszewski & Brunke from Ontario (Brunke et al. 2012), and the adventive Palaearctic species D. angustula (Gyllenhal) (Muona 1984, Klimaszewski et al. 2010, Brunke et al. 2012). We were not able to examine *D. planaris* (Mäklin) but instead used the redescription and drawing of the median lobe of the aedeagus of this species provided by Lohse and Smetana (1985). During the course of the present study we discovered six additional species new to science from Canada, all distributed east of the Rocky Mountains. Many species of this genus may have implications for forest pest management as potential natural enemies of bark beetles and other economically important subcortical insects.

Material and methods

We examined about 250 specimens of *Dinaraea* in this study. Nearly all specimens were dissected. Genitalic structures, tergite VIII, and sternite VIII were dehydrated in absolute alcohol, mounted in Canada balsam on celluloid microslides, and pinned with the specimens from which they originated. Specimens and dissected structures were examined using a Nikon SMZ 1000 stereomicroscope. Photographs were taken using an image processing system (Nikon SMZ 1500 stereoscopic microscope, Nikon Digital Camera DXM 1200F, and Adobe Photoshop software). Habitus photographs of all included species are provided, while genitalia are illustrated only for those species whose genitalia have not been shown in recent publications. In the species accounts, distributions are given by province or state (Canada, U.S.A.) or by country (elsewhere). These territories are abbreviated using Canada Post and United States Postal Service standards. Data for distribution maps were extracted from specimens in collections, as well as from literature records. Geographic coordinates were standard-ized using NAD83 datum, and maps were projected onto a Lambert Conic Conformal using ESRI ArcMap version 10 for Windows.

Morphological terminology mainly follows that used by Seevers (1978) and Ashe (2000). The ventral (= parameral) part of the median lobe of the aedeagus is considered to be the part of the bulbus containing the foramen mediale, the entrance of the ductus ejaculatorius, and the adjacent venter of the tubus; the opposite side is referred to as the dorsal (= abparameral) part.

Specimens were examined from the following collections:

AAEC SI	Agriculture and Agri Food Canada St. John's Newfoundland and Labrador
AAPC-5J	Agriculture and Agri-rood Canada, St. John S, Newfoundiand and Labrador,
	Canada
ACPE	Agriculture and Agri-Food Canada, Charlottetown, Prince Edward Island,
	Canada
CNC	Canadian National Collection of Insects, Ottawa, Ontario, Canada
DEBU	Guelph University Collection, Guelph University, Guelph, Ontario, Canada
	(temporarily at LFC)
FMNH	Field Museum of Natural History, Chicago, Illinois, USA
LFC	Laurentian Forestry Centre, Canadian Forest Service, Québec, Quebec, Canada
MUN	Memorial University of Newfoundland, St. John's, Newfoundland and
	Labrador, Canada (currently on long-term loan to David Langor, Canadian
	Forest Service, Edmonton, Alberta, Canada)
NBM	New Brunswick Museum, Saint John, New Brunswick, Canada
NOFC	Northern Forestry Centre, Canadian Forest Service, Edmonton, Alberta,
	Canada
NSM	Nova Scotia Museum, Halifax, Nova Scotia, Canada
RWC	Reginald Webster Collection, 24 Mill Stream Dr., Charters Settlement, New
	Brunswick, Canada
UAM	Museum of the North, University of Alaska, Fairbanks, Alaska, USA

Taxonomic review

Genus Dinaraea Thomson, 1858: 33.

http://species-id.net/wiki/Dinaraea

Type species. Homalota aequata Erichson, 1837.

Diagnosis. Body subparallel, flattened, integument with distinct meshed microsculpture, punctation distinct; head large, subquadrate to slightly elongate, genae usually longer than eyes, suborbital carina absent; clypeus long, nearly horizontal, not depressed as in other genera of Athetini; mandibles strong and slightly curved apically, left one with smooth edge and right one with small subapical tooth in apical third on inner edge; maxillary palpus 4-segmented, basal segment small and apical segment short and needleshaped; lacinia and galea moderately elongate, lacinia with fringe of long hairs subapically; labial palpus 3-segmented; ligula V-shaped and each arm narrow; pronotum usually of trapezoidal form, usually widest in apical third, with pubescence at midline of disc directed posteriad in apical two-thirds, anteriad in basal third, and laterad at sides; elytra short, at suture as long as pronotum or only slightly longer; abdominal tergites 3-5 each with distinct basal impression; tarsal formula 4-5-5; male tergite VIII in majority of species with small teeth at apical margin and sometimes also in adjacent area of disc; median lobe of aedeagus with athetine bridge and of a simple form, with inconspicuous structures of internal sac; spermatheca with conical capsule and long slim stem coiled posteriorly.

Comments. Based on the morphology of the male tergite VIII, two groups of species are recognized. One group, consisting of the majority of species, is characterized by tergite VIII bearing two-to-several small teeth on the apical margin. Species in the second group (*D. borealis, D. curtipenis, D. longipenis, D. planaris, D. subdepressa*), have tergite VIII truncate and without teeth on the apical margin.

Biology. Many species are known from the subcortical galleries of other insects but their diet is unknown.

Checklist of Nearctic species

- 1. *Dinaraea angustula* (Gyllenhal), adventive in Nearctic region [AB, LB, NB, NF, NS, ON, PE, QC, YT]
- 2. *Dinaraea backusensis* Klimaszewski & Brunke, in Brunke et al. 2012: 175 [MA, NB, ON]
- 3. Dinaraea bicornis Klimaszewski & Webster, sp. n. [NB, ON]
- 4. Dinaraea borealis Lohse et al., 1990: 198 [NB, ON, QC]
- 5. Dinaraea curtipenis Klimaszewski & Webster, sp. n. [NB]
- 6. Dinaraea longipenis Klimaszewski & Webster, sp. n. [NB]
- 7. *Dinaraea pacei* Klimaszewski & Langor, in Klimaszewski et al. 2011: 159 [AB, BC, LB, NB, QC]
- 8. Dinaraea piceana Klimaszewski & Jacobs, sp. n. [QC]
- 9. Dinaraea planaris (Mäklin 1852: 309) [AK, YT]
- 10. Dinaraea subdepressa (Bernhauer 1907: 386) [NH]
- 11. Dinaraea quadricornis Klimaszewski & Webster, sp. n. [NB]
- 12. Dinaraea worki Klimaszewski & Jacobs, sp. n. [QC]

Key to Nearctic species

(Excluding *D. planaris* (Mäklin), which is only known from the lectotype that was not available for study; see illustration of median lobe of the aedeagus (Fig. 11b (original image) and Fig. 11a (a redescription in Lohse and Smetana (1985))). This species sensu Lohse and Smetana (1985) keys to couplet with *D. pacei* but has a different shape of the median lobe of aedeagus).

Elytra at suture shorter than pronotum (Figs 1a, 4a, 10a)2
 Elytra at suture at least as long as pronotum (e.g., Figs 2a, 3a)4

2 Maximum width of elytra equal to maximum width of pronotum (Fig. 4a); median lobe of aedeagus and spermatheca as illustrated (Fig. 4b, e) Maximum width of elytra greater than maximum width of pronotum (Figs 1a, 10a).....**3** 3 Pronotum trapezoidal in shape, broadest in apical third, punctures very dense, pronotum appearing matte (Fig. 1a); male tergite VIII with two teeth (Fig. 1c); median lobe of aedeagus and spermatheca as illustrated (Fig. 1b, e) Dinaraea bicornis Klimaszewski & Webster, sp. n. Pronotum rectangular in shape, broadest at middle (Fig. 10a); male tergite VIII without teeth (Fig. 10c); median lobe of aedeagus as illustrated (Fig. 10b); female undescribed Antennal articles VIII-X strongly transverse (Figs 2a, 3a, 8a, 9a)......5 4 Antennal articles VIII-X moderately transverse (Figs 5a, 6a, 7a)......8 5 Pronotum rectangular in shape, broadest at middle, punctures very dense (pronotum appearing matte) and distanced from each other by a diameter of a puncture (Fig. 2a); male tergite VIII, median lobe of aedeagus, and spermatheca as illustrated (Fig. 2c, b, e) Dinaraea quadricornis Klimaszewski & Webster, sp. n. Pronotum trapezoidal in shape, broadest in apical third, punctures moderately dense, distanced from each other by more than diameter of a puncture (Figs 3a, 8a, 9a, 10a); genital structures different (e.g., Figs 3b, c, h; 9b, e; 10b).....**6** 6 Body moderately broad (Fig. 3a); male tergite VIII with four apical teeth (Fig. 3d); tubus of median lobe of aedeagus broad and rounded apically (Fig. 3b, h); spermatheca as illustrated (Fig. 3c)Dinaraea backusensis Klimaszewski & Brunke Tubus of median lobe of aedeagus narrow and sharply pointed apically (Figs 8b, 9b); spermatheca as illustrated (Fig. 5e, 6e, 7e, 8e); females of D. curtipe-7 Body dark brown almost black (Fig. 9a); tubus of median lobe of aedeagus short and sinuate ventrally, and with broad sclerites of internal sac (Fig. 9b); female unknown Dinaraea curtipenis Klimaszewski & Webster, sp. n. Body dark brown with reddish tinge (Fig. 8a); tubus of median lobe of aedeagus long and straight ventrally, and with narrow sclerites of internal sac (Fig. 8b); spermatheca as illustrated (Fig. 8e)Dinaraea borealis Lohse 8 Pronotum trapezoidal in shape, broadest in apical third (Figs 5a, 7a); male tergite VIII with or without apical teeth, but never with additional teeth-like structures in subapical part of disc (Figs 5c, 7c); spermatheca as illustrated Pronotum rectangular in shape, broadest at middle (Fig. 6a); male tergite VIII with four apical teeth and additional teeth-like structures in subapical

