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# ZOOTAXA

4314

## **Revision of the Nearctic *Parathalassius* Mik (Diptera: Dolichopodidae: Parathalassiinae), with a review of the world fauna**

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## Abstract

The Nearctic species of *Parathalassius* Mik are revised and the world species are reviewed. Twelve species are recorded from the Nearctic Region including nine new species: *P. abela* **sp. nov.**, *P. aldrichi* Melander, *P. candidatus* Melander, *P. dilatatus* **sp. nov.**, *P. infuscatus* **sp. nov.**, *P. melanderi* Cole, *P. midas* **sp. nov.**, *P. sinclairi* **sp. nov.**, *P. socali* **sp. nov.**, *P. susanae* **sp. nov.**, *P. uniformus* **sp. nov.**, and *P. wheeleri* **sp. nov.** Lectotype designations are made for *P. aldrichi* Melander and *P. melanderi* Cole. A key to the 15 world species is provided and the distributions of the Nearctic species are mapped. COI mitochondrial DNA barcode sequences were obtained for 12 species of *Parathalassius*. A morphological phylogenetic analysis of the included species is presented and known ecological information is summarized.

**Key words:** Empidoidea, Dolichopodidae, Parathalassiinae, *Parathalassius*, Nearctic, Palaearctic, new species, morphology, DNA barcodes, cryptic diversity, phylogeny, zoogeography, ecology, sandy coastal beaches, dunes, El Segundo

## Introduction

*Parathalassius* Mik is a little known genus of predaceous flies that is now classified in an expanded concept of the Dolichopodidae (Sinclair & Cumming 2006), within the subfamily Parathalassiinae (Brooks & Cumming 2011, 2016). The genus contains several species of small greyish flies (Figs 1–10) that are found along sandy sea coasts (Figs 11–22) in both the Palaearctic and Nearctic Regions (Shamshev 1998). The Palaearctic species include *P. blasigii* Mik from the Mediterranean region and the Azores (Chvála 1988, 1989), as well as *P. maritimus* Shamshev and *P. ulrichi* Shamshev from Far East Asia (Shamshev 1998). In the Nearctic Region, *P. candidatus* Melander, *P. aldrichi* Melander and *P. melanderi* Cole have been recorded from the Pacific coast (Melander 1928, 1965).

We have been actively collecting and accumulating Nearctic specimens of this poorly known genus, including discovery of several undescribed species. The purpose of this paper is to revise the Nearctic fauna and review the world species of *Parathalassius*. In addition, we analyze the phylogenetic relationships of the included species, and discuss what is known of their ecology and zoogeographic history.



**FIGURES 1–4.** *Parathalassius* habitus photographs. 1–3. Males of *Parathalassius abela* sp. nov., resting on *Ambrosia chamissonis* (Less.) Greene (beach bur), at Surf Beach, California. 4. Female *Parathalassius abela* sp. nov., resting on sand at Oso Flaco Dunes, California. Photographs by Alice Abela.



5 (*P. blasigii* ♂)



6 (*P. blasigii* ♀)



7 (*P. infuscatus* ♂)



8 (*P. uniformus* ♂)



9 (*P. uniformus* ♂)



10 (*P. uniformus*)

**FIGURES 5–10.** *Parathalassius* habitus photographs. **5.** Male of *Parathalassius blasigii* Mik resting on sand at Parque Natural do Litoral Norte, Portugal. **6.** Female of *Parathalassius blasigii* Mik resting on sand at Parque Natural do Litoral Norte, Portugal. **7.** Male of *Parathalassius infuscatus* **sp. nov.**, resting on sand at Oso Flaco Dunes, California. **8–9.** Male of *Parathalassius uniformus* **sp. nov.**, resting on *Ambrosia chamissonis* (Less.) Greene (beach bur) at Surf Beach, California. **10.** Male and female mating pair of *Parathalassius uniformus* **sp. nov.**, on sand at Surf Beach, California. Photographs by Rui Andrade (Figs 5–6), and Alice Abela (Figs 7–10).



**FIGURES 11–16.** Collection localities and habitats of Nearctic *Parathalassius*. **11.** Island View Beach, British Columbia. **12.** Sidney Spit, British Columbia. **13–14.** Cape Disappointment, Washington. **15.** Bandon, Oregon. **16.** Samoa Dunes Recreation Area, California.



**FIGURES 17–22.** Collection localities and habitats of Nearctic *Parathalassius*. **17–18.** Morro Bay, California. **19.** Surf Beach, California. **20.** Surf Beach, California, with biologist and photographer Alice Abela collecting *Parathalassius* from a patch of beach bur, *Ambrosia chamissonis* (Less.) Greene. **21.** Crystal Cove State Park, California. **22.** Crystal Cove State Park, California, vegetation at back of beach.

## Materials and methods

This study is based on the examination of over 5400 specimens, which are deposited in the following institutions: California Academy of Sciences, San Francisco, USA (CAS); Canadian National Collection of Insects, Ottawa, Canada (CNC); California State Collection of Arthropods, Sacramento, USA (CSCA); Cornell University Insect Collection, Ithaca, USA (CUIC); Essig Museum of Entomology, University of California, Berkeley, USA (EMEC); Los Angeles County Natural History Museum, Los Angeles, USA (LACM); Lyman Entomological Museum, Ste-Anne-de-Bellevue, Canada (LEMQ); Museum of Comparative Zoology, Harvard University, Cambridge, USA (MCZ); Spencer Entomological Museum, University of British Columbia, Vancouver, Canada (UBCZ); Bohart Museum of Entomology, University of California, Davis, USA (UCDC); Entomology Research Museum, University of California, Riverside, USA (UCRC); University of Guelph Insect Collection, Guelph, Canada (UGIC); United States National Museum of Natural History, Washington D.C., USA (USNM); M.T. James Museum, Washington State University, Pullman, USA (WSU); and the Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK). Label data for primary types are cited verbatim. Labels are listed with data from each label in quotation marks and separated by a semicolon. Lines on labels are delimited by a slash (/) and annotations are placed in square brackets, i.e., [ ].

As in our previous papers (e.g., Brooks & Cumming 2011, 2012, 2016), terms used for adult structures primarily follow Cumming & Wood (2009), except for the antenna and wing venation where Stuckenberg (1999) and Saigusa (2006) are followed, respectively. Homologies of the male terminalia follow Brooks & Cumming (2011, 2012, 2016) and Brooks & Ulrich (2012).

Male and female terminalia dissections were macerated in 85% lactic acid heated in a microwave oven for multiple 20–30 second intervals, until muscle tissue was dissolved. As in Brooks & Cumming (2011, 2012, 2016) and Brooks & Ulrich (2012), figures of male genitalia in lateral view are oriented with the anatomically dorsal and ventral parts directed towards the top and bottom of the page, respectively, following Sinclair & Cumming (2006, figs 347–350). Macrotrichia are referred to as bristles, setae, setulae, or hairs depending on relative decreasing size.

To provide additional evidence for species identity, numerous specimens of *Parathalassius* were submitted for DNA barcoding to the Biodiversity Institute of Ontario in Guelph, ON, Canada. A single leg was removed from each specimen to obtain mitochondrial DNA barcodes (658 base pairs from the 5' end of COI). The DNA was extracted, amplified, purified and sequenced following the protocols given by Hajibabaei *et al.* (2005). Successful COI sequences were deposited in GenBank. COI sequences of >300 base pairs (bp) were analyzed with a Neighbour-joining tree (Fig. 154) created in the Barcode of Life Data Systems (BOLD) using the BOLD Aligner (Amino Acid based HMM) (Ratnasingham & Hebert 2007). In general, species identities were confirmed by comparing COI sequences from males and females that clustered together with <2% genetic divergence (Hebert *et al.* 2003).

Sixty-five morphological characters were used in the phylogenetic analysis, including 45 binary and 20 multistate characters (see “Phylogenetic analysis of *Parathalassius* species relationships”). All characters were equally weighted and treated as unordered. Characters were scored for 15 ingroup taxa and four outgroup taxa. Ingroup taxa consisted of the entire world species of *Parathalassius*, including the new species described herein. The four outgroup taxa selected for the analysis were single exemplar species in the genera *Schistostoma* Becker (Microphorinae), *Plesiothalassius* Ulrich (Parathalassiinae) and two different species groups of *Microphorella* Becker (Parathalassiinae). Character polarity was determined by rooting the tree with the four outgroups, which together were constrained to be paraphyletic in relation to the ingroup. Parsimony analysis of the character state matrix (Table 1) was performed using PAUP\* version 4.0b10 (Swofford 2002). A heuristic search using stepwise addition, random addition sequence of taxa and tree-bisection-reconnection (TBR) branch swapping with a 1000 random replications, was conducted to find the most parsimonious trees. Tree statistics such as consistency index (CI), retention index (RI), and rescaled consistency index (RC) were calculated to assess the fit of data to the cladograms. Character state distributions were examined using MacClade version 4 (Maddison & Maddison 2003).



## Systematics

### Genus *Parathalassius* Mik

*Parathalassius* Mik, 1891: 217 (*nec* Dussart 1986). Type species: *Parathalassius blasigii* Mik, by original designation.

**Diagnosis.** Body covered with dense pale pruinosity that gives a grey or brownish-grey appearance; prosternum fused with proepisternum to form precoxal bridge; scutellum with 2–3 pairs of marginal bristles; tarsi with apex of tarsomere 5 lacking medial finger-like process; wing with pterostigma indistinct, anal lobe weakly to partially developed, cell dm present, cell cua truncate apically with CuA straight or nearly straight, vein CuA+CuP short to relatively long; hypopygium globular, about 1/3–1/2 length of abdomen, asymmetrical with hypopygial foramen not formed, left ventral epandrial process present and basally articulated, bifurcate or unbranched, ventral lobe of left surstylus with complex upturned projection arising medioventrally, right epandrial lamella not fused to right side of hypandrium, dorsal lobe of right surstylus usually with frayed prensiseta on medial surface, hypandrium reniform and broadly notched posteriorly where phallus protrudes, left and right postgonite lobes complex and protruding out from between dorsal and ventral surstylar lobes, phallus tubular and bent upwards with ventral spur-like projection near base, ejaculatory apodeme keel-like and laterally flattened, hypoproct projected as pair of lobes below cerci, cerci well-sclerotized and asymmetrical with right cercus larger than left cercus, female terminalia partially retracted into segment 5 with tergite 10 medially divided into 2 subtriangular hemitergites with each bearing 2 or rarely 3 flattened and blunt-tipped acanthophorite spines apically.