part of disc (Fig. 6c); spermatheca as illustrated (Fig. 6e) 9 Pronotum dark brown and elytra yellowish-brown (Fig. 5a); male tergite VIII, median lobe of aedeagus and spermatheca as illustrated (Fig. 5b, c, e).. Pronotum and elytra dark brown (Fig. 7a); genital structures differently shaped10 Median lobe of aedeagus with tubus slightly sinuate apically and slightly pro-10 duced ventrally at apex, internal sac structures short and straight (Fig. 13a); male tergite VIII without apical teeth (Fig. 13b), sternite VIII as illustrated (Fig. 13c)......Dinaraea subdepressa (Bernhauer) Median lobe of aedeagus with tubus sinuate and strongly produced ventrally, internal sac structures long and arcuate (Fig. 7b); male tergite VIII with small apical teeth (Fig. 7c); spermatheca S-shaped (Fig. 7e)...... Dinaraea pacei Klimaszewski & Langor [based on comparison of D. pacei with the Yukon specimen (CNC), which was compared with the lectotype of *D. planaris* by A. Lohse and Smetana (1985), there are no major external differences between the two species and they key to the same couplet. The two species differ by the shape of median lobe of aedeagus. See comments under D. pacei

1. Dinaraea bicornis Klimaszewski & Webster, sp. n.

http://zoobank.org/299D97AC-B15D-4D4A-A4DD-F11E2E8DA77A http://species-id.net/wiki/Dinaraea_bicornis Fig. 1a–g, Map 1

HOLOTYPE (male): CANADA, NEW BRUNSWICK, York Co., Kingsclear, Mazerolle Settlement, 45.872288°N, 66.83105°W, 9.IV.2006, R.P. Webster // Margin of stream, in litter at base of northern white cedar (LFC). PARATYPES: CANADA, NEW BRUNSWICK: Charlotte Co., 5 km NW of Pomeroy Ridge, 45.3059°N, 67.4343°W, 5.VI.2008, R.P. Webster // Red maple and eastern white cedar swamp, in moss & leaf litter near small vernal pools (RWC) 1 male; Charlotte Co., 3.5 km NW of Pomeroy Ridge, 45.3087°N, 67.4362°W, 16.VI.2008, R.P. Webster // Red maple swamp, in leaves and moss near small vernal pools (RWC) 1 female; York Co., Canterbury, Trail to Browns Mtn. Fen., 45.9033°N, 67.6260°W, 2.V.2005 // Mixed forest with cedar, margin of vernal pond in moist leaf litter (LFC) 1 sex undetermined; York Co., New Maryland, off Hwy 2, E of Baker Brook, 45.8760°N, 66.6252°W, 26.IV.2005, R.P. Webster // Old growth cedar swamp, in moss and litter at base of cedar (RWC) 1 female; York Co., NE of Exit 271 off Hwy 2, 45.8776°N, 66.8254°W, 8.VI.2008, R.P. Webster // Alder swamp with poplar, sifting leaf litter & moss near vernal pool (RWC) 1 female; ONTARIO: Leeds and Grenville. Co., 2 km SE Spencerville, 30.IV.1979, A. & Z. Smetana (CNC) 1 male, 1 female.



Figure 1. *Dinaraea bicornis* Klimaszewski & Webster, sp. n.: **a** habitus **b** median lobe of aedeagus in lateral view **c** male tergite VIII **d** male sternite VIII **e** spermatheca in lateral view **f** female tergite VIII **g** female sternite VIII. Habitus scale bar = 1.0 mm, other scale bars = 0.2 mm.

Etymology. The specific name *bicornis* means 'with two horns' in allusion to the two teeth on the male tergite VIII.

Diagnosis. *Dinaraea bicornis* (habitus Fig. 1a) may be distinguished from congeners by the following combination of characters: body length 3.1-3.4 mm; head and pronotum matte with dense microsculpture; pronotum broadest at apical third; elytra at suture shorter than pronotum, with asperate punctation; antennal articles



Map 1–4. Distribution map of: I Dinaraea bicornis sp. n. 2 Dinaraea quadricornis sp. n. 3 Dinaraea backusensis 4 Dinaraea worki sp. n.
7-10 strongly transverse; male tergite VIII with two small sharp apical teeth (Fig. 1c); median lobe of aedeagus with straight and short tubus narrowly rounded apically (Fig. 1b); spermatheca with pear-shaped capsule and moderately deep apical invagination, stem narrow, long and looped posteriorly, slightly swollen at apex (Fig. 1e).

Description. Body length 3.1–3.4 mm; body dark brown with at least posterior part of elytra paler, with legs, antennae and labial palpi yellowish-brown; head and pronotum with dense microsculpture and appearing matte; elytral and particularly pronotal microsculpture less dense and their integument appears glossy; head about as broad as pronotum, genae slightly longer than eyes in dorsal view; pronotum broadest in apical third, slightly transverse, longer than elytra at suture; elytra transverse, shorter than pronotum at suture, truncate posteriorly; abdomen arcuate laterally, broadest in apical third; male tergite VIII with two small sharp medial teeth at apical margin (Fig. 1c), sternite VIII slightly produced posteriorly, antecostal suture arcuate (Fig. 1d); median lobe of aedeagus with short and straight venter of tubus and narrowly rounded apex (Fig. 1b); female tergite VIII slightly sinuate apically on each side of disc (Fig. 1f), sternite VIII rounded apically, antecostal suture sinuate (Fig. 1g); spermatheca with pear-shaped capsule and moderately deep apical invagination, stem narrow, long and looped posteriorly, slightly swollen at apex (Fig. 1e).

Distribution. Known from New Brunswick and Ontario.

Collection and habitat data. Most adults were collected in April and May, and one specimen in October. The New Brunswick specimens were found in moss and leaf litter near the edges of small vernal pools in forests containing eastern white cedar (*Thuja occidentalis* L.) and red maple (*Acer rubrum* L.), and sometimes alder and poplar.

2. Dinaraea quadricornis Klimaszewski & Webster, sp. n.

http://zoobank.org/F1252FB1-064A-49FF-8619-1C741088FED7 http://species-id.net/wiki/Dinaraea_quadricornis Fig. 2a–g, Map 2

HOLOTYPE (male): CANADA, NEW BRUNSWICK, Queens Co., Cambridge, W of Jemseg at "Trout Creek", 45.8227°N, 66.1240°W, 3.VI.2007, R.P. Webster // Silver maple forest, under tight bark of *Ulmus americana* L. (White elm) (LFC) 1 male. PARATYPES: CANADA, NEW BRUNSWICK: Albert Co., Caledonia Gorge P.N.A., 45.7930°N, 64.7764°W, 1.VII.2011, R.P. Webster // Small rocky clear-cold river (Caledonia Creek), sifting drift material (tree bud material) in eddy area (RWC) 1 male; Albert Co., Caledonia Gorge P.N.A., 45.7941°N, 64.7736°W, 13.IX.2011, R.P. Webster // Near Crooked Creek, mixed forest (red spruce & yellow birch) in decaying mushrooms (NBM) 1 male; Carleton Co., Richmond, Hovey Hill Protected Area, 46.1115°N, 67.7770°W, 24.V.2005, R.P. Webster // Hardwood forest, under bark of beech log (RWC) 1 male; Queens Co., Canning, Grand Lake near Scotchtown, 45.8762°N, 66.1816°W, 30.IV.2006, R.P. Webster // Oak forest, under bark of oak (RWC) 1 female (NBM) 1 female; same locality and habitat data, and collector



Figure 2. *Dinaraea quadricornis* Klimaszewski & Webster, sp. n.: **a** habitus **b** median lobe of aedeagus in lateral view **c** male tergite VIII **d** male sternite VIII **e** spermatheca in lateral view **f** female tergite VIII **g** female sternite VIII. Habitus scale bar = 1.0 mm, other scale bars = 0.2 mm.

except 25.V.2006 (RWC) 1 male; Queens Co., Cranberry Lake P.N.A., 46.1125°N, 65.6075°W, 5–11.VI.2009 // R. Webster & M.-A. Giguère, Red oak forest, Lindgren funnel trap (RWC) 1 female; same locality and habitat data, and collectors except 25.VI-1.VII.2009 (RWC) 1 male; Queens Co. Grand Lake Meadows P.N.A., 45.8227°N, 66.1209°W, 17–30.VIII.2011, C. Hughes & R.P. Webster // Old silver maple forest and seasonally flooded marsh, Lindgren funnel trap (NBM) 1 female; Sunbury Co., Lakeville Corner, 45.9007°N, 66.2423°W, 10.IX.2006, R.P. Webster // Silver maple forest, on ridge with oaks, on gilled mushroom (RWC) 1 male; Sunbury Co., Gilbert Island, 45.8769°N, 66.2954°W, 18.VII.2012, C. Hughes & R.P. Webster // Hardwood forest on island, under bark of hardwood (AFC) 1 female York Co., New Maryland, Charters Settlement, 45.8340°N, 66.7450°W, 29.III.2006, R.P. Webster (LFC) 1 female; same locality data except 22.IV.2006, R.P. Webster // Mixed forest in wood pile under bark of spruce (RWC) 1 male; same locality data except 30.IV.2006, R.P. Webster // Mixed forest in wood pile under bark of spruce (RWC) 1 male; 1 female; York Co., New Maryland, Charters Settlement, 45.8404°N, 66.7360°W, 27.V.2008, R.P. Webster // Mixed forest, under bark of spruce (RWC) 1 female; York Co., New Maryland, Charters Settlement, 45.8404°N, 66.7360°W, 27.V.2008, R.P. Webster // Mixed forest, under bark of spruce (RWC) 1 female; York Co., New Maryland, Charters Settlement, 45.8404°N, 66.7360°W, 27.V.2008, R.P. Webster // Mixed forest, under bark of spruce (RWC) 1 female; York Co., New Maryland, Charters Settlement, 45.8404°N, 66.7360°W, 27.V.2008, R.P. Webster // Mixed forest, under bark of spruce (RWC) 1 female.

Etymology. The specific name *quadricornis*, means 'with four horns' in allusion to the four teeth on the male tergite VIII.

Diagnosis. *Dinaraea quadricornis* (habitus Fig. 2a) may be distinguished from congeners by the following combination of characters: body length 3.2–3.5 mm; head, pronotum and elytra matte with dense microsculpture; pronotum broadest at middle; elytra at suture as long as pronotum, with dense punctation similar to that on pronotum; antennal articles 7–10 strongly transverse; male tergite VIII with four small sharp apical teeth (Fig. 2c); median lobe of aedeagus with straight and short tubus, narrowly rounded apically and slightly produced ventrally (Fig. 2b); spermatheca with pear-shaped capsule and moderately deep apical invagination, stem narrow, long and looped posteriorly, slightly swollen at apex (Fig. 2e).

Description. Body length 3.2–3.5 mm; body dark brown with legs, antennae (at least basally) and labial palpi yellowish- or reddish-brown; head, pronotum and elytra matte, elytra less so, with dense microsculpture; abdominal microsculpture moderately dense and integument glossy; head about as broad as pronotum, genae slightly longer than eyes in dorsal view; pronotum broadest at middle, slightly transverse, as long as elytra at suture; elytra transverse, truncate posteriorly; abdomen arcuate laterally, broadest at middle; male tergite VIII with four small sharp teeth at apical margin (Fig. 2c), sternite VIII slightly produced posteriorly, antecostal suture sinuate (Fig. 2d); median lobe of aedeagus with short and straight tubus, venter of tubus and narrowly rounded apex slightly produced ventrally (Fig. 2b); female tergite VIII slightly sinuate apically on each side of the disc (Fig. 2f), sternite VIII truncate apically, antecostal suture sinuate (Fig. 2g); spermatheca with pear-shaped capsule and moderately deep apical invagination, stem narrow, long and looped posteriorly, slightly swollen at apex (Fig. 2e).

Distribution. Known only from New Brunswick.

Collection and habitat data. Adults were collected from March to September in several microhabitats: under tight bark of white elm in a silver maple (*Acer sac-charinum* L.) forest; in a gilled mushroom located on a ridge with oaks in a silver

maple forest; in a hardwood forest with silver maple and butternut (*Juglans cinerea* L.); under the bark of a hardwood tree; in a wood pile; under the bark of spruce (*Picea* sp.) in a mixed forest; under the bark of a spruce log in an old mixed forest; in a hardwood forest under the bark of a beech (*Fagus grandifolia* Ehrh.) log; in decaying mushrooms in a mixed forest with red spruce (*Picea rubens* Sarg.) and yellow birch (*Betula alleghaniensis* Britt.); and in a red oak (*Quercus rubra* L.) forest under the bark of red oak. Flying adults were also captured in Lindgren funnel traps in an old red oak forest and in an old silver maple forest and seasonally flooded marsh. One individual was sifted from drift material (tree buds) in an eddy area along a fast-flowing, clear, cold and rocky river.

3. Dinaraea backusensis Klimaszewski & Brunke

http://species-id.net/wiki/Dinaraea_backusensis\according to Klimaszewski et al 2013 Fig. 3a–g, Map 3

Dinaraea backusensis Klimaszewski & Brunke, in Brunke et al. 2012: 175.

HOLOTYPE (male): CANADA, ONTARIO, Haldimand-Norfolk Reg., 6 km W of Saint Williams, Backus Woods, Wetland trail, sugar maple-dominated mesic forest, 42.3954°N, 80.2934°W, 2.IV.2010, A. Brunke // Accession No. 00331025 (DEBU). Holotype examined.

Diagnosis. *Dinaraea backusensis* (habitus Fig. 3a) may be distinguished from congeners by the following combination of characters: body length 2.4–2.6 mm; head, pronotum and elytra moderately glossy with dense microsculpture; pronotum broadest in about apical third and narrowest at base; elytra at suture as long as pronotum, with dense punctation similar to that on pronotum; antennal articles 7–10 moderately transverse; male tergite VIII with four small apical median teeth, median ones rounded (Fig. 3d); median lobe of aedeagus with straight and short tubus, narrowly rounded apically (Fig. 3b, h); spermatheca with large pear-shaped capsule and moderately shallow apical invagination, stem moderately long and looped posteriorly, apical end strongly swollen (Fig. 3c).

Description. Body length 2.4–2.6 mm; body dark brown with legs, antennae (at least basally) and labial palpi yellowish- or reddish-brown; head, pronotum and elytra slightly glossy, with dense microsculpture; abdominal microsculpture moderately dense and integument glossy; head about as broad as pronotum, genae slightly longer than eyes in dorsal view; pronotum broadest in apical third, slightly transverse, as long as elytra at suture; elytra transverse, truncate posteriorly; abdomen arcuate laterally, broadest in middle; male tergite VIII with four small and short teeth at apical margin, all about the same size, median teeth rounded (Fig. 3d), sternite VIII slightly rounded posteriorly, antecostal suture arcuate and anterior margin concave (Fig. 3e); median lobe of aedeagus with short and straight venter of tubus and narrowly rounded apex (Fig. 3b, h); female tergite VIII broadly arcuate apically (Fig. 3f), sternite VIII rounded



Figure 3. *Dinaraea backusensis* Klimaszewski & Brunke: **a** habitus **b** median lobe of aedeagus in lateral view **c** male tergite VIII **d** male sternite VIII **e** spermatheca in lateral view **f** female tergite VIII **g** female sternite VIII **h** median lobe of aedeagus in lateral view based on holotype. Habitus scale bar = 1.0 mm, other scale bars = 0.2 mm.

apically, antecostal suture arcuate (Fig. 3g); spermatheca with large pear-shaped capsule and moderately shallow apical invagination, stem moderately long, and looped posteriorly, apical part strongly swollen (Fig. 3c).

Distribution. Known from Ontario and New Brunswick in Canada and Massachusetts in the USA.

Collection and habitat data. Adults were collected from March to August mostly from under the bark of rotting logs (spruce, maples) in a variety of hardwood and mixed hardwood-conifer forest types. Some adults were found in polypore fungi on a large fallen basswood (*Tilia americana* L.) and in moss and litter at the base of cedar in an old-growth eastern white cedar swamp. Flying adults were also captured in Lind-gren funnel traps in a red spruce forest with red maple and balsam fir (*Abies balsamea* (L.) Mill.) and in an old red pine (*Pinus resinosa* Ait.) forest.

Material examined. CANADA: NEW BRUNSWICK: Albert Co., Caledonia Gorge P.N.A., 45.8175°N, 64.7770°W, 6.VII.2011, R.P. Webster // Mature hardwood forest, rotten sugar maple log, under bark (RWC) 1 male; Caledonia Gorge P.N.A., 45.7760°N, 64.7935°W, 1.VII.2011, R.P. Webster // Old-growth sugar maple & yellow birch forest, under bark of sugar maple log (NBM) 1 male; Caledonia Gorge P.N.A., 45.8380°N, 64.8484°W, 3.VII.2011, R.P. Webster // Oldgrowth sugar maple & yellow birch forest, under bark of sugar maple log (NBM) 1 male; Carleton Co., Jackson Falls, "Bell Forest Preserve", 46.2200°N, 67.7231°W, 13.VIII.2006, R.P. Webster // Hardwood forest, on slightly dried Pleurotus sp., on dead standing maple (RWC) 1 female; Carleton Co., Jackson Falls, "Bell Forest Nature Preserve", 46.2199°N, 67.7231°W, 7.VI.2007, R.P. Webster // Rich Appalachian hardwood forest, in polypore fungi on large fallen basswood (RWC) 1 male; Charlotte Co., 5 km NW of Pomeroy Ridge, 45.3059°N, 67.4343°W, 5.VI.2008, R.P. Webster // Red maple and eastern white cedar swamp, under bark of red maple (RWC) 1 female; Sunbury Co., Acadia Research Forest, 46.0188°N, 66.7450°W, 17.VIII.2007, R.P. Webster // Road 16 Control, Mature red spruce & red maple forest, under bark of red maple (RWC) 1 female; Sunbury Co., Acadia Research Forest, 45.9866°N, 66.3841°W, 24-30.VI.2009, R. Webster & M.-A. Giguère // Red spruce forest with red maple & balsam fir, Lindgren funnel trap (RWC) 1 male; York Co., New Maryland, Charters Settlement, 45.8342°N, 66.7452°W, 23.IV.2004, R.P. Webster (LFC) 1 male; York Co., New Maryland, Charters Settlement, 45.8340°N, 66.7450°W, 27.IV.2005, R.P. Webster // Mixed forest, in wood pile, under bark of spruce (RWC, LFC) 2 males, 1 female; York Co., New Maryland, Charters Settlement, 45.8395°N, 66.7391°W, 1.V.2004, R.P. Webster // Mixed forest, under bark of conifer log (RWC) 1 female; York Co., New Maryland, 45.8395°N, 66.7391°W, 6.VI.2006, R.P. Webster // Mixed forest, in fungus covered log (punky wood) (RWC) 1 female; York Co., New Maryland, 45.8395°N, 66.7391°W, 18.VI.2008, R.P. Webster // Mixed forest, in rotten log (RWC) 1 female; York Co., New Maryland, off Hwy 2, E of Baker Brook, 45.8760°N, 66.6252°W, 6.IV.2005, R.P. Webster // Old growth cedar swamp, in moss & litter at base of cedar (RWC) 1 male; York Co., 15 km E of Tracy, off Rt. 645, 45.6848°N, 66.8821°W, 4-16.VI.2010, R. Webster & C. MacKay // Old red pine forest, Lindgren funnel trap (RWC) 1 male; York Co., 14 km WSW of Tracy, S of Rt. 645, 45.6741°N, 66.8661°W, 9.VI.2010, R.P. Webster // Old mixed forest, under bark of rotten red maple log (RWC) 1 male. USA: MASSACHUSETTS: Framingham, 10.III.1947, C.A. Frost (CNC) 1 female.