**Redescription. Male:** Body length 1.5–3.9 mm, wing length 1.4–3.5 mm. Dark brown ground colour mostly covered with dense greyish-white or brownish-grey pruinosity, with golden-yellow pruinosity on head of certain species. Setae and pubescence of body and legs white, yellow, brown, or golden. **Head** (Figs 23, 25–30, 33–36): Ovoid in lateral view, slightly broader than high in anterior view. Neck inserted slightly above middle of head. Ocellar triangle conspicuous. Occiput weakly concave on upper median part above occipital foramen. Dichoptic; eyes entirely covered with ommatrichia, medial edge with weak emargination adjacent to antenna; ommatidia slightly smaller anterodorsally. Frons greyish, over 2X broader than high, widening above. Face narrowest at middle, about 1.75–2.75X width of anterior ocellus. Clypeus not separated from face; about as high as broad, widening below; apical margin truncate, weakly produced. Bristles of head well-differentiated; dorsal bristles strong: 1 pair of inclinate fronto-orbitals well-separated from base of antenna and arising lateral to anterior ocellus, 1 pair of lateroconate anterior ocellars, 1 pair of small posterior ocellars, 1 pair of strong widely spaced inclinate postocellars, 2–4 pairs of lateroconate verticals; postocular setae short and mainly uniserial; postgena with longer scattered setae usually extending onto gena around edge of mouth-opening. Gena narrow. Antenna (Figs 38–42, 44–47) brown to dark brown, inserted above middle of head in profile; scape short, funnel-shaped; pedicel subequal in length to scape, spheroidal with subapical circling of setulae; postpedicel short-subtriangular, subtriangular, subquadrate, or elongate-conical, 1.25–1.8X longer than wide, clothed in fine setulae, sensory pit present on outer lateral surface; arista-like stylus about 1.4–2.0X length of postpedicel, with minute hairs. Palpus ovoid apically, dark brown, clothed with minute pile, apical half with several short setae on outer surface, sensory pit present. Proboscis short, projecting ventrally; epipharyngeal carina present; epipharyngeal blades narrow; labellum with 6 geminately sclerotized pseudotracheae. **Thorax:** Mesoscutum slightly arched, prescutellar depression apparent. Prosternum fused with proepisternum forming precoxal bridge. Proepisternum with 1–2 setulae per side. Antepronotum narrow with 3–4 setulae per side. Postpronotal lobe distinct with several small setulae (with one distinct short bristle in *P. ulrichi* Shamshev). Mesonotum shield-shaped in dorsal view, longer than wide, bristles well-differentiated. Acrostichal setulae present, biserial or quadriserial, not extended posteriorly onto prescutellar depression; 5–8 dorsocentral bristles (posteriormost bristle strongest), 0–2 presutural intra-alar bristles, 1–2 presutural supra-alar (posthumeral) bristles, 2–4 postsutural supra-alar bristles, 2–4 notopleural bristles, and 1 postalar bristle per side, with accessory setulae between rows. Scutellum crescent-shaped in dorsal view with 2–3 pairs of marginal bristles, subapical pair longest. Mesopleuron bare. Halter pale yellowish-white. **Legs:** Mostly clothed with pale setae or setulae, tarsal claws, pulvilli and empodium normally developed on all legs. *Foreleg:* Coxa with numerous setae on anterior surface. Femur slightly longer than tibia, with well-developed setae on posterior surface, setae shorter on anterior surface. Tibia slender. Tarsus slightly longer than tibia; tarsomere 1 slightly shorter than combined length of tarsomeres 2–5, apparently lacking spinose anterior tubercle at

base; tarsomeres 2–4 decreasing in length apically; tarsomere 5 subequal in length to tarsomere 3, apex lacking medial finger-like process. *Midleg*: Coxa with several setae on anterior surface. Femur slightly shorter than tibia, with well-developed setae on anterior surface and few short setae on posterior surface. Tibia slender with at least 1 apicoventral bristle. Tarsus longer than tibia; tarsomere 1 slightly shorter than combined length of tarsomeres 2–5; tarsomeres 2–4 decreasing slightly in length apically; tarsomeres 1–4 each with dark spine-like apicoventral setae; tarsomere 5 subequal in length to tarsomere 3, apex lacking medial finger-like process. *Hindleg*: Coxa with 2–4 setae on outer surface. Femur slightly longer than tibia, with well-developed setae on anterior surface and few short setae on posterior surface. Tibia slender. Tarsus of variable length, slightly shorter, subequal, or longer than tibia; tarsomere 1 shorter than combined length of tarsomeres 2–4, with minute spinose posteroventral tubercle at base; tarsomeres 2–4 usually decreasing in length apically; tarsomere 5 usually subequal in length to tarsomere 3 (or 4 in certain species), apex lacking medial finger-like process. **Wing** (Figs 56–60, 62, 64–67): Hyaline to infusate with yellowish to dark brown veins, about 2.5–3.0X longer than wide. Pterostigma indistinct, membrane entirely covered with minute microtrichia. Anal lobe partially developed (weakly developed in *P. infuscatus* sp. nov.), alula absent. Costa circumambient. Extreme anterior base of costa with short row of anterodorsal setae, apical seta strongest. Anterior costal section bearing row of short spine-like setae intermixed with fine setae from Sc to R<sub>2+3</sub>, posterior part of costa beyond R<sub>2+3</sub> with only fine setae. Longitudinal veins complete (except CuA+CuP), reaching wing margin. Sc faint apically. R<sub>1</sub> straight, reaching costa beyond middle of wing (or beyond base of M<sub>2</sub>). Base of Rs originating opposite humeral crossvein. R<sub>2+3</sub> diverging from R<sub>4+5</sub> in basal half, running nearly parallel to R<sub>4+5</sub> in distal half. R<sub>4+5</sub> straight. M<sub>1</sub> running nearly parallel to R<sub>4+5</sub> beyond cell dm. M<sub>2</sub> and M<sub>4</sub> nearly straight and subparallel beyond cell dm. Costal section between M<sub>1</sub> and M<sub>2</sub> distinctly longer than costal section between M<sub>2</sub> and M<sub>4</sub>. Short r-m crossvein present in basal portion of wing, distal to base of R<sub>4+5</sub>. Crossvein bm-m incomplete. Cell dm present, closed by base of M<sub>2</sub> and crossvein dm-m, cell extended to middle of wing. Cells br, bm and cua in basal fourth of wing. Cells bm and cua broader than br. Cell cua closed, truncate apically with CuA straight or nearly straight. Vein CuA+CuP short to relatively long. Calypter with fine setae. **Abdomen**: Abdominal muscle plaques present, prominent on lateral margins of tergites 2–4; tergite and sternite 2 with transverse band of muscle plaques anteriorly. Tergite 1 with short fine setae; sternite 1 bare. Tergites 2–6 clothed with well-developed setae (setae on tergites 5 and 6 sometimes restricted to posterior margin); sternites 2–4 clothed with short weaker setae; sternite 4 usually with posterior edge emarginate; sternite 5 usually with short setae present near posterior margin; sternite 6 with short sparse setae present; tergite 7 usually bare, sometimes with 1–2 setae present; sternite 7 usually bare, sometimes with 1–2 or occasionally several setae present. Segment 1 reduced and very short; segments 2–4 mostly symmetrical with simple tergites and sternites, segment 2 relatively long; segments 5–7 narrowed, somewhat more heavily sclerotized (especially segments 6 and 7) and laterally compressed to form cavity on right side for hypopygium. Sternite 5 with or without projecting pregenitalic process, with desclerotized region medially or with posterior edge deeply and/or broadly emarginate (behind pregenitalic process if present). Sternite 8 subquadrate to subrectangular, forming dome-like cap over anterodorsal region of hypopygium, setose with some marginal setae stronger; tergite 8 reduced to narrow band-like sclerite, or indistinct and partially to mostly membranous medially. *Hypopygium* (Figs 68–126): Lateroflexed to right; inverted with posterior end directed anteriorly; globular, about 1/3–1/2 length of abdomen; asymmetrical; hypopygial foramen not formed. Epandrium divided into left and right lamellae. Left epandrial lamella narrowly constricted at middle with broad dorsal and ventral portions, ventral epandrial portion partially overlapping left side of hypandrium with lower margin distinct but fused to hypandrium; ventral epandrial process (Figs 80–94) present, basally articulated, bifurcate or unbranched (dorsal arm absent), ventral arm with minute apicodorsal seta and 1–2 minute to small setae along lateroventral margin, apex of most species with expanded lamelliform concavity, apex of certain species laterally flattened and narrow with ventral edge and medial surface serratulate. Left surstylus with dorsal and ventral lobes separated by shallow U-shaped cleft through which left postgonite lobe protrudes. Dorsal lobe of left surstylus with 1 basidorsal seta and 1 basilateral seta, most species with apical seta and knob- or stalk-like medial projection present. Ventral lobe of left surstylus with complex upturned projection arising medioventrally. Right epandrial lamella partially overlapping right side of hypandrium, not fused with hypandrium; apical portion of epandrial lamella broad with ventral epandrial process present or absent; basal portion of epandrial lamella narrowed with variably developed emargination bordering ventral margin of right cercus. Right surstylus with dorsal and ventral lobes separated by deep cleft through which right postgonite lobe protrudes. Dorsal lobe of right surstylus with 3 lateral or marginal setae, apex narrowed with thick apically-frayed preniseta on medial surface in most species.

Ventral lobe of right surstylus projecting dorsally. Hypandrium reniform with posterior end broadly notched where phallus protrudes. Postgonite with basal internal portion cradling base of phallus; left and right postgonite lobes complex, protruding out from between dorsal and ventral surstylar lobes. Phallus (Figs 95–114) tubular, bent upwards, well-sclerotized, basal internal portion with ventral spur-like projection abutting medioventral margin of postgonite cradle, distal external portion varying in length, curvature and armature. Ejaculatory apodeme keel-like, laterally flattened, subrectangular to broadly subtriangular in lateral view. Hypoproct projected as pair of usually slender lobes below cerci. Cerci (Figs 115–126) well-sclerotized, asymmetrical, medial margin of each cercus with longitudinal row of 3 setae adjacent anal region (anal setae), right cercus larger than left cercus, with basal portion distended and rounded laterally in most species.