http://species-id.net/wiki/Dinaraea_worki Fig. 4a–g, Map 4

HOLOTYPE (male): CANADA, QUEBEC, Villebois, *Picea mariana*, coll. J. Jacobs, 2008, DB-ID 2913 (LFC). PARATYPES: CANADA, QUEBEC: Villebois, *Picea mariana*, coll. J. Jacobs, 2008, DB-ID 305 (LFC) 1 female; same data except: DB-ID 490 (LFC) 1 female; DB-ID 2749 (LFC) 1 female; DB-ID 2758 (LFC) 1 female; DB-ID 2765 (LFC) 1 female; DB-ID 2768 (LFC) 1 female; DB-ID 2770 (LFC) 1 female; DB-ID 2778 (LFC) 1 female; DB-ID 2780 (LFC) 1 female; DB-ID 2918 (LFC) 1 male; DB-ID 2994 (LFC) 1 female; Quebec, Sept Iles, 2.XI.1985 (LFC) 5 males, 7 females. NON-TYPES: CANADA, QUEBEC: Lac-St-Jean, Compagnie forestière Arbec, 50°22'54"N, 70°33'29"W, 12.VIII–25.VIII.2009, Annelage 2009, C. Hébert, pessière à mousses (LFC) 1 female; Lac-St-Jean, Compagnie forestière Arbec, 50°22'06"N, 70°33'22"W, 17.VI–01.VII.2009, Annelage 2009, C. Hébert, pessière à mousses (LFC) 1 females have slightly damaged spermathecae].

Etymology. Named for Dr. Timothy Work, Université du Québec à Montréal, Quebec, Canada, who provided many insect specimens for this study and who has advanced the ecological knowledge of epigaeic beetles in Canada.

Diagnosis. *Dinaraea worki* (habitus Fig. 4a) may be distinguished from congeners by the following combination of characters: body length 2.3–2.6 mm; head, pronotum and elytra moderately glossy with moderately dense microsculpture; pronotum broadest in middle and narrowest at base; elytra at suture as long as pronotum, with dense punctation similar to that on pronotum; antennal articles 7–10 strongly transverse; male tergite VIII with four small apical teeth, all short and rounded (Fig. 4c); median lobe of aedeagus with straight and short tubus narrowly rounded apically (Fig. 4b); spermatheca with large pear-shaped capsule and long apical invagination, stem short and looped posteriorly, with slightly swollen apical part (Fig. 4e).

Description. Body length 2.3–2.6 mm; body dark brown with legs, antennae (at least basally), labial palpi and posterior part of elytra yellowish- or reddish-brown; head, pronotum and elytra moderately glossy, with moderately dense microsculpture; abdominal microsculpture moderately dense and integument more glossy; head about as broad as pronotum, genae slightly longer than eyes in dorsal view; pronotum broadest in middle, slightly transverse, about as long as elytra at suture; elytra transverse, truncate posteriorly; abdomen arcuate laterally, broadest in middle; male tergite VIII with four small rounded teeth at apical margin (Fig. 4c), sternite VIII rounded posteriorly, antecostal suture arcuate and anterior margin broadly arcuate (Fig. 4d); median lobe of aedeagus with short and straight venter of tubus and narrowly rounded apex (Fig. 4b); female tergite VIII slightly sinuate apically on each side of disc (Fig. 4f), sternite VIII rounded apically, antecostal suture sinuate (Fig. 4g); spermatheca with large pear-shaped capsule, and long apical invagination, stem short and looped posteriorly, with slightly swollen apical part (Fig. 4e).



Figure 4. *Dinaraea worki* Klimaszewski & Jacobs, sp. n.: **a** habitus **b** median lobe of aedeagus in lateral view **c** male tergite VIII **d** male sternite VIII **e** spermatheca in lateral view **f** female tergite VIII **g** female sternite VIII. Habitus scale bar = 1.0 mm, other scale bars = 0.2 mm.

Distribution. Known from Quebec.

Collection and habitat data. Several adults were collected in November. Specimens from western Quebec were collected from dead and decaying black spruce (*Picea mariana* Mill. (BSP)) in a boreal forest dominated by black spruce.

5. Dinaraea piceana Klimaszewski & Jacobs, sp. n.

http://zoobank.org/18BB3EFB-5A12-4A99-A6F6-31969051AEFE http://species-id.net/wiki/Dinaraea_piceana Fig. 5a–g, Map 7

HOLOTYPE (male): CANADA, QUEBEC: Villebois, *Picea mariana*, coll. J. Jacobs, 2008, DB-ID 2797 (LFC) 1 male. PARATYPES: same data as the holotype except: DB-ID 333 (LFC) 1 female; DB-ID 847 (LFC) 1 male; DB-ID 1255 (LFC) 1 female; DB-ID 2722 (LFC) 1 female; DB-ID 1745 (LFC) 1 male; DB-ID 1747 (LFC) 1 female; DB-ID 2756 (LFC) 1 male; DB-ID 2774 (LFC) 1 female; DB-ID 2784 (LFC) 1 female; DB-ID 2785 (LFC) 1 male; DB-ID 2840 (LFC) 1 female; DB-ID 2844 (LFC) 1 female; DB-ID 2869 (LFC) 1 male; DB-ID 2870 (LFC) 1 male; DB-ID 2876 (LFC) 1 female; DB-ID 2879 (LFC) 1 male; DB-ID 2880 (LFC) 1 female; DB-ID 2884 (LFC) 1 male; DB-ID 2885 (LFC) 1 female; DB-ID 2893 (LFC) 1 female; DB-ID 2907 (LFC) 1 female; DB-ID 2908 (LFC) 1 male; DB-ID 2909 (LFC) 1 female; DB-ID 3265 (LFC) 1 male; MRC Manic, Réservoir Outardes 4, 50°37'N, 69°35'W, 2.VII–10.VII.2007, Chaire Côte-Nord, J.P. Légaré, Bloc Abitibi Sud, CP2 (CJSP) 3–10 m, Piège à impact, 2007-3-0520 (LFC) 1 female.

Etymology. *Piceana* is an adjective derived from the tree name *Picea mariana* Mill. (BSP), in allusion to the black spruce forest where it was found.

Diagnosis. *Dinaraea piceana* (habitus Fig. 5a) may be distinguished from congeners by the following combination of characters: body length 3.1–3.3 mm; head, pronotum and elytra matte with dense microsculpture; pronotum broadest in apical third and narrowest at base; elytra at suture slightly longer than pronotum, with dense punctation similar to that on pronotum; antennal articles 7–10 moderately transverse; male tergite VIII with four small apical teeth, all short and rounded (Fig. 5c); median lobe of aedeagus with straight and short tubus narrowly rounded apically and slightly produced ventrally (Fig. 5b); spermatheca with elongate pear-shaped capsule, and moderately long apical invagination, stem long, sinuate and looped posteriorly, with slightly larger apical part (Fig. 5e).

Description. Body length 3.1–3.3 mm; body dark brown with legs, antennae (at least basally), labial palpi and elytra yellowish- or reddish-brown; head, pronotum and elytra matte, with dense microsculpture; abdominal microsculpture less dense than that of pronotum and elytra and integument more glossy; head about as broad and as large as pronotum, genae slightly longer than eyes in dorsal view; pronotum broadest in apical third, slightly transverse, longer than elytra at suture; elytra transverse, truncate posteriorly; abdomen subparallel; male tergite VIII with four small rounded teeth at apical margin (Fig. 5c), sternite VIII rounded posteriorly, antecostal suture and anterior margin of disc sinuate (Fig. 5d); median lobe of aedeagus with short and straight venter of tubus and narrowly rounded apex (Fig. 5b); female tergite VIII concave basally and truncate apically (Fig. 5f); sternite VIII rounded apically and emarginated medially, antecostal suture slightly sinuate (Fig. 5g); spermatheca with elongate pear-



Figure 5. *Dinaraea piceana* Klimaszewski & Jacobs, sp. n.: **a** habitus **b** median lobe of aedeagus in lateral view **c** male tergite VIII **d** male sternite VIII **e** spermatheca in lateral view **f** female tergite VIII **g** female sternite VIII. Habitus scale bar = 1.0 mm, other scale bars = 0.2 mm.

shaped capsule and moderately long apical invagination, stem long, sinuate and looped posteriorly, with slightly swollen apical part (Fig. 5e).