**Female:** Body length 1.9–4.3 mm, wing length 1.5–4.0 mm. Similar to male except as follows: Pruinosity and setae of head concolourous with pruinosity and setae of body. **Head** (Figs 24, 31–32, 37): Face wider, at middle about 3.0–5.0X width of anterior ocellus. **Legs:** Setae on fore, mid and hindleg somewhat less developed, with individual setae slightly shorter and more slender. **Wing** (Figs 61, 63): Hyaline, with at most slight shading at apex of cell dm (infusate like male, in one species). **Abdomen** (Figs 127–132): Tapering posteriorly, apical segments partially retracted into segment 5. Tergites 2–5 clothed with well-developed setae, setae slightly weaker and less erect than in males of most species; sternites 2–5 clothed with short weaker setae. Terminalia with tergite 6, segments 7 and 8 usually glabrous (except for a few minute setulae), sternite 6 setose (at least on posterior portion); tergite 6 broader than long with anterior edge broadly or deeply emarginate; sternite 6 broader than long, subrectangular; tergite 7 usually broader than long with anterior edge deeply emarginate; sternite 7 broader than long and usually with anterior edge (and sometimes posterior edge) broadly emarginate; tergite 8 divided medially, articulated with sternite 8 anterolaterally; sternite 8 trough-like or plate-like, apical portion with well-developed ridges in certain species (Figs 133–141); sternite 9 variably developed; spermatheca developed as unpigmented membraneous sac-like terminal expansion of spermathecal duct; spermathecal duct narrow elongate and coiled, arising from broad ridged sperm pump; tergite 10 medially divided into broad subtriangular hemitergites, each with 2 or rarely 3 flattened and blunt-tipped acanthophorite spines apically and 1–3 setae laterally; sternite 10 narrow and V-shaped, weakened or divided medially, with 1 small seta per side; cercus well-sclerotized, setose, with apex pointed or blunt-tipped.

**Immatures:** Nothing is known of the eggs, larvae, or pupae.

**Included species, distribution and habitat.** The genus is Holarctic in distribution and currently comprises 15 species (including the new species described herein). All species of *Parathalassius* occur on sandy sea coasts (Figs 11–22). Most species appear restricted to fore dune beach habitats on either wet or loose sand, or on associated beach vegetation. Some species however (e.g., *P. aldrichi* Melander, *P. sinclairi* sp. nov.), also occur in remnant back dune habitats that border the fore dune beaches. The Palaearctic fauna includes the type species *Parathalassius blasigii* Mik from the western Mediterranean and Azores (Chvála 1988, 1989), and two species (*P. maritimus* Shamshev and *P. ulrichi* Shamshev) from the Russian Far East (Kuril Islands) (Shamshev 1998) and now Japan. The Nearctic fauna includes *Parathalassius abela* sp. nov., *P. aldrichi* Melander, *P. candidatus* Melander, *P. dilatatus* sp. nov., *P. infuscatus* sp. nov., *P. melanderi* Cole, *P. midas* sp. nov., *P. sinclairi* sp. nov., *P. socali* sp. nov., *P. susanae* sp. nov., *P. uniformis* sp. nov. and *P. wheeleri* sp. nov., all of which occur on the Pacific coast of North America (Figs 142–153). *Parathalassius susanae* sp. nov. is also known from a single locality on the Atlantic coast of the USA (Sapelo Island, Georgia) (Fig. 151).

### Key to the world species of *Parathalassius*

This key treats all 15 species of *Parathalassius* currently known, including the 12 species comprising the newly expanded Nearctic fauna, and the three described Palaearctic species. This key may be used to identify both sexes of each species, except *P. dilatatus* sp. nov., for which females are unknown. Females of most species can be identified using this key, except for those of *P. abela* sp. nov. and *P. candidatus*, which are apparently indistinguishable morphologically.

- 1 Males, abdomen ending in moderate to large sized globular genital capsule (hypopygium) lateroflexed to right and inverted into cavity formed by pregenitalic segments (Figs 68–71) . . . . . 2
- Females, abdomen tapered posteriorly with apical segments partially retracted into segment 5 (Figs 127–132) . . . . . 16

2	Tibiae and tarsi pale yellow to yellowish-brown (Figs 5–6) . . . . .	3
-	Tibiae dark, tarsi dark at least apically . . . . .	5
3	Head with golden-yellow setae on gena and postgena (Figs 29–30); wing with dark apical spot (Fig. 62); Nearctic . . . . .	<i>P. midas</i> <b>sp. nov.</b>
-	Head with pale setae on gena and postgena; wing without dark apical spot, entirely hyaline; Palaearctic . . . . .	4
4	Antenna with postpedicel subtriangular, 1.45–1.5X longer than wide (cf. Figs 38–39); western Palaearctic . . . . .	<i>P. blasigii</i> Mik
-	Antenna with postpedicel short-subtriangular, 1.1X longer than wide (cf. Fig. 45); eastern Palaearctic . . . . .	<i>P. maritimus</i> Shamshev
5	Head and thorax with dark setae; eastern Palaearctic . . . . .	<i>P. ulrichi</i> Shamshev
-	Head and thorax with pale setae; Nearctic . . . . .	6
6	Thorax with 2 notopleural setae, smaller sized species . . . . .	7
-	Thorax with 3 or 4 notopleural setae, medium to larger sized species . . . . .	13
7	Wing darkened at least towards apex (Figs 59–60) . . . . .	8
-	Wing entirely hyaline (Figs 57, 65, 67) . . . . .	10
8	Foreleg with tarsomere 1 dilated, tarsomere 2 slightly expanded (Figs 48–49) . . . . .	<i>P. dilatus</i> <b>sp. nov.</b>
-	Foreleg with tarsomeres 1–2 narrow, not dilated . . . . .	9
9	Wing broadly infusate with base of M <sub>2</sub> usually appearing indistinct (Fig. 59) . . . . .	<i>P. infuscatus</i> <b>sp. nov.</b>
-	Wing darkened only towards apex with base of M <sub>2</sub> distinct (Fig. 60) . . . . .	<i>P. melanderi</i> Cole
10	Eyes with ommatrichia of nearly uniform length, without dense reflective mat of long thickened hairs on lower third (Fig. 36) . . . . .	<i>P. uniformus</i> <b>sp. nov.</b>
-	Eyes with ommatrichia of lower third distinctly longer and thickened, forming dense reflective mat of long whitish hairs (Figs 25, 34) . . . . .	11
11	Antenna with postpedicel short-subtriangular, 1.25–1.4X longer than wide (Fig. 45); hind tarsomere 1 with long erect setae dorsally; hypopygium compact, with parts somewhat concealed . . . . .	<i>P. socali</i> <b>sp. nov.</b>
-	Antenna with postpedicel subtriangular, 1.5–1.6X longer than wide (Fig. 39); hind tarsomere 1 without long erect setae dorsally; hypopygium larger, with parts more exposed (cf. Figs 70–71) . . . . .	12
12	Hypopygium with right cercus truncate at apex, apicomedial margin short and blunt (Fig. 121); phallus with pointed dentiform process near apex (Figs 103–104); dorsal lobe of left surstylus with apex broadly rounded (Figs 73–74); central California, from Mendocino County south to San Luis Obispo County (Fig. 143) . . . . .	<i>P. aldrichi</i> Melander
-	Hypopygium with right cercus pointed at apex, apicomedial projection long and narrow (Fig. 122); phallus with pointed dentiform process more basal at 3/4 length (Figs 105–106); dorsal lobe of left surstylus with apex narrow and digitiform (Fig. 72); British Columbia, south through Washington and Oregon to Humboldt County in northern California (Fig. 153) . . . . .	<i>P. wheeleri</i> <b>sp. nov.</b>
13	Head with golden-yellow pruinosity on face and clypeus, not concolourous with greyish-white frons and vertex (Figs 1, 3, 23) . . . . .	<i>P. abela</i> <b>sp. nov.</b>
-	Head with face and clypeus mostly concolourous with greyish-white frons and vertex (Figs 26, 33, 35) . . . . .	14
14	Hind tibia with short anterodorsal row of erect comb-like setae (Fig. 51); hind tarsus with tarsomeres 2–4 bearing several short thick perpendicular peg-like setae dorsally (Fig. 54) . . . . .	<i>P. sinclairi</i> <b>sp. nov.</b>
-	Hind tibia with relatively long anterodorsal setae (Figs 50, 52); hind tarsus with tarsomeres 2–4 bearing short thin or thick angled setae dorsally, setae not perpendicular and peg-like (Fig. 53) . . . . .	15
15	Hind tarsomere 2 distinctly longer than tarsomere 3 (Fig. 53); hind tibia with anterodorsal setae mostly longer than width of tibia, evenly curved towards apex of tibia (Fig. 50); antenna with postpedicel subtriangular (Fig. 40); wing with vein CuA+CuP ending close to wing margin, slightly curved in most specimens (Fig. 58) . . . . .	<i>P. candidatus</i> Melander
-	Hind tarsomeres 2 and 3 nearly subequal in length (Fig. 55); hind tibia with anterodorsal setae mostly subequal or equal to width of tibia, barely curved towards apex of tibia (Fig. 52); antenna with postpedicel elongate-conical (Fig. 46); wing with vein CuA+CuP ending far from wing margin, straight (Fig. 66) . . . . .	<i>P. susanae</i> <b>sp. nov.</b>
16	Wing broadly infusate with base of M <sub>2</sub> usually appearing indistinct (cf. Fig. 59) . . . . .	<i>P. infuscatus</i> <b>sp. nov.</b>
-	Wing entirely hyaline, with at most slight infusate shading along veins near apex of cell dm, base of M <sub>2</sub> distinct (Figs 61, 63) . . . . .	17
17	Tibiae and tarsi pale yellow to yellowish-brown (Figs 5–6) . . . . .	18
-	Tibiae dark, tarsi dark at least apically . . . . .	20
18	Terminalia prominent with long pointed hemitergites (divided tergite 10) that each bear 2 acanthophorite spines (Figs 127–128); sternite 8 with apex distinctly bifurcate (Figs 129, 134); Nearctic . . . . .	<i>P. midas</i> <b>sp. nov.</b>
-	Terminalia small with short broad hemitergites (divided tergite 10) that each bear 2 acanthophorite spines (cf. Figs 130–131); sternite 8 with apex truncate or weakly emarginate (cf. Figs 133, 139); Palaearctic . . . . .	19
19	Antenna with postpedicel subtriangular, 1.45–1.5X longer than wide (cf. Figs 38–39); western Palaearctic . . . . .	<i>P. blasigii</i> Mik
-	Antenna with postpedicel short-subtriangular, 1.1X longer than wide (cf. Fig. 45); eastern Palaearctic . . . . .	<i>P. maritimus</i> Shamshev
20	Head and thorax with dark setae; eastern Palaearctic . . . . .	<i>P. ulrichi</i> Shamshev
-	Head and thorax with pale setae (Figs 24, 37); Nearctic . . . . .	21
21	Thorax with 2 notopleural setae, smaller sized species . . . . .	22
-	Thorax with 3 or 4 notopleural setae, medium to larger sized species . . . . .	26
22	Wing with slight infusate shading along veins near apex of cell dm (most specimens) (Fig. 61); hind tarsomere 2 usually pale on basal half; sternite 8 without longitudinal ridges on apical third or half (Fig. 136) . . . . .	<i>P. melanderi</i> Cole