Distribution. Known from Quebec.

Collection and habitat data. Most adults were collected in dead black spruce logs in boreal black spruce forests, and one was captured in an intercept trap in a boreal forest during July.

6. Dinaraea angustula (Gyllenhal)

http://species-id.net/wiki/Dinaraea_angustula\according to Klimaszewski et al 2013 Fig. 6a–g, Map 5

Aleochara angustula Gyllenhal, 1810: 393; as Dinaraea: Klimaszewski et al. 2011: 159.

Diagnosis. *Dinaraea angustula* (habitus Fig. 6a) may be distinguished from congeners by the following combination of characters: body length 3.3–3.7 mm; head, pronotum and elytra slightly glossy with dense microsculpture; pronotum broadest at middle and narrowest at apex and base; elytra at suture as long as or slightly shorter than pronotum, with dense punctation similar to that on pronotum; antennal articles 7–10 moderately transverse; male tergite VIII with four small apical teeth, all short and rounded and some additional tooth-like subapical structures (Fig. 6c); median lobe of aedeagus with straight and short tubus narrowly rounded apically and sometimes slightly hooked at apex (Fig. 6b); spermatheca with short pear-shaped capsule, and small apical invagination, stem long, straight medially and looped posteriorly, with slightly swollen apical part (Fig. 6e).

Description. Body length 3.3–3.7 mm; body dark brown with legs, antennae (at least basally), labial palpi and elytra yellowish- or reddish-brown, pronotum and abdomen lighter than head, sometimes entire body appears brown; head, pronotum and elytra slightly glossy, with dense microsculpture; abdominal microsculpture less dense and integument more glossy than that of pronotum and elytra; head about as broad as pronotum, genae slightly longer than eyes in dorsal view; pronotum broadest at middle, slightly transverse, usually longer than elytra at suture; elytra transverse, truncate posteriorly; abdomen subparallel; male tergite VIII with four small apical teeth, all short and rounded and some additional tooth-like subapical structures (Fig. 6c), sternite VIII produced apically (Fig. 6d); median lobe of aedeagus with short and straight venter of tubus and narrowly ventrally pointed apex (Fig. 6b); female tergite VIII concave basally and truncate apically (Fig. 6f), sternite VIII rounded apically and emarginated medially, antecostal suture slightly sinuate (Fig. 6g); spermatheca with short pear-shaped capsule, and small apical invagination, stem long, straight medially and looped posteriorly, with slightly swollen apical part (Fig. 6e).

Distribution. This Palaearctic species is adventive in North America (Klimaszewski et al. 2010). The earliest Canadian records are: Elora, Ontario in 1975 (DEBU); St. Andrews, New Brunswick in 1978 (DEBU); Fairview, Alberta in 1982 (DEBU). The first North American records are: Buffalo and New York before 1889 (Fauvel 1889); Davis, California before 1984 (Muona 1984). In Canada, the species is known from Newfoundland and Labrador, Nova Scotia, Prince Edward Island, New Brunswick, Quebec, Ontario, Alberta and Yukon Territory (Klimaszewski et al. 2007, 2010, 2011, 2012, Majka and Klimaszewski 2008, Webster et al. 2009). In the USA, it is reported from New York, Pennsylvania and California, but is likely more widely distributed in the northeastern states.



Figure 6. *Dinaraea angustula* (Thomson): **a** habitus **b** median lobe of aedeagus in lateral view **c** male tergite VIII **d** male sternite VIII **e** spermatheca in lateral view **f** female tergite VIII **g** female sternite VIII. Habitus scale bar = 1.0 mm, other scale bars = 0.2 mm.

Collection and habitat data. In North America, this species is associated with soil and organic debris in agricultural fields and disturbed urban meadows. It is also found in marsh litter, in leaf litter in mixed forests, in compost, under bark of decaying spruce logs, amongst vegetation on a coastal sand dune, in litter in a cattail marsh, in

leaf litter along a vernal pond, and in drift material along a lakeshore (Webster at al. 2009, Klimaszewski et al. 2010, 2011, 2012). Illustrations and a description of the larva were published in Topp (1975).

Material examined. CANADA, NOVA SCOTIA: Kings County, Sheffield Mills, July 22, 2002, Pitfall trap, Ken Neal (LFC) 1 male; Hants Co., Upper Rawdon, VII.18, 2008, J. Renkema, highbush blueberry field R2T1E (LFC) 1 male; Cape Breton Highlands National Park, Lone Shielding, PG729861, 28.VI.1983, R. Vockeroth, Malaise (CNC) 1 sex?; Bible Hill, 45.376°N, 63.260°W, 2005 (CNC) 1 sex?; Sheffield Mills, 45.151°N, 64.477°W, 1998 (NSM) 1 sex?; Sydney Tar Ponds, 46.150°N, 60.167°W, 1996 (NSM) 1 sex?; Upper Rawdon, 45.068°N, 63.712°W, 2005 (NSM) 1 sex? NEW BRUNSWICK: Albert Co., Shepody NWA, Germantown Section, 45.7056°N, 64.7642°W, 2004 (NBM) 1 female; Carleton Co., Wakefield (Belleville), Meduxnekeag Valley Nature Preserve, 46.1965°N, 67.6340°W, 11.V.2005, M.-A. Giguère & R. Webster // Mixed forest, margin of vernal pond in leaf litter (RWC) 1 female; Charlotte Co., St. Andrews, 45.067°N, 67.033°W, 1978 (DEBU) 1 sex?; Kent Co., N.P., Kouchibouguac, 24.V.1977, S.J. Miller, Code 51370 (CNC) 2 females; Queens Co., Canning, Grand Lake near Scotchtown, 45.8762°N, 66.1816°W, 30.IV.2006, R.P. Webster // Lake margin, in drift material (RWC) 1 female; York Co. New Maryland, Charters Settlement, 45.8395°N, 66.7391°W, 22.VII.2006, 17.IX.2006, 5.IX.2007, 23.IV.2008, 19.IX.2010, R.P. Webster // Mixed forest, in pile of decaying (mouldy) corncobs and corn husks (RWC) 2 males, 3 females. NEW-FOUNDLAND and LABRADOR: Red Bay, 51.734°N, 56.426°W, 2009 (MUN) 1 sex?; Shalloway, 49.409°N, 53.869°W, 2001 (MUN) 1 sex?; St. John's, Agriculture Canada Research Centre, 47.516°N, 52.785°W, 1982 (AAFC-SJ) 1 sex? PRINCE EDWARD ISLAND: Harrington, 46.350°N, 63.168°W, 1996 (ACPE) 1 sex? QUE-BEC: Cookshire, Co. Compton, SAB, Lum. 1, 13-V-1996 // 96-3-0218, Downey R., Plantation (LFC) 1 sex?; same data except: Lum. 4, 23-V-1996/ 96-3-0277 (LFC) 1 sex?; Lum. 2, 3-VI-1999/ 96-3-0242 (LFC) 1 female; Lum. 5, 8-VII-1996 // 96-3-0308 (LFC) 1 sex?; 45.420°N, 71.630°W (lit) (LFC) 1 sex?; Dorval, 11-IV-1985, in deciduous forest, LeSage & Smetana (CNC) 1 male; Montreal, VII-22-1969 & VII-30-1972, E.J. Kiteley (CNC) 2 sex?; Portneuf Co., Deschambault, 30.III.2007, Coll. Michel Racine // Sous rocher et débris, talus boisé déneigé, en bordure carrière (LFC) 1 female; Réserve Portneuf, Lac Poissonneux, 47.049°N, 72.125°W, 2000 (LFC) 1 sex?; 47.050°N, 72.120°W, 2000 (LFC) 1 sex?; ZEC B-Nelson, Lacdes-Étangs, 46.963°N, 72.050°W, 2000 (LFC) 2 sex?; Co. Charlevoix, Rte. 381, 47°42'N, 70°44'W, 13-21.VI.2000, Grands-Jardins 2000/ Coupe 53 (CP53), Luminoc, piège-fosse, Pessière noire, brulée, Coupe 50 ans, 2000-3-0053 (LFC) 1 female; Québec Co., Charlesbourg, 8.X.2007, Coll. Michel Racine // Sous debris végétaux en bordure plate-bande de fleurs cultivées (LFC) 1 female; Downey River Plantation, 1996, 1 sex?, P. Downey, Lum. 1, 23-27.6.96 (LFC) 2 males. ONTARIO: 3 mi N. Ramore, 1–14.VIII.1973, J. Redman & C. Starr (LFC) 1 female; Hamilton, 10-13-VII.1980, M. Sanbourne (CNC) 1 female; same data except: 15.VII.1981 (CNC) 1 sex?, 19.VII.1982 (CNC) 1 sex?; Pinery Pr. Pk., Grand Bend, 16–17.V.79,