- Wing entirely hyaline, without infusate shading along veins (cf. Figs 57, 65, 67); hind tarsomere 2 usually entirely darkened (rarely pale basally); sternite 8 with or without longitudinal ridges on apical third or half ..... 23
- 23 Sternite 8 with longitudinal ridges absent or barely apparent (Fig. 139), at most slightly developed laterally along apical margin and not present medially ..... *P. socali* **sp. nov.**
- Sternite 8 with longitudinal ridges on apical third or half, extended across sternite including medial margin (Figs 138, 140). . . . . 24
- 24 Sternite 8 with longitudinal ridges on apical third, with weak basal bulge, apex emarginate (Fig. 138) . . . *P. uniformus* **sp. nov.**
- Sternite 8 with longitudinal ridges on apical half, with distinct basal bulge, apex truncate (Fig. 140) . . . . . 25
- 25 Central California, from Mendocino County south to San Luis Obispo County (Fig. 143). . . . . *P. aldrichi* Melander
- British Columbia, south through Washington and Oregon to Humboldt County in northern California (Fig. 153) . . . . . *P. wheeleri* **sp. nov.**
- 26 Sternite 8 with apical quarter rugose (Fig. 137) . . . . . *P. sinclairi* **sp. nov.**
- Sternite 8 without apical rugosity, apical half with longitudinal ridges (Figs 133, 135, 141) . . . . . 27
- 27 Hind tarsomeres 2 and 3 nearly subequal in length (cf. Fig. 55); wing with vein CuA+CuP ending far from wing margin, straight (cf. Fig. 66); sternite 8 not distinctly narrowed apically (Fig. 141). . . . . *P. susanae* **sp. nov.**
- Hind tarsomere 2 distinctly longer than tarsomere 3 (cf. Fig. 53); wing with vein CuA+CuP ending close to wing margin, slightly curved or straight (cf. Figs 56, 58); sternite 8 widened near base, distinctly narrowed apically (Figs 133, 135). . . . . *P. abela* **sp. nov.** or *P. candidatus* Melander

***Parathalassius abela* sp. nov.**

(Figs 1–4, 23–24, 38, 56, 80, 95–96, 115, 133, 142)

**Type material.** **HOLOTYPE** ♂ labelled: “USA: CA: Santa Barbara Co.:/ Surf Beach, Vandenberg Air/ Force Base, 34.683801°N/ 120.605520°W, 6.iv.2016/ A.J. Abela, ex: *Ambrosia chamissonis* on coastal dunes”; “HOLOTYPE/ *Parathalassius abela*/ Brooks & Cumming [red label]” (CNC). **PARATYPES: USA: California:** same data as holotype (42♂, 34♀, CNC); same data as holotype except, 21.iii.2016 (18♂, 8♀, CNC; 2♂, USNM); same data except CNC588227 (1♂, barcoded, CNC), CNC588228 (1♀, barcode-associated, CNC); same data as holotype except, 5.iv.2016 (2♂, 1♀, CNC).

**Other material examined. USA: California:** Monterey County: Marina dunes [ca. 36°41'33"N 121°48'38"W], 22.v.1982 (12♂, 6♀, EMEC); Salinas River State Beach [ca. 36°46'33"N 121°47'50"W], 26.vii.1994, sandy beach, H. Ulrich (3♂, ZFMK); same data except, dunes (3♀, ZFMK); same data except, 27.vii.1994 (8♂, 8♀, ZFMK); Santa Barbara County, Surf Beach, Vandenberg AFB, 34.683801°N 120.605520°W, 4.vi.2016, ex: *Ambrosia chamissonis* & coastal dunes, A.J. Abela (6♂, 19♀, CNC); same data except, S.E. Brooks (23♂, 24♀, CNC; 2♂, 2♀, CSCA); same data except, CNC573323, CNC573299 (2♂, barcoded, CNC), CNC573298, CNC573301 (2♀, barcode-associated, CNC); same data except, J.M. Cumming (26♂, 56♀, CNC); same data except, CNC582818, CNC582864 (2♂, barcoded, CNC), CNC582808, CNC582832 (2♀, barcode-associated, CNC); same data except, S.H. Cumming (2♀, CNC); San Luis Obispo County, Morro Bay, dunes nr. Morro Rock, 35°22'16.4"N 120°51'52.0"W, 3.vi.2016, swept sandy seacoast & beach vegetation, S.E. Brooks (11♂, 4♀, CNC); same data except CNC573213, CNC573203 (2♂, barcoded, CNC), CNC573207, CNC573212 (2♀, barcode-associated, CNC); same data except, J.M. Cumming (2♂, CNC); same data except CNC580878 (1♂, barcoded, CNC); Morro Bay, 30.iv.1962, C.A. Toschi (1♂, EMEC); same data except, P.D. Hurd (1♀, EMEC); same data except, 26.iv.1968, P.A. Opler (1♂, EMEC); same data except, 16.vi.1947, A.L. Melander (2♀, USNM); Morro Dunes, 17.vi.1947, A.L. Melander (1♀, USNM); Oso Flaco Dunes [35.032931°N 120.629882°W], 8.iii.2015, A. Abela (1♀, photograph, see Fig. 1D).

**Diagnosis.** This relatively large species is characterized by 3–4 notopleural bristles, dark legs, relatively long vein CuA+CuP, males with golden-yellow pruinosity on the face and clypeus, and longer lower male ommatrichia. *Parathalassius abela* is very similar to *P. candidatus*, but males can be distinguished by the golden-yellow pruinosity plus yellow setae and ommatrichia on the lower part of the head. Females of these two species are virtually identical.

**Description. Male** (Figs 1–3): Body length 2.4–3.3 mm, wing length 2.7–3.2 mm. Dark brown ground colour covered mostly with dense greyish-white pruinosity. Setae of body and legs generally white. **Head** (Figs 1, 3, 23): Eyes with ommatrichia of lower third distinctly longer and slightly flattened, forming dense reflective mat of yellowish coloured hair. Face and clypeus covered with golden-yellow pruinosity (apparently faded in some specimens through preservation), not concolourous with greyish-white frons and vertex. Face narrowest at middle, about 2.0X width of anterior ocellus. Gena and postgena with moderately long pale yellowish setae, forming short

beard flanking mouthparts. Antenna (Fig. 38) including arista-like stylus, entirely dark brown; postpedicel subtriangular, 1.5–1.7X longer than wide; arista-like stylus long, about 2.0X length of postpedicel. Palpus with 2–3 moderately long setae and several short setulae on outer surface of apical half. **Thorax:** Acrostichal setulae quadriseriate; 6–7 dorsocentral bristles, 0–1 presutural intra-alar bristles, 1–2 presutural supra-alar (posthumeral) bristles, 2–3 postsutural supra-alar bristles, 3–4 notopleural bristles. Scutellum with 3 pairs of bristles. **Legs:** *Foreleg:* Dark grey, pale only at knee. Coxa with moderately long pale white to yellowish setae on anterior surface. Femur with numerous long setae on posterior surface, posterodorsal and posteroventral rows prominent. Tibia with short setae and setulae. Tarsus with setulae; tarsomeres 1–2 not dilated. *Midleg:* Dark grey, pale only at knee, tarsus greyish-brown. Femur with anteroventral and posteroventral row of setae prominent. Tibia with pair of apicoventral bristles. Tarsomeres 1–4 each with pair of dark spine-like apicoventral setae. *Hindleg:* Dark grey, femur dark brown posteriorly, tarsus greyish-brown. Femur with ventral row of setae prominent. Tibia with anterodorsal and anteroventral rows of setae prominent, subequal or longer than width of tibia, with anterodorsal row of setae not or barely curved towards apex of tibia. Tarsus slightly shorter than tibia with short setae and setulae; tarsomere 1 slightly shorter than combined length of tarsomeres 2–4; tarsomeres 2–3 with some slightly thickened angled setae dorsally, not perpendicular and peg-like; tarsomere 2 distinctly longer than tarsomere 3; tarsomere 3 slightly longer than tarsomere 4; tarsomere 5 subequal in length to tarsomere 3. **Wing** (Fig. 56): Hyaline with dark brown veins. Cell dm produced apically, dm-m crossvein concave. Vein CuA+CuP relatively long, slightly curved to straight. **Abdomen:** Tergites 2–4 with setae well-developed and relatively long. Sternite 5 with slender anteriorly curved digitiform pregenitalic process present, base with short blunt anterior projection, apex blunt and covered with microtrichia, posterior edge of sternite 5 (behind process) deeply emarginate. Sternite 8 subquadrate, with prominent elongate setae on posterolateral margins. *Hypopygium* (Figs 80, 95–96, 115): Large. Left epandrial lamella with ventral portion elongate (about 2X longer than high); ventral epandrial process broadly bifurcate, dorsal arm curved ventrally, narrow in middle portion, apex expanded and hook-like, ventral arm thick with minute apicodorsal seta and pair of minute setae along distiventral margin, apex with expanded lamelliform concavity. Dorsal lobe of left surstylus subtriangular with basiventral edge weakly rounded, with long basidorsal seta, short lateral seta and long apical seta, medial surface with knob-like projection bearing lamelliform apical process. Ventral lobe of left surstylus shallowly bilobate in lateral view, dorsal lobe short with apex subquadrate, ventral lobe with rounded base bearing short lateral seta and complex upturned multilobate projection arising medioventrally. Right epandrial lamella with ventral epandrial process not developed; basal portion of epandrial lamella narrowed and dorsally curved, with deep dorsal emargination bordering ventral margin of right cercus. Dorsal lobe of right surstylus with 3 lateral setae (apical-most seta somewhat stronger), apex narrowed with squared-off tip bearing thick apically-frayed preniseta on medial surface. Ventral lobe of right surstylus with lateral seta near middle, distal half recurved and tapered with tubercle bearing strong seta proximal to rounded apex. Hypandrium very large, elongate-reniform with convex anterior and posterior ends extending to or beyond margins of epandrial lamellae in lateral view, mainly bare except for a few short setae lateroventrally on left side, and posteriorly on right side. Left postgonite lobe subquadrate basally, constricted near middle, with distal portion broadly lamelliform with claw-like apical process, base of lobe with slender medial projection. Right postgonite lobe with broad lateral protuberance and bulbous medial projection, apex bifurcate with short digitiform process and rounded lamelliform process. Phallus short and weakly curved, broad in basal 2/3 with apical 1/3 narrower (in lateral view), dorsal flange and left lateral bump-like protuberance present at 2/3 length. Ejaculatory apodeme broadly subtriangular. Hypoproct strongly projected dorsally as pair of slender blade-like lobes. Cerci with anal setae well-developed and differentiated from surrounding hairs; right cercus much larger than left cercus with basal portion distended and rounded laterally, apex strongly deflected dorsally, elongate narrow and pointed with 2 short preapical setae on lateral margin; left cercus oblong-subrectangular in dorsal view, apex short and truncate, with 2 long, dorsally-directed setae.

**Female** (Fig. 4): Body length 2.7–4.3 mm, wing length 2.9–3.8 mm. Similar to male except as follows: **Head** (Fig. 24): Eyes with ommatrichia of nearly uniform length, not distinctly longer on lower third. Face and clypeus without golden-yellow pruinosity, concolourous with greyish-white frons and vertex. Face wider, at middle about 4.0X width of anterior ocellus. **Legs:** *Foreleg:* Coxa with shorter more slender pale white setae on anterior surface. Femur with posteroventral row of setae only prominent apically. *Midleg:* Femur with anteroventral and posteroventral setae less prominent. *Hindleg:* Tarsomeres 2–3 without slightly thickened setae dorsally. **Abdomen:** Tergite 5 broadly subtriangular to semicircular in dorsal view with posterior margin rounded (cf. Fig. 131).

Terminalia distinctly narrower than base of segment 5 (cf. Figs 131–132); sternite 8 trough-like, lacking basal bulge, widened just beyond base and narrowed apically, apical half with longitudinal ridges, apex broadly truncate (Fig. 133); sternite 9 reduced to a narrow transverse sclerotized band; tergite 10 with hemitergites subtriangular and short, each with 2 acanthophorite spines; cercus short, pointed apically.

**Distribution and seasonal occurrence.** *Parathalassius abela* is currently known only from coastal dunes in Monterey County, San Luis Obispo County and Santa Barbara County, in southern California (Fig. 142). Adults have been collected or photographed from early March to late July.

**Etymology.** The species name honours Alice Abela (Santa Barbara County) (Fig. 20), who first alerted us to the existence of this species, as well as *P. infuscatus* **sp. nov.** and *P. uniformis* **sp. nov.**, through her excellent photographs of these flies and subsequent collection of specimens of all three previously unknown species.

**Remarks.** COI barcode sequences (Fig. 154) and morphology confirm the separation of this species from the very similar allopatric *P. candidatus* (with minimally 3.6% genetic divergence). A small degree of genetic divergence (minimally 1.1%) between populations of *P. abela* on Surf Beach and Morro Bay, suggests some isolation of the two populations of this species on these nearby beaches (45 km apart).

Adults of *P. abela* were frequently found towards the back of the fore dune beach habitat on the leaves of beach bur (*Ambrosia chamissonis* (Less.) Greene) (Fig. 20).



**FIGURES 23–28.** Heads of Nearctic *Parathalassius* in anterior view. **23.** *Parathalassius abela* **sp. nov.**, male. **24.** *Parathalassius abela* **sp. nov.**, female. **25.** *Parathalassius wheeleri* **sp. nov.**, male. **26.** *Parathalassius candidatus* Melander, male. **27.** *Parathalassius infuscatus* **sp. nov.**, male. **28.** *Parathalassius melanderi* Cole, male.

***Parathalassius aldrichi* Melander**

(Figs 73–75, 92, 103–104, 121, 140, 143)

*Parathalassius aldrichi* Melander, 1906: 374.

**Type material examined.** **LECTOTYPE** (here designated in order to fix identity of the species), ♂, from Pacific Grove [ca. 36°37'08"N 121°54'9"W], Monterey County, California, USA, labelled: "Pacific Grove/ v.7.[19]06 Cal. [J.M. Aldrich]"; "COTYPE/ *Parathalassius Aldrichii*[sic.]/ ♂ Mel."; "LECTOTYPE/ *Parathalassius/ aldrichi* Melander/ des. Brooks & Cumming 2016 [red label]" (USNM). **PARALECTOTYPES: USA: California:** same locality and date as lectotype (8♂, 7♀, USNM; 1♂, 1♀, AMNH). Our paralectotype label has additionally been attached to each specimen.

**Other material examined. USA: California:** Marin County: Abbott's Lagoon [ca. 38°07'11"N 122°57'08"W], 3.vi.2000, W.H. Lenarz (1♀, EMEC); Point Reyes National Seashore, North Beach [ca. 38°06'23"N 122°57'45"W], el. <100 ft, 13.v.1972, D.E. Schultz (1♂, EMEC); Point Reyes, North Beach, 13.v.1978, M.E. Buegler (1♀, EMEC); Stinson Beach, 37°53'51"N 122°38'28"W, 27.iii.2017, swept sandy seacoast & beach vegetation, S.E. Brooks (9♂, 10♀, CNC); same data except, J.M. Cumming (7♂, 6♀, CNC); same data except, S.H. Cumming (2♂, CNC); Mendocino County: Inglenook Fen, 4 mi. N. Ft. Bragg [ca. 39°30'55"N 123°46'38"W], 7.v.1975, M.E. Buegler (1♂, EMEC); same data except, 26.v.1975 (1♀, EMEC); same data except, 6.vi.1975, M.E. Buegler & E.I. Schlinger (1♂, 3♀, EMEC); same data except, 9.vi.1975 (1♀, EMEC); same data except, 17.vii.1975 (2♂, 2♀, EMEC); same data except, 14.vi.1973, E.I. Schlinger (1♀, EMEC); same data except, dune area, 30.vi.1973 (2♂, 2♀, EMEC); Monterey County: Asliomar [ca. 36°36'60"N 121°56'19"], 17.v.1959, D.J. Burdick (4♂, 1♀, EMEC); San Francisco County: San Francisco, beach west end Judah St., 37°45'37"N 122°30'38"W, swept beach vegetation, 8.viii.1999, S.E. Brooks (6♂, 8♀, LEM); same data except, CNC DIPTERA #'s 103906, 103907 (2♂, barcoded, LEMQ); San Luis Obispo County: Morro Bay, dunes nr. Morro Rock, 35°22'16.4"N 120°51'52.0"W, 3.vi.2016, swept sandy seacoast & beach vegetation, S.E. Brooks (82♂, 43♀, CNC; 2♂, 2♀, CSCA); same data except, CNC573170, CNC573167 (2♂, barcoded, CNC), CNC573158, CNC573157 (2♀, barcode-associated, CNC); same data except, J.M. Cumming (9♂, 7♀, CNC); same data except, CNC580872, CNC580869 (2♂, barcoded, CNC), CNC580879, CNC580886 (2♀, barcode-associated, CNC); Morro Bay, 26.ix.1946, A.L. Melander (1♀, USNM); same data except, 16.vi.1947, (7♂, 1♀, USNM); Morro Dunes, 6.ix.1945, A.L. Melander (1♀, USNM); same data except, 17.vi.1947 (3♂, 2♀, USNM); San Mateo County: Half Moon Bay [ca. 37°27'36"N 122°26'41"W], dunes, 11.v.1981 (14♂, 8♂, EMEC); Santa Cruz County: Ano Nuevo dunes [ca. 37°06'60"N 122°18'21"W], 8.v.1981 (19♂, 12♀, EMEC).

**Diagnosis.** This relatively small Californian species is characterized by a subtriangular antennal postpedicel, longer lower male ommatrichia, 2 notopleural bristles, hyaline wing, and relatively dark legs. *Parathalassius aldrichi* is very similar to *P. wheeleri* sp. nov., but males can be distinguished from this more northern species by the shape of the apex of the right cercus and dorsal lobe of the left surstylus, as well as the more apical position of the dentiform process of the phallus.

**Redescription. Male:** Body length 1.6–2.2 mm, wing length 1.5–1.9 mm. Dark brown ground colour covered mostly with dense greyish-white pruinosity. Setae of body and legs white. **Head** (cf. Fig. 25): Eyes with ommatrichia of lower third distinctly longer and slightly flattened, forming dense reflective mat of whitish coloured hair. Face and clypeus concolourous with greyish-white frons and vertex. Face narrowest at middle, about 2.5X width of anterior ocellus. Gena and postgena with moderately long white setae, forming short beard flanking mouthparts. Antenna (cf. Fig. 39) including arista-like stylus, entirely dark brown; postpedicel subtriangular, 1.5–1.6X longer than wide; arista-like stylus of medium length, about 1.5X length of postpedicel. Palpus with 7–8 setae on outer surface of apical half. **Thorax:** Acrostichal setulae primarily biserial; 6–7 dorsocentral bristles, 0 presutural intra-alar bristles, 1 presutural supra-alar (posthumeral) bristle, 2–3 postsutural supra-alar bristles, 2 notopleural bristles. Scutellum with 2–3 pairs of bristles. **Legs:** *Foreleg:* Dark grey, pale at knee and extreme apex of tibia, tarsus pale brown. Coxa with short pale setae on anterior surface. Femur with moderately long setae on posterior surface. Tibia and tarsus with setulae; tarsomeres 1–2 not dilated. *Midleg:* Dark grey, pale only at knee, tarsus greyish-brown. Femur with anterodorsal setae most prominent. Tibia with pair of apicoventral bristles. Tarsomeres 1–4 each with several dark spine-like apicoventral setae. *Hindleg:* Dark grey, femur dark brown posteriorly, pale at knee, tarsus pale brown to greyish-brown. Femur with anteroventral row of setae prominent. Tibia with anterodorsal and anteroventral rows of setae of moderate length, subequal or slightly longer than width