M. Sanbourne (CNC) 3 sex?; Guelph, 30.VII-13.VIII.1982, D. Yu (CNC) 1 male; 18.VI.1982 (LFC) 1 male; Guelph, 43.536°N, 80.229°W, 1977 (DEBU) 1 sex?; 5 mi. Wye, VI-VII-1973, J. Redner & C. Starr (CNC, LFC) 3 males; same data except VII-VIII-1973 (CNC) 1 female; New Liskeard, 10.VII-1.VIII.1973, J. Redner & C. Starr (CNC) 1 male; Rondeau Pr. Pk., South Beach, 5.VI.1985, A. Davies, J.M. Campbell // In debris on beach at high water line (CNC) 1 male; Rondeau Pr. Park, sandy beach, 31.V.1985, A. Smetana (CNC) 4 females; Ancaster, 28.III.1963, J.E.H. Martin (CNC, LFC) 1 male, 27 sex?; Leeds Co., Chaffeys Locks, Lake Opinicon, mossy shore, 18.V.1975, I.M. Smith (CNC) 1 female; Ottawa, Kanata, 9.VII.79, A. Smetana (CNC) 1 sex?; Pr. Edward Co. (CNC) 24.X.1920, Brimley // J.F. Brimley Collection, Bequeathed 1976 (CNC) 1 male; same data except: 27.3.21 (LFC) 1 sex?; 8.V.46 (LFC) 1 sex?; Chatham, 22.V.1957, L.A. Miller (CNC, LFC) 2 males, 4 females; Windsor, Prairie area, 18.V-6.VII.1976, Dondale & Redner (CNC) 1 male; Windsor, prairie-oak woodland, 28.VI-18.V.1976, Dondale & Redner (CNC) 1 sex?; same data except: 8.VII-27.VIII.1976, pitfall (CNC) 1 female, 4 sex?; Pin oak woods (CNC) 8 sex?; Blair, Rare, The Dells, 43.383°N, 80.388°W, 2006 (DEBU) 1 sex?; Chatham, 42.434°N, 82.129°W, 2007 (DEBU) 1 sex?; Elora, 43.685°N, 80.427°W, 1975 (DEBU) 1 sex?; Owen Sound, 44.570°N, 80.930°W, 1978 (DEBU) 1 sex?; Pembroke, 45.820, 77.III.1980 (CNC) 1 sex?; Sarnia, 42.987°N, 82.318°W, 1983 (DEBU) 1 sex?; Tavistock, 43.322°N, 80.836°W, 1983 (DEBU) 1 sex?; Wilde Lake Bog, 8 km E Arthur, 43.846°N, 80.447°W, 1987 (DEBU) 1 sex?; Cottage Beaulieu, Beaulieu, 14.IV.06 (CNC) 1 sex? ALBERTA: Lacombe, Ag. Canada Sta., 52°28'N, 0113°44'W, 20.VII.2001, Jim Broatch // Pitfall Group EXP 53, Canada plots (harvested in 2001) VII.20-119 and VII.20-107 (LFC) 2 females; Lacombe, 54.467°N, 113.733°W, 2001 (lit) (LFC) 1 sex?; Fairview, 56.067°N, 118.384°W, 1982, (DEBU) 1 sex? YUKON: Alaska Hwy., Burwash Creek, 61.35°N, 139°W, 1987 (DEBU) 1 sex? USA, PENNSYLVANIA: Harrisburg, 22.IV.1980, E.J. Kiteley (CNC) 1 female.

7. Dinaraea pacei Klimaszewski & Langor

http://species-id.net/wiki/Dinaraea_pacei Fig. 7a–g, Map 6

Dinaraea pacei Klimaszewski & Langor, in Klimaszewski et al. 2011: 159.

HOLOTYPE (male): CANADA, NEWFOUNDLAND: LABRADOR, Goose Bay, Rts. 500 and 520 jct., 53°16.9'N, 60°24.6'W, 13–26.VIII.2001, S. and J. Peck // flight intercept trap, elevation 10 m, spruce-poplar forest, 2001-45 (LFC). Holotype examined.

Diagnosis. *Dinaraea pacei* (habitus Fig. 7a) may be distinguished from congeners by the following combination of characters: body length 2.2–2.5 mm; head, pronotum and elytra slightly glossy with dense microsculpture; pronotum broadest in apical third and narrowest at base; elytra at suture slightly longer than pronotum, with dense punctation similar to that on pronotum; antennal articles 7–10 moderately transverse; male tergite



Figure 7. *Dinaraea pacei* Klimaszewski & Langor: **a** habitus **b** median lobe of aedeagus in lateral view **c** male tergite VIII **d** male sternite VIII **e** spermatheca in lateral view **f** female tergite VIII **g** female sternite VIII. Habitus scale bar = 1.0 mm, other scale bars = 0.2 mm.

VIII with four minute apical teeth, all short and rounded, and scarcely visible (Fig. 7c); median lobe of aedeagus with strongly produced ventrally and narrowly rounded apically tubus (Fig. 7b); spermatheca with short pear-shaped capsule, and small apical invagination, stem short and looped posteriorly, with slightly swollen apical part (Fig. 7e).

Dinaraea pacei is not distinguishable externally from *Dinaraea subdepressa* (Bernhauer), which was described from New Hampshire. However, the two species can be readily separated by the structures of the internal sac of the median lobe. The internal sac of *D. subdepressa* has two simple, straight, narrowly elongate sclerites (Fig. 13a), while the sclerites of *D. pacei* are complex as illustrated in Fig. 7b. The apical part of the median lobe is straight and slightly produced ventrally at the apex in *D. subdepressa* (Fig. 13a), while it is sinuate and strongly produced ventrally in *D. pacei* (Fig. 7b). The two species apparently represent sister taxa.

Description. Body length 2.2–2.5 mm; body dark brown with legs, antennae (at least basally), labial palpi and elytra slightly paler and appearing reddish-brown, pronotum and abdomen lighter than head, sometimes entire body appears brown; head, pronotum and elytra slightly glossy, with dense microsculpture; abdominal microsculpture less dense and integument more glossy than pronotum and elytra; head about as large and broad as pronotum, genae slightly longer than eyes in dorsal view; pronotum broadest in apical third, slightly transverse, usually shorter than elytra at suture; elytra transverse, truncate posteriorly; abdomen subparallel; male tergite VIII with four minute apical teeth, all short and rounded, and scarcely visible (Fig. 7c); sternite VIII arcuate apically (Fig. 7d); median lobe of aedeagus with short and sinuate tubus and narrowly dorsally pointed apex (Fig. 7b); female tergite VIII concave basally and truncate apically (Fig. 7f), sternite VIII rounded apically and emarginated medially, antecostal suture slightly sinuate (Fig. 7g); spermatheca with short pear-shaped capsule, and small apical invagination, stem short and looped posteriorly, with slightly swollen apical part (Fig. 7e).

Distribution. This species was previously recorded only from southwest Labrador (Klimaszewski et al. 2011). Here, we provide new distribution data from British Columbia, New Brunswick, Quebec and Alaska.

Collection and habitat data. Adults in Newfoundland and Labrador were collected from June to August using pitfall traps and flight intercept traps in various coniferous forest types, and one specimen was collected under the bark of a dead red pine (Klimaszewski et al. 2011). In British Columbia, adults were caught in July and September in emergence traps attached to the trunks of lodgepole pine (Pinus contorta Dougl. ex Loud. latifolia Engelm.) infested by mountain pine beetle (Dendroctonus ponderosae Hopkins). In New Brunswick, adults were found: under the bark of large fallen spruce in an old-growth eastern white cedar swamp; under tight bark of American elm; in a silver maple forest; in fleshy polypore fungi at the base of a dead standing Populus sp. in a wet alder swamp; and in a group of Pholiota sp. at the base of a dead Populus sp. in a mixed forest. In Quebec, adults were found in dead black spruce in a black spruce forest. Adults were also captured in Lindgren funnel traps deployed in an old-growth white spruce (Picea glauca (Moench) Voss) and balsam fir forest, an old mixed forest with red and white spruce, red and white pine (Pinus strobus L.), and a rich Appalachian hardwood forest with some conifers. Adults were collected from March to September.



Map 5-6. Distribution map of: 5 Dinaraea angustula sp. n. 6 Dinaraea pacei.



Map 7–10. Distribution map of: 7 *Dinaraea piceana* sp. n. 8 *Dinaraea borealis* 9 *Dinaraea curtipenis* sp. n. 10 *Dinaraea longipenis* sp. n.

Material examined. PARATYPES: CANADA, NEWFOUNDLAND: SW Labrador, 76 km E Churchill Falls, Rt. 500, km 345, 53°18.8'N, 62°57.9'W, 12–26. VIII.2001, S. and J. Peck // flight intercept trap, elevation 530 m, spruce-moss forest, 2001-40 (LFC) 1 male; Labrador, 75 km SW Goose Bay, Rt. 500, 53°02.6'N, 61°16.6'W, 13–26.VIII.2001, S. and J. Peck // Flight intercept trap, elevation 100 m, spruce-lichen forest, 2001-43 (LFC) 1 female; SW Labrador, 72 km E Labrador City, Rt. 500, km 93, 53°08.6'N, 66°05.9'W, 12–27.VIII.2001, S. and J. Peck // Flight intercept trap, elevation 600 m, spruce-moss forest, 2001-34 (LFC) 1 female; NW Newfoundland, Doctor's Hill, St. John Bay, No. 185, 29.VII.1949, Ernst Palmén (MZH) 1 female; Little Grand Lake, Bakeapple Brook, old fir, pitfall, 13.VII-15.VIII.1992 (CFS-CB) 1 female; Avalon Pen., Cape St. Mary's, 7.VI.1978, D. Larson, Lot 5, (MUN) 1 male; Grand L., 6.VI.1984, D. Langor, (MUN) 1 male; 3.5 km E. Gambo Junction, 1.VI.1982, Langor and Raske, under red pine bark, L1, (MUN) 1 female.