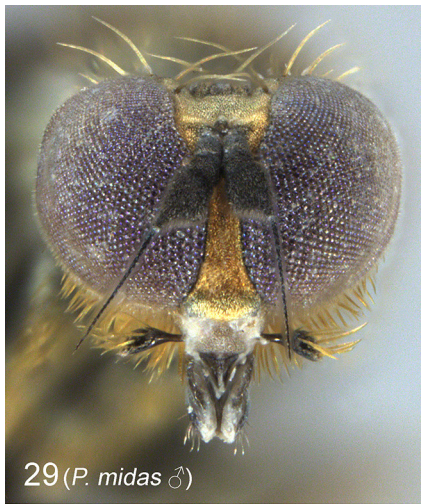
of tibia. Tarsus subequal in length to tibia with short setae and setulae; tarsomere 1 shorter than combined length of tarsomeres 2–4; tarsomeres 1–4 lacking peg-like or thickened setae dorsally; tarsomere 2 longer than tarsomere 3; tarsomere 3 longer than tarsomere 4; tarsomere 5 subequal in length to tarsomere 3. **Wing** (cf. Fig. 57): Hyaline with dark brown veins. Cell dm produced apically, dm-m crossvein nearly straight. Vein CuA+CuP short, straight. **Abdomen:** Tergites 2–4 with setae well-developed and relatively long. Sternite 5 without projecting pregenitalic process, with desclerotized region medially. Sternite 8 subquadrate with setae longer along posterolateral margins. *Hypopygium* (Figs 73–75, 92, 103–104, 121): Large. Left epandrial lamella with ventral portion elongate (about 2X longer than high); ventral epandrial process narrowly bifurcate, dorsal arm with apex expanded, blunt or hook-like, ventral arm thick and long with minute apicodorsal seta and minute distiventral seta, apex with expanded lamelliform concavity. Dorsal lobe of left surstylus with basiventral edge rounded and flap-like, apex broadly rounded, with long basidorsal seta (sometimes on bump-like protuberance or tubercle), short lateral seta and long apical seta, medial surface with stalk-like projection bearing lamelliform apical seta. Ventral lobe of left surstylus shallowly bilobate in lateral view, dorsal lobe short with apex subquadrate or broadly rounded, ventral lobe broadly rounded with short marginal seta (sometimes on short tubercle) and complex upturned bifurcate projection arising medioventrally. Right epandrial lamella with ventral epandrial process not developed; basal portion of epandrial lamella narrowed and dorsally curved, with deep dorsal emargination bordering ventral margin of right cercus. Dorsal lobe of right surstylus with 3 lateral setae of similar size, apex narrowed with rounded to subtriangular tip bearing thick apically-frayed preniseta on medial surface. Ventral lobe of right surstylus with lateral seta near basal third, distal 2/3 recurved, slender with narrow apically pointed lamelliform process proximal to lamelliform apex. Hypandrium large, reniform and bare. Left postgonite lobe ovoid basally, constricted near middle, distal portion subquadrate to subrectangular and flat without claw-like apicodorsal process, base of lobe with curved medial projection. Right postgonite lobe with broad lateral protuberance present or indistinct and continuous with apex, with rounded medial projection, apex bifurcate with well-developed digitiform ventral process and lamellate dorsal process. Phallus elongate with prominently projecting narrow curve and pointed dentiform process near apex. Ejaculatory apodeme subrectangular to subtriangular. Hypoproct projected dorsally as pair of slender pointed lobes, each lobe with 1–2 ventral setae proximal to apex, left lobe also with piliferous region ventrally. Cerci with anal setae well-developed and differentiated from surrounding hairs; right cercus much larger than left cercus with basal portion distended and rounded laterally, apex weakly dorsally deflected, truncate with apicomedial margin blunt, with 2 marginal setae; left cercus oblong in dorsal view, apex truncate, not dorsally deflected, with pair of thickened setae at apicolateral margin, outermost seta sometimes on short tubercle.

**Female:** Body length 1.9–2.8 mm, wing length 1.7–2.1 mm. Similar to male except as follows: **Head:** Eyes with ommatrichia of nearly uniform length, not distinctly longer on lower third. Face wider, at middle about 4.0X width of anterior ocellus. **Abdomen:** Tergite 5 broadly subtriangular to semicircular in dorsal view with posterior margin rounded (cf. Fig. 131). Terminalia distinctly narrower than base of segment 5 (cf. Figs 131–132); sternite 8 trough-like, with distinct basal bulge, not narrowed apically, apical half with longitudinal ridges, apex truncate (Fig. 140); sternite 9 unsclerotized and indistinct; tergite 10 with hemitergites subtriangular and short, each with 2 acanthophorite spines; cercus short, pointed apically.

**Distribution and seasonal occurrence.** *Parathalassius aldrichi* is currently known to occur on sandy seashores along the California coast from Fort Bragg in Mendocino County south to the dunes of Morro Bay in San Luis Obispo County (Fig. 143). Adults have been collected from late March to late September.

**Remarks.** Some paralectotypes bear separate labels reading “JMAldrich/ Coll” and “sand dune(s)”. Melander (1906) also indicates that the type series of *P. aldrichi* was collected by J.M. Aldrich on “dry sands in back of the beach”. We also collected numerous specimens of *P. aldrichi* by sweeping vegetation along the back dune area of Morro Bay (Fig. 17).

COI barcode sequences (Fig. 154) and morphology confirms the separation of this species from the similar allopatric *P. wheeleri* sp. nov. (with minimally 8.2% genetic divergence). However within *P. aldrichi*, the San Francisco population shows significant genetic divergence (with minimally 6.2% divergence) from the Morro Bay population, suggesting the possibility of another cryptic species in this complex. All the populations of *P. aldrichi*, including the type locality population from Pacific Grove, appear morphologically identical. Because the unsequenced Pacific Grove type locality population is located midway between the two sequenced populations, it seemed prudent to treat all populations together as *P. aldrichi*, until additional sampling and sequencing is completed.



29 (*P. midas* ♂)



30 (*P. midas* ♂)



31 (*P. midas* ♀)



32 (*P. midas* ♀)



33 (*P. sinclairi* ♂)



34 (*P. sociali* ♂)



35 (*P. susanae* ♂)

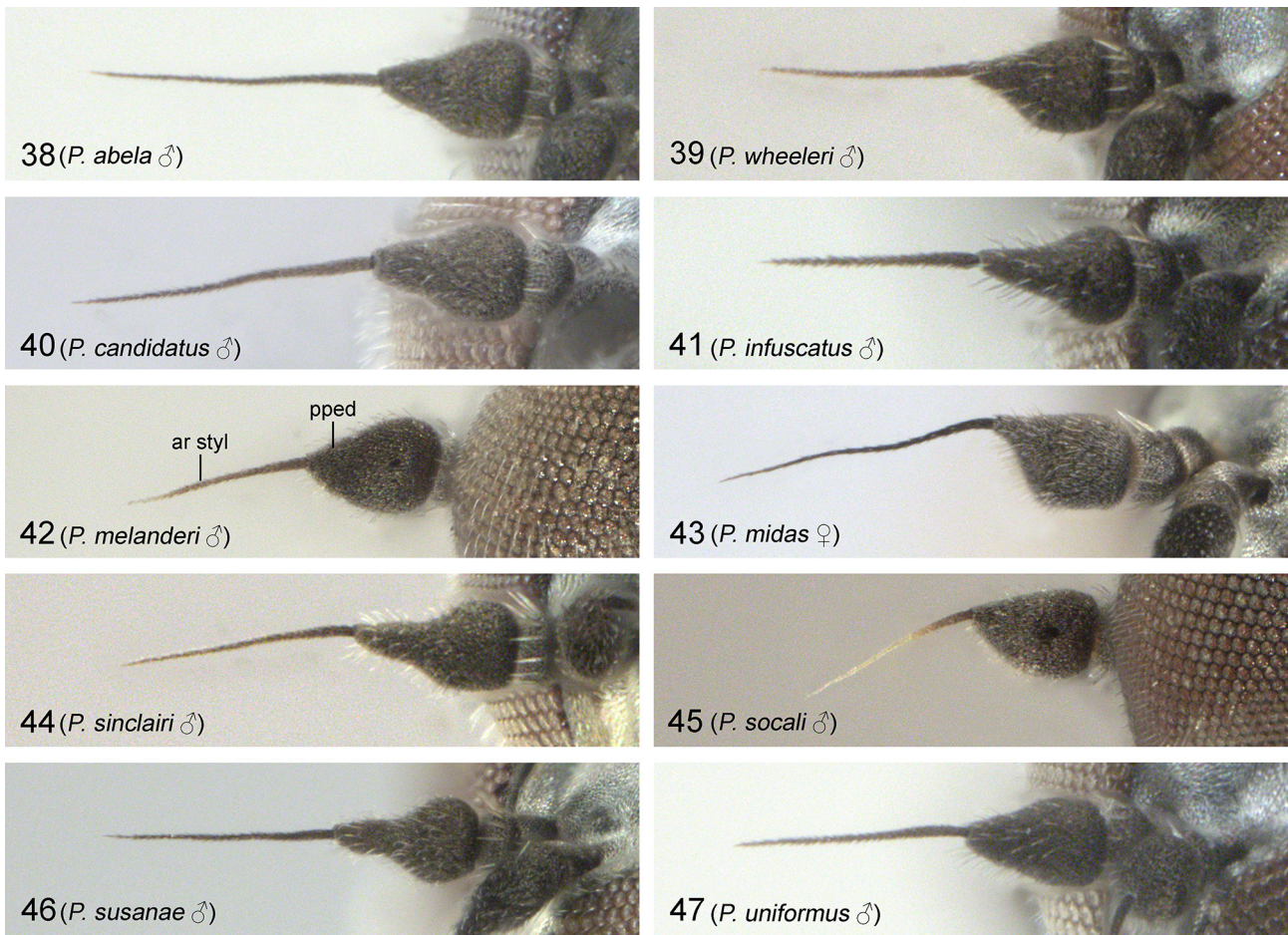


36 (*P. uniformus* ♂)



37 (*P. uniformus* ♀)

**FIGURES 29–37.** Heads of Nearctic *Parathalassius*. 29–30. *Parathalassius midas* sp. nov., male, anterior and lateral views. 31–32. *Parathalassius midas* sp. nov., female, anterior and lateral views. 33. *Parathalassius sinclairi* sp. nov., male, anterior view. 34. *Parathalassius sociali* sp. nov., male, anterior view. 35. *Parathalassius susanae* sp. nov., male, anterior view. 36. *Parathalassius uniformus* sp. nov., male, anterior view. 37. *Parathalassius uniformus* sp. nov., female, anterior view.



**FIGURES 38–47.** Antennae of Nearctic *Parathalassius* (male left antenna in medial view, unless otherwise noted). **38.** *Parathalassius abela* sp. nov. **39.** *Parathalassius wheeleri* sp. nov. **40.** *Parathalassius candidatus* Melander. **41.** *Parathalassius infuscatus* sp. nov. **42.** *Parathalassius melanderi* Cole, right antenna in lateral view. **43.** *Parathalassius midas* sp. nov., female. **44.** *Parathalassius sinclairi* sp. nov. **45.** *Parathalassius socali* sp. nov., right antenna in lateral view. **46.** *Parathalassius susanae* sp. nov. **47.** *Parathalassius uniformus* sp. nov. Abbreviations: ar styl—arista-like stylus; pped—postpedicel.

### *Parathalassius blasigii* Mik

(Figs 5–6)

*Parathalassius blasigii* Mik, 1891: 217.

*Schistostoma alterum* Becker, 1907: 119.

**Material examined.** **PORTUGAL:** Minho, Braga, Esposende, Apúlia, Parque Natural do Litoral Norte, 41°28'24.0"N 08°46'26.6"W, 11.vii.2011, ex: sandy beach, Rui Andrade, CNC487196 (1♂, barcoded, CNC), CNC487197 (1♀, barcode-associated, CNC). **TUNISIA:** La Marsa, 8.v.1913 (1♂, 1♀, USNM).

**Diagnosis.** This medium sized Palaearctic species (Figs 5–6) is characterized by a subtriangular antennal postpedicel, longer lower male ommatrichia, white setae on the lower part of the head, 2 notopleural bristles, pale legs, and entirely hyaline wing in both sexes.

**Distribution.** This western Palaearctic species is known from the Azores, the western Mediterranean region including Spain, the Italian mainland, Sicily and North Africa (Tunisia) (Chvála 1988, 1989, 2013), and is here newly recorded from the northwestern coast of Portugal.

**Remarks.** The shape and setation of the cerci examined in the male specimen of *P. blasigii* from Portugal, appears noticeably different from the illustration of the male cerci of this species (specimen from the type locality).

in Venice, Italy) depicted in Shamshev (1998). This may indicate the presence of at least one additional undescribed cryptic species within the current concept of *P. blasigii*.

### ***Parathalassius candidatus* Melander**

(Figs 26, 40, 50, 53, 58, 81, 116, 135, 144)

*Parathalassius candidatus* Melander, 1906: 375.

**Type material examined.** HOLOTYPE, ♀, from Friday Harbor [ca. 48°32'15"N 123° 1'10.97"W], San Juan Island, San Juan County, Washington, USA, labelled: "Friday Harbor, Wash. [summer, 1905, J.M. Aldrich]"; "TYPE/ *Parathalassius/ candidatus/* Mel. [red label]"; "ALMelander/ Collection/ 1961" (USNM).

**Other material examined.** CANADA: British Columbia: Haida Gwaii, Graham Island, 3km N Tlell [ca. 53°33'37"N 131°55'39"W], 13.vii.1988, meadow behind dunes, T.A. Wheeler, CNC DIPTERA #103909 (1♂, barcoded, CNC); Vancouver, Point Grey [ca. 49°15'58"N 123°15'52"W], 31.v.1973, on tidal flat, J.R. Vockeroth (2♂, 1♀, CNC); same data except, 5.vii.1973 (1♂, 5♀, CNC); same data except, 12.vii.1973 (12♂, 7♀, CNC); same data except, 19.vii.1973 (1♀, CNC); same data except, 23.vii.1973 (1♂, 1♀, CNC); same data except, 31.vii.1973 (1♀, CNC); Vancouver, 2.vii.1988, J.R. Vockeroth (2♂, ZFMK); Vancouver, beach SW of University, lower course of Fraser River north arm, 10.vii.1988, gravel and sand, H. Ulrich (12♂, 20♀, ZFMK); Vancouver Island: Deep Bay nr. Bowser [ca. 49°27'33"N 124°43'59"W], 21.vi.1955, R. Coyles (2♂, 1♀, CNC); Sidney Is., Sidney Spit, 48°38'28.06"N 123°19'50.05"W, 8.viii.2008, sandy beach, J.M. Cumming (1♂, 2♀, CNC); same data except, CNC DIPTERA #103910 (1♀, barcode-associated, CNC); Cordova Bay [ca. 48°31'12"N 123°21'60"W], 11.vii.1924, A.L. Melander (1♀, USNM); same data except, 11.vii.1925 (1♂, USNM; 1♀, CUIC). USA: California: Del Norte County: Smith River [ca. 41°55'03"N 124°12'17"W], 25.vii.1932, dry beach sand, J.M. Aldrich (3♂, USNM); Smith River, Tolowa Dunes State Park, 15.vi.1981, M.E. Buegler (1♀, EMEC); Smith River Dunes, 15.vi.1981 (2♂, EMEC); Humboldt County: Clam Beach [ca. 40°59'40"N 124°06'58"W], 21.vi.1935, A.L. Melander (1♂, 1♀, USNM); Clam Beach Co. Park N of Eureka [ca. 40°59'40"N 124°06'58"W], 15.v.1978, D.D. Wilder (9♂, 7♀, CAS); same data except, 16.v.1978 (2♂, 1♀, CAS); Loleta, W, sand dunes at end of Table Bluff Rd. [ca. 40°41'50"N 124°16'34"W], 28.v.2003, R. Wielgus (1♀, EMEC); Samoa Peninsula, Samoa Dunes Recreation Area, 40°45'41"N 124°13'37"W, 21.v.2009, J.M. Cumming (1♀, CNC); same data except, S.E. Brooks, CNC DIPTERA # 103912 (1♂, barcoded, CNC); Samoa Beach & dunes, 18.vi.1907, J.C. Bradley (1♀, CUIC); Marin County: Abbott's Lagoon [ca. 38°07'11"N 122°57'08"W], A37, 3.vi.2000, W.H. Lenarz (1♀, EMEC); Dillon Beach, 38°14'57"N 122°58'00"W, 26.iii.2017, swept sandy seacoast & beach vegetation, S.E. Brooks (1♂, CNC); same data except, J.M. Cumming (3♀, CNC); same data except, S.H. Cumming (1♂, CNC); Muir Beach [ca. 37°51'34"N 122°34'43"W], 30.v.1946, E.L. Kessel (1♂, 1♀, EMEC); Stinson Beach, 37°53'51"N 122°38'28"W, 27.iii.2017, swept sandy seacoast & beach vegetation, S.E. Brooks (1♂, CNC); same data except J.M. Cumming (2♂, CNC); Mendocino County: Manchester Dunes [ca. 38°57'19"N 123°43'52"W], 19.vi.1981 (5♂, 4♀, EMEC); San Francisco County: San Francisco [ca. 37°45'37"N 122°30'38"W], 1.vii.1952, C.E. Kaufeldt (1♂, USNM); same data except, 22.vi.1947, A.L. Melander (2♂, USNM); same data except 12.v.1915, M.C. Van Duzee (1♀, MCZ); same data except, 22.v.1915 (1♂, CAS); same data except, Sand Dunes, 13.v.1927, C.L. Fox (1♀, EMEC); Sonoma County: Bodega Dunes [ca. 38°20'16"N 123°04'02"W], 22.vi.1981 (1♀, EMEC); Salmon Creek, North Salmon Creek State Beach, 38°21'21"N 123°03'59"W, 24.iii.2017, swept sandy seacoast & beach vegetation, S.E. Brooks (1♂, CNC); same data except, 25.iii.2017 (1♂, CNC). Oregon: Coos County: Bandon, Bullards Beach, 43°08'44"N 124°24'56"W, 29.v.2009, swept beach-grass, S.E. Brooks (2♂, 1♀, CNC); same data except, J.M. Cumming (1♀, CNC); Curry County: Winchuck River, [ca. 42°00'17"N 124°12'54"W], 23.vii.1932, J.M. Aldrich (2♂, 1♀, USNM); Lane County: Heceta Beach, 44°02'14.7"N 124°07'57.2"W, 7.vii.2014, swept dunes & beach grass (*Ammophila*), J.M. Cumming, CNC487110 (1♀, barcode-associated, CNC); Suislaw North Jetty, nr. Florence, 44°01'07.0"N 124°08'12.6"W, 8.vii.2014, swept dunes & beach grass (*Ammophila*), S.E. Brooks (3♂, 2♀, CNC); same data except, J.M. Cumming (1♂, 1♀, CNC); same data except, CNC588238 (1♂, barcoded, CNC), CNC588237 (1♀, barcode-associated, CNC); Lincoln County: South Beach State Park, 44°36'05.6"N 124°03'54.0"W, 3.vii.2014, swept dunes & beach grass (*Ammophila*), S.E. Brooks (3♂, 1♀, CNC); same data except, CNC588235 (1♂, barcoded, CNC), CNC588236 (1♀, barcode-associated, CNC). Washington: Clallam

County: Twin [ca. 48°09'54"N 123°56'58"W], 13.vi.1988, sandy beach, H. Ulrich (1♀, ZFMK); Pacific County: Cape Disappointment State Park nr. Ilwaco, Benson Beach, 46°16'20.4"N 124°04'25.4"W, 1.vii.2014, swept dunes & beach grass (*Ammophila*), S.E. Brooks (2♂, 2♀, CNC; 1♂, 1♀, CSCA); same data except, CNC487204 (1♀, barcode-associated, CNC); same data except, J.M. Cumming (1♂, 5♀, CNC); same data except, CNC487203 (1♂, barcoded, CNC); same data except, 2.vii.2014, S.E. Brooks (3♀, CNC); same data except, 2.vii.2014, J.M. Cumming (5♂, 1♀, CNC); same data except, 1.vii.2014, swept dunes & beach vegetation, S.H. Cumming (3♀, CNC); same data except, 2.vii.2014, (1♀, CNC); Ilwaco, Cape Disappointment, 23.vii.1993, H. Ulrich (14♂, 8♀, ZFMK); same data except, 24.vii.1993 (21♂, 20♀, ZFMK); same data except, 25.vii.1993 (15♂, 23♀, ZFMK); same data except, 26.vii.1993 (62♂, 1♀, ZFMK); same data except, Benson Beach, 24.vii.1993, dunes (1♂, ZFMK); same data except, 5.viii.1994 (9♂, 12♀, ZFMK); same data except, 9.viii.1994 (9♂, 2♀, ZFMK); same data except, 27.vii.1993, on wet sand (5♂, 6♀, ZFMK); same data except, 5.viii.1994, sandy beach (27♂, 2♀, ZFMK); same data except, 8.viii.1994 (32♂, 3♀, ZFMK); same data except, 10.viii.1994 (15♂, ZFMK); same data except, Waikiki Beach, 15.vii.1988, on sand (22♂, 8♀, ZFMK); same data except, 17.vii.1988, on rock (1♀, ZFMK); same data except, 22.vii.1993, dunes (1♂, ZFMK); same data except, 26.vii.1993, on wet sand (19♀, ZFMK); same data except, 22.vii.1993, sandy beach (3♂, 3♀, ZFMK); same data except, 9.viii.1994 (30♂, 2♀, ZFMK); Ilwaco [ca. 46°16'20"N 124°04'25"W], vii.1917, A.L. Melander (2♂, 2♀, USNM); San Juan County: San Juan Island, Kanaka Bay [ca. 48°29'03"N 123°05'4"W], 8.vii.1924, A.L. Melander (1♂, USNM).