NON-TYPES: CANADA, BRITISH COLUMBIA: 13 km E of Princeton, 49.5056°N, 120.3097°W, ex. MPB trap on pine, col. Bleiker, 27 Sept. 2011 // MPB Predator Study, PR5-S104, September 27, 2011, Emerge @ 70° (NOFC) 1 male; 27 km NE Princton, 49.5640°N 120.1477°W, ex. MPB trap on pine, col. Bleiker, 28 Sept. 2011 // MPB Predator Study, PR7-S102, September 28, 2011, Emerge @ 290° (NOFC) 1 female; 82 km N Fort St. John, 56.8054°N 121.7437°W, ex. MPB trap on pine, col. Bleiker, 13 July 2011 // MPB Predator Study, FSJ1-S103, July 13, 2011, Emerge @ 46° (NOFC) 1 female; same except FSJ1-S102, Emerge @ 150° (NOFC) 1 female. NEW BRUNSWICK: Carleton Co., Belleville, Meduxnekeag Valley Nature Preserve, 46.1897°N, 67.6710°W, 12.IX.2008, R.P. Webster // Mixed forest, in group of *Pholiota* sp. at base of *Populus* sp. (RWC) 1 female; Carleton Co., Jackson Falls, "Bell Forest", 46.2200°N, 67.7231°W, 21-28.VI.2009, R. Webster & M.-A. Giguère // Rich Appalachian hardwood forest with some conifers, Lindgren funnel trap (RWC) 1 female; Queens Co., Cambridge, W of Jemseg at "Trout Creek", 45.8227°N, 66.1240°W, 3.VI.2007, R.P. Webster // Silver maple forest, under tight bark of Ulmus americana (RWC) 1 male; Restigouche Co., Dionne Brook P.N.A., 47.9064°N, 68.3431°W, 31.V-15.VI.2011, M. Roy & V. Webster // Old-growth white spruce and balsam fir forest, Lindgren funnel trap (RWC) 1 female; York Co., 8.4 km W of Tracy, off Rt. 645, 45.6821°N, 66.7894°W, 6.V.2008, R.P. Webster // Wet alder swamp in fleshy polypore fungi at base of dead standing *Populus* sp. (RWC) 1 male; York Co., 14 km WSW of Tracy, S of Rt. 645, 45.6741°N, 66.8661°W, 26.V-2.VI.2010, 2-16.VI.2010, R. Webster & C. MacKay // Old mixed forest with red and white spruce, red and white pine, balsam fir, eastern white cedar, red maple and poplar forest, Lindgren funnel traps (RWC) 2 females. QUEBEC: MRC Manic, Lac Lacoursière, 51.28°N, 67.99°W, 18-26.VI.2007, Chaire Côte-Nord, J.P. Légaré; Block Arbec, CP1 (CJST) 3-10 m, Multi-Pher, fosse passif, 2007-3-0396 (LFC) 1 male; Ste Julie, 2.IV.1995 (LFC) 1 female; Villebois, Picea mariana, J. Jacobs, 2008 (LFC) 2 males, 19 females; Lac-St-Jean, Compagnie forestière Arbec, 50°22'54"N, 70°33'29"W, 3.VI-16.VI.2009, Annelage 2009, C. Hébert, pessière à mousses (LFC) 1 female; Lac-St-Jean, Compagnie forestière Arbec, 50°21'22"N, 70°31'17"W, 4.VI- 18.VI.2009, Annelage 2009, C. Hébert, pessière à mousses (LFC) 2 females; Lac-St-Jean, Compagnie forestière Arbec, 50°22'24"N, 70°33'29"W, 16.VI–01.VII.2009, Annelage 2009, C. Hébert, pessière à mousses (LFC) 5 females; Lac-St-Jean, Compagnie forestière Arbec, 50°21'22"N, 70°31'17"W, 18.VI–02.VII.2009, Annelage 2009, C. Hébert, pessière à mousses (LFC) 1 female; Lac-St-Jean, Compagnie forestière Arbec, 502°2'37"N, 703°3'03"W, 01.VII-14.VII.2009, Annelage 2009, C. Hébert, pessière à mousses (LFC) 1 female; Mare-du-Sault, Parc des Laurentides, 2700', 15–17.VIII.1970, J.M. & B.A. Campbell (CNC) 1 male, 1 female.

USA, ALASKA: Fairbanks, 930 Fitz Ct., el. 280 m, 64.901296°N, 147.528609°W, +/- 15 m small stand *Betula & Pop. trem.*, FIT, 29 IV–29 V.2008, D. Sikes, UAM100032370 (UAM) 2 females; 35.5 mi Dalton Hwy, el. 271 m, 65.74425°N, 149.34564°W, +/- 4 m *Betula*, *Salix*, white spruce, FIT, 31 V-5 VI.2008, D.S. Sikes, UAM100024452 (UAM) 1 female.

Comments. Several attempts, lasting about one year, to borrow lectotype of *D. planaris* (Mäklin), described from Alaska, and housed in the Museum of Helsinki have failed because the specimen is on loan and there are difficulties to get it back. This is the reason that we were not able to establish a concept of this species based on the lectotype. There is one specimen from Yukon (Dempster Hwy. mi 42, N of Klondike Riv., 1978, CNC, Ottawa), which Lohse and Smetana (1985) compared with the lectotype of *D. planaris* and according to them it is conspecific with this species. We have examined this specimen including its median lobe of aedeagus in dorsal and lateral view. Lohse and Smetana (1985) used this specimen for illustrating the median lobe of *D. planaris* in ventral view. The Yukon specimen examined by Lohse and Smetana is similar externally to *D. pacei* but differs from it by differently shaped median lobe of aedeagus (Fig. 11b). The male tergite VIII of the Yukon specimen is damaged and only about half of it is well preserved, it has small lateral tooth and minute crenulations from tooth towards the midline of disc.

8. Dinaraea borealis Lohse

http://species-id.net/wiki/Dinaraea_borealis Fig. 8a–g, 12, Map 8

Dinaraea borealis Lohse, in Lohse et al. 1990: 198 (based on a single female description).

HOLOTYPE (female): **CANADA**, **QUEBEC**, Gt. Whale River, 30.VI.1949, J.R. Vockeroth, No. 20341 (CNC). Holotype examined.

Diagnosis. *Dinaraea borealis* (habitus Fig. 8a) may be distinguished from congeners by the following combination of characters: body length 2.8–3.0 mm; head, pronotum and elytra slightly glossy with dense microsculpture; pronotum broadest in apical third and narrowest at base; elytra at suture as long as pronotum, with dense punctation similar to that on pronotum; antennal articles 7–10 moderately transverse; male tergite VIII without apical teeth (Fig. 8c); median lobe of aedeagus with straight,



Figure 8. *Dinaraea borealis* Lohse: **a** habitus **b** median lobe of aedeagus in lateral view **c** male tergite VIII **d** male sternite VIII **e** spermatheca in lateral view **f** female tergite VIII **g** female sternite VIII. Habitus scale bar = 1.0 mm, other scale bars = 0.2 mm.

long tubus pointed at apex and slightly pointed ventrally (Fig. 8b); spermatheca elongate with pear-shaped capsule, and long apical invagination, stem long and looped posteriorly, with strongly swollen apical part (Fig. 8e).

Description. Body length 2.8–3.0 mm; body variable in colour, either entirely black with brown or reddish appendages and part of elytra, or dark brown with legs,

antennae (at least basally), and labial palpi appearing reddish-brown; head, pronotum and elytra slightly glossy, the latter more so, with dense microsculpture; abdominal microsculpture less dense and integument more glossy than that of pronotum and elytra; head moderately large, as broad as pronotum, genae slightly longer than eyes in dorsal view; pronotum broadest in apical third, slightly transverse, usually as long as elytra at suture; elytra transverse, truncate posteriorly; abdomen arcuate laterally. MALE (**new description**): tergite VIII truncate apically and without apical teeth (Fig. 8c); sternite VIII rounded apically (Fig. 8d); median lobe of aedeagus with long and straight tubus with apex pointed ventrally (Fig. 8b). FEMALE: tergite VIII concave basally and truncate apically (Fig. 8f); sternite VIII rounded apically, antecostal suture strongly sinuate (Fig. 8g); spermatheca elongate with pear-shaped capsule, and long apical invagination, stem long and looped posteriorly, with strongly swollen apical part (Figs 8e, 12).

Distribution. This species was previously recorded only from Gt. Whale River in Quebec (Lohse et al. 1990). Here, we provide new distribution data for New Brunswick, Quebec, and Ontario.

Collection and habitat data. Adults were collected from March to August from: under bark of large fallen spruce in old-growth eastern white cedar forests; leaf litter under alders near a small stream in a mixed forest; and moss in a black spruce forest. Specimens were also captured in Lindgren funnel traps in an old-growth eastern white cedar forest and an old-growth white spruce and balsam fir forest.

Material examined. CANADA, NEW BRUNSWICK: Charlotte Co., 10 km NW of New River Beach, 45.2110°N, 66.6170°W, 15–29.VI.2010, R. Webster & C. MacKay // Old-growth eastern white cedar forest, Lindgren funnel trap (LFC) 1 female; Restigouche Co., Little Tobique River near Red Brook, 47.44616°N, 67.06888°W, 24.V.2007, R.P. Webster // Old-growth eastern white cedar forest, under bark of large fallen spruce (LFC, RWC) 2 males, 2 females; Restigouche Co., MacFarlane Brook Protected Area, 47.6018°N, 67.6263°W, 25.V.2007, R.P. Webster // Old-growth eastern white cedar swamp, under bark of large fallen spruce (RWC) 1 male, 2 females; Restigouche Co., Dionne Brook P.N.A., 47.9064°N, 68.3441°W, 31.V-15.VI.2011, M. Roy & V. Webster // Old-growth white spruce and balsam fir forest, Lindgren funnel trap (RWC) 3 males, 2 females; York Co. New Maryland, Charters Settlement, 45.8395°N, 66.7391°W, 29.III.2006, R.P. Webster // Mixed forest, under alders near small stream, in leaf litter (RWC) 1 female. QUEBEC: MRC Manic, Réservoir Outardes 4, 50.60°N, 69.37°W, 30.VII-07.VIII.2007, Chaire Côte-Nord, J.P. Légaré, Block Abitibi Nord, Témoin 1-10 m, Piège à impact, 2007-3-1306 (LFC) 1 male; MRC Manic, Lac Lacoursière, 51.27°N, 67.99°W, 18.VI-26.VI.2007, Chaire Côte-Nord, J.P. Légaré, Bloc Arbec, Témoin 3-10 m, Piège à impact, 2007-3-0168, CPRS 4-15 m, 2007-3-01153 (LFC) 2 females; same data except: 30.VII-07.VIII.2007, CPRS 3-10 m, 2007-3-1352 (LFC) 1 female; Lac-St-Jean, Compagnie forestière Arbec, 50°22'54"N, 70°33'29"W, 3.VI-16.VI.2009, Annelage 2009, C. Hébert, pessière à mousses (LFC) 1 female; Lac-St-Jean, Compagnie forestière Arbec, 50°21'22"N, 70°31'17"W, 4.VI–18.VI.2009, Annelage 2009, C. Hébert, pessière à mousses (LFC) 2 males; Lac-St-Jean, Compagnie forestière Arbec, 50°22'54"N, 70°33'29"W, 16.VI–01. VII.2009, Annelage 2009, C. Hébert, pessière à mousses (LFC) 1 male, 2 females; Compagnie forestière Arbec, 50°22'37"N, 70°33'08"W, 17.VI–01.VII.2009, Annelage 2009, C. Hébert, pessière à mousses (LFC) 3 males, 2 females; Lac-St-Jean, Compagnie forestière Arbec, 50°21'22"N, 70°31'17"W, 18.VI–02.VII.2009, Annelage 2009, C. Hébert, pessière à mousses (LFC) 1 female. **ONTARIO**: Moosonee, 2.VII.1973, Parry & Campbell (CNC) 1 female.

9. Dinaraea curtipenis Klimaszewski & Webster, sp. n. http://zoobank.org/214D0779-559A-4512-AC42-1D0B9B353A1B http://species-id.net/wiki/Dinaraea_curtipenis Fig. 9a–d, Map 9

HOLOTYPE (male): CANADA, NEW BRUNSWICK: York Co., New Maryland, Charters Settlement, 45.8395°N, 66.7391°W, 1.V.2004, R.P. Webster // Mixed forest, under bark of conifer log (LFC). PARATYPE: CANADA, NEW BRUNSWICK: York Co., New Maryland, Charters Settlement, 45.8395°N, 66.7391°W, 22.VII.2005, R.P. Webster // Mixed forest, in well-rotted fungus-covered log (RWC) 1 male.

Etymology. *Curtipenis* means 'possessing a short penis', in allusion to the short tubus of the median lobe of the aedeagus in this species.

Diagnosis. *Dinaraea curtipenis* (habitus Fig. 9a) may be distinguished from congeners by the following combination of characters: body length 3.0 mm; head, pronotum and elytra slightly glossy with dense microsculpture and bluish tinge; pronotum broadest in the middle and narrowest at base; elytra at suture as long as pronotum, with dense punctation similar to that on pronotum; antennal articles 7–10 moderately transverse; male tergite VIII without apical teeth (Fig. 9c); median lobe of aedeagus with straight, short tubus pointed at apex and slightly pointed ventrally (Fig. 9d), internal sac with distinct sclerites (Fig. 9b). *Dinaraea curtipenis* is superficially similar to *D. subdipressa* but can be distinguished from it by lacking a strongly depressed posterior edge of pronotum, while it is strongly depressed at the posterior angle of the disc and medially at base forming a groove in the latter species; and it has more elongate bulbus of median lobe of aedeagus with additional dorsal and ventral sclerotized structures (Fig. 9b).

Description. Body length 3.0 mm; body dark brown with reddish-brown tarsi, tibia and bases of antennae; head, pronotum and elytra slightly glossy, elytra more so, with dense microsculpture; abdominal microsculpture less dense and integument more glossy than that of pronotum and elytra; head large, as broad as pronotum, genae slightly longer than eyes in dorsal view; pronotum broadest in middle, slightly transverse, usually as long as elytra at suture; elytra transverse, truncate posteriorly; abdomen subparallel; male tergite VIII truncate apically and without apical teeth (Fig. 9c); sternite VIII rounded apically (Fig. 9d); median lobe of aedeagus with short and straight tubus with apex pointed ventrally (Fig. 9b). Female undescribed.



Figure 9. *Dinaraea curtipenis* Klimaszewski & Webster, sp. n.: **a** habitus **b** median lobe of aedeagus in lateral view **c** male tergite VIII **d** male sternite VIII. Habitus scale bar = 1.0 mm, other scale bars = 0.2 mm.

FEMALE. We have several females from New Brunswick localities found without male association that may belong to this species but because they are very similar externally and have similar genitalia to those of *D. pacei* we hesitate to formally associate them with *D. curtipenis*. These females have a more coarsely punctate pronotum than those of *D. pacei* but have similar rounded posterior angles of pronotum. We anticipate that this problem will be solved by finding females associated with males at the same locality.

Distribution. This species is known only from New Brunswick.

Collection and habitat data. The holotype was collected from under the bark of a conifer log in a mixed forest. Other individuals were captured in Lindgren funnel traps in an old red oak forest, an old-growth eastern white cedar forest, an old-growth white spruce and balsam fir forest, and old red pine forests. The paratype was collected from a well-decayed and fungus-covered log in a mixed forest. Adults were collected during May and July.

10. *Dinaraea longipenis* Klimaszewski & Webster, sp. n. http://zoobank.org/BE14DE6E-C25E-4DDC-8E43-60E72F3F7D69 http://species-id.net/wiki/Dinaraea_longipenis Fig. 10a–d, Map 10

HOLOTYPE (male): CANADA, NEW BRUNSWICK: York Co., New Maryland, Charters Settlement, 45.8267°N, 66.7343°W, 3.V.2006, R.P. Webster // *Carex* marsh, treading, sp. # 444 (LFC). PARATYPE: CANADA, NEW BRUNSWICK: Restigouche Co., Jacquet River Gorge P.N.A., 47.7491°N, 66.1114°W, 24.VI.2008, R.P. Webster // Hardwood forest, in well-rotted log (RWC) 1 male.

Etymology. *Longipenis* means 'possessing a long penis', in allusion to the long tubus of the median lobe of the aedeagus in this species.

Diagnosis. *Dinaraea longipenis* (habitus Fig. 10a) may be distinguished from congeners by the following combination of characters: body length 3.5 mm; head, pronotum and elytra slightly glossy with dense microsculpture; pronotum broadest in the middle and narrowest at base; elytra at suture shorter than pronotum, with dense punctation similar to that on pronotum; antennal articles 7–10 strongly transverse; male tergite VIII without apical teeth (Fig. 10c); median lobe of aedeagus with straight, long tubus rounded at apex and slightly pointed ventrally (Fig. 10b), internal sac with thin sclerites (Fig. 10b). FEMALE: We have one female from New Brunswick found without male association that may belong to this species. This female is externally very similar to the male of *D. longipenis* but the spermatheca and tergite and sternite VIII are indistinguishable from that of *D. piceana*. We need more specimens of this species, with male and female association, to confirm and formally describe the female of this species.

Description. Body length 3.5 mm; body dark black with light reddish-brown tarsi, tibia and bases of antennae; head, pronotum and elytra slightly glossy, the elytra more so, with dense microsculpture; abdominal microsculpture less dense and integument more glossy than that of pronotum and elytra; head large, about as broad as pronotum, genae slightly longer than eyes in dorsal view; pronotum broadest in middle, slightly transverse, longer than elytra at suture; elytra transverse, truncate posteriorly; abdomen arcuate laterally; male tergite VIII truncate apically and without apical teeth, slightly angular laterally at apical margin (Fig. 10c), sternite VIII rounded apically (Fig. 10d); median lobe of aedeagus with long



Figure 10. *Dinaraea longipenis* Klimaszewski & Webster, sp. n.: **a** habitus **b** median lobe of aedeagus in lateral view **c** male tergite VIII **d** male sternite VIII. Habitus scale bar = 1.0 mm, other scale bars = 0.2 mm.

and straight tubus with apex rounded and pointed ventrally (Fig. 10b). Female undescribed (see above).

Distribution. This species is known only from New Brunswick.

Collection and habitat data. The holotype was captured during May in a *Carex* marsh by treading emergent vegetation. The paratype was collected from a well-rotted log in a hardwood forest.



13. Dinaraea subdepressa

Figures 11–13. Genital structures of *Dinaraea*: **IIa** *D. planaris* (Mäklin), median lobe of aedeagus in ventral view, after Lohse and Smetana (1985), and **IIb** in lateral view **I2** *D. borealis* Lohse, spermatheca in lateral view, after Lohse (in Lohse et al. 1990) **I3a–c** *D. subdepressa* (Bernhauer), original images based on the type specimen: **I3a** median lobe of aedeagus in lateral view **I3b** male tergite VIII **I3c** male sternite VIII. Scale bars = 0.2 mm.

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