**Diagnosis.** This relatively large species is characterized by 3–4 notopleural bristles, dark legs, relatively long vein CuA+CuP, males with greyish-white pruinosity on the face and clypeus, and longer lower male ommatrichia. *Parathalassius candidatus* is very similar to *P. abela*, but males of the former species can be distinguished by a face and clypeus that is concolourous with the greyish-white frons. Females of these two species are virtually identical. *Parathalassius candidatus* is also similar to *P. sinclairi* **sp. nov.** and *P. susanae* **sp. nov.**, but all three species can be differentiated by the structure of the hindleg and female sternite 8, as indicated in the key

**Redescription. Male:** Body length 3.0–3.9 mm, wing length 3.0–3.5 mm. Dark brown ground colour covered mostly with dense greyish-white pruinosity. Setae of body and legs white. **Head** (Fig. 26): Eyes with ommatrichia of lower third distinctly longer and slightly flattened, forming dense reflective mat of whitish coloured hair. Face and clypeus concolourous with greyish-white frons and vertex. Face narrowest at middle, about 2.0X width of anterior ocellus. Gena and postgena with moderately long white setae, forming short beard flanking mouthparts. Antenna (Fig. 40) including arista-like stylus, entirely dark brown; postpedicel subtriangular, 1.5–1.7X longer than wide; arista-like stylus long, about 2.0X length of postpedicel. Palpus with 2–3 moderately long setae and several short setulae on outer surface of apical half. **Thorax:** Acrostichal setulae quadriseriate; 6–8 dorsocentral bristles, 0–1 presutural intra-alar bristles, 1–2 presutural supra-alar (posthumeral) bristles, 2–3 postsutural supra-alar bristles, 3–4 notopleural bristles. Scutellum with 3 pairs of bristles. **Legs:** *Foreleg:* Dark grey, pale only at knee. Coxa with moderately long pale setae on anterior surface. Femur with numerous long setae on posterior surface, posterodorsal and posteroventral rows prominent. Tibia with short setae and setulae. Tarsus with setulae; tarsomeres 1–2 not dilated. *Midleg:* Dark grey, pale only at knee, tarsus greyish-brown. Femur with anteroventral and posteroventral row of setae prominent. Tibia with pair of apicoventral bristles. Tarsomeres 1–4 each with pair of dark spine-like apicoventral setae. *Hindleg* (Figs 50, 53): Dark grey, femur dark brown posteriorly, tarsus greyish-brown. Femur with ventral row of setae prominent. Tibia with anterodorsal and anteroventral rows of setae prominent, mostly longer than width of tibia, with anterodorsal row of setae evenly curved towards apex of tibia. Tarsus slightly shorter than tibia with short setae and setulae; tarsomere 1 slightly shorter than combined length of tarsomeres 2–4; tarsomeres 1–3 with several short thickened angled setae dorsally, not perpendicular and peg-like; tarsomere 2 distinctly longer than tarsomere 3; tarsomere 3 slightly longer than tarsomere 4; tarsomere 5 subequal in length to tarsomere 3. **Wing** (Fig. 58): Hyaline with dark brown veins. Cell dm produced apically, dm-m crossvein concave. Vein CuA+CuP relatively long, slightly curved to straight. **Abdomen:** Tergites 2–4 with setae well-developed and relatively long. Sternite 5 with slender anteriorly curved digitiform pregenitalic process present, base with short blunt anterior projection, apex blunt and covered with microtrichia, posterior edge of sternite 5 (behind process) deeply emarginate. Sternite 8 subquadrate with prominent elongate setae on posterolateral margins. *Hypopygium* (virtually indistinguishable from that of *P. abela* **sp. nov.**) (Figs 81, 116): Large. Left epandrial lamella with ventral portion elongate (about 2X longer than high); ventral epandrial process broadly bifurcate, dorsal arm curved ventrally, narrow in middle portion, apex expanded and hook-like, ventral arm thick with minute apicodorsal seta and pair of minute setae along distiventral margin, apex with expanded lamelliform concavity. Dorsal lobe of left

surstylus subtriangular with basiventral edge weakly rounded, with long basidorsal seta, short lateral seta and long apical seta, medial surface with knob-like projection bearing lamelliform apical process. Ventral lobe of left surstylus shallowly bilobate in lateral view, dorsal lobe short with apex subquadrate, ventral lobe with rounded base bearing short lateral seta and complex upturned multilobate projection arising medioventrally. Right epandrial lamella with ventral epandrial process not developed; basal portion of epandrial lamella narrowed and dorsally curved, with deep dorsal emargination bordering ventral margin of right cercus. Dorsal lobe of right surstylus with 3 lateral setae (apical-most seta somewhat stronger), apex narrowed with squared-off tip bearing thick apically-frayed preniseta on medial surface. Ventral lobe of right surstylus with lateral seta near middle, distal half recurved and tapered with tubercle bearing strong seta proximal to rounded apex. Hypandrium very large, elongate-reniform with convex anterior and posterior ends extending to or beyond margins of epandrial lamellae in lateral view, mainly bare except for a few short setae lateroventrally on left side, and posteriorly on right side. Left postgonite lobe subquadrate basally, constricted near middle, with distal portion broadly lamelliform with claw-like apical process, base of lobe with slender medial projection. Right postgonite lobe with broad lateral protuberance and bulbous medial projection, apex bifurcate with short digitiform process and rounded lamelliform process. Phallus (cf. Figs 95–96) short and weakly curved, broad in basal 2/3 with apical 1/3 narrower (in lateral view), dorsal flange and left lateral bump-like protuberance present at 2/3 length. Ejaculatory apodeme broadly subtriangular. Hypoproct strongly projected dorsally as pair of slender blade-like lobes. Cerci with anal setae well-developed and differentiated from surrounding hairs; right cercus much larger than left cercus with basal portion distended and rounded laterally, apex strongly deflected dorsally, elongate narrow and pointed with 2 short preapical setae on lateral margin; left cercus oblong-subrectangular in dorsal view, apex short and truncate, with 2 long, dorsally-directed setae.

**Female:** Body length 3.4–4.1 mm, wing length 3.0–4.0 mm. Similar to male except as follows: **Head:** Eyes with ommatrichia of nearly uniform length, not distinctly longer on lower third. Face wider, at middle about 4.0–5.0X width of anterior ocellus. **Legs:** *Foreleg:* Coxa with shorter more slender pale setae on anterior surface. Femur with posteroventral row of setae only prominent apically. *Midleg:* Femur with anteroventral and posteroventral setae less prominent. *Hindleg:* Tarsomeres 1–3 without slightly thickened setae dorsally. **Abdomen:** Tergite 5 broadly subtriangular to semicircular in dorsal view with posterior margin rounded (cf. Fig. 131). Terminalia distinctly narrower than base of segment 5 (cf. Figs 131–132); sternite 8 trough-like, lacking basal bulge, widened just beyond base and narrowed apically, apical half with longitudinal ridges, apex broadly truncate (Fig. 135); sternite 9 reduced to narrow transverse sclerotized band; tergite 10 with hemitergites subtriangular and short, each with 2 acanthophorite spines; cercus short, pointed apically.

**Distribution and seasonal occurrence.** *Parathalassius candidatus* is currently known to occur on sandy seashores from Haida Gwaii, Vancouver Island and Vancouver, British Columbia, south along the Washington, Oregon and California coasts to San Francisco (Fig. 144). Adults have been collected from late March to mid August.

**Remarks.** Although the locality label of the holotype does not indicate collection date or collector, Melander (1906) states that the specimen was collected in the summer of 1905 by J.M. Aldrich.

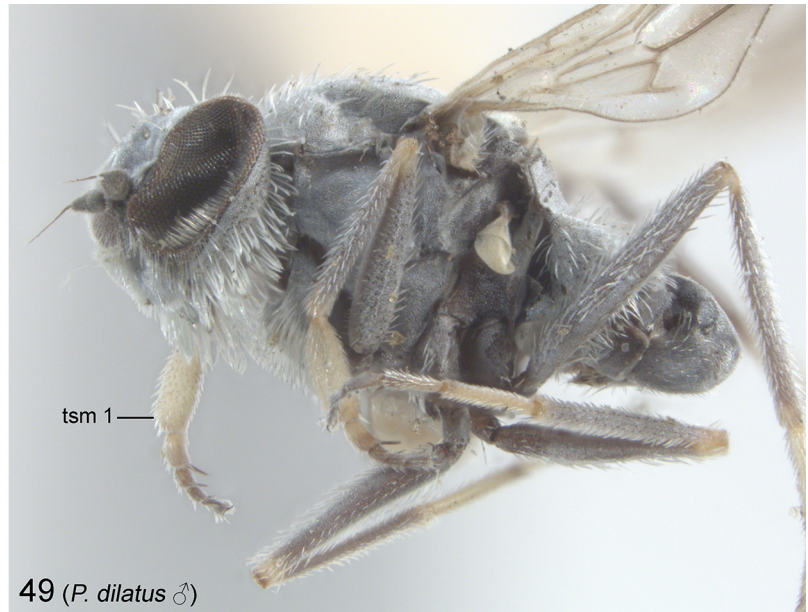
COI barcode sequences (Fig. 154) and morphology confirm separation of this species from the very similar allopatric *P. abela* (with minimally 3.6% genetic divergence).

### ***Parathalassius dilatus* sp. nov.**

(Figs 48–49, 85, 101–102, 126, 145)

**Type material.** **HOLOTYPE** ♂ from Naples [ca. 33°45'07"N 118°08'00"W], Los Angeles County, California, labelled: “Naples/ Cal/ IV-7-18”; “C.W. Johnson/ Collection”; “*Parathalassius*/ n.sp. [handwritten on both sides]”; “*Parathalassius melanderi*/ Cole/ det WJ Turner 1978”; “MCZ-ENT [barcode symbol] 00529580 [printed on both sides]” “HOLOTYPE/ *Parathalassius dilatus* / Brooks & Cumming [red label]” (MCZ). **PARATYPE: USA: California:** Los Angeles County, El Segundo Dunes [ca. 33°55'N 118°26'W], 29.IV.1986, UCRC ENT 461755 (1♂, UCRC).

**Diagnosis.** This relatively small distinctive species is characterized by a male with foretarsomeres 1–2 dilated, longer lower male ommatrichia, 2 notopleural bristles, and wing that is apically infuscate.



**FIGURES 48–49.** *Parathalassius dilatus* sp. nov., partial and full habitus photographs, male holotype. **48.** Head and anterior portion of thorax, lateral view. **49.** Body, anterolateral view. Abbreviation: tsm 1—tarsomere 1 (foreleg).

**Description. Male** (Figs 48–49): Body length 2.4 mm, wing length 2.3 mm. Dark brown ground colour covered mostly with dense greyish-white pruinosity. Setae of body and legs white. **Head** (Figs 48–49): Eyes with ommatrichia of lower third distinctly longer and slightly flattened, forming dense reflective mat of whitish coloured hair. Face and clypeus concolourous with greyish-white frons and vertex. Face narrowest at middle. Gena and postgena with long white setae, forming distinct beard flanking mouthparts. Antenna (Fig. 49) including arista-like stylus, dark brown; postpedicel subtriangular, 1.5X longer than wide; arista-like stylus of medium length, about 1.5X length of postpedicel. Palpus with dense brush of 10–12 setae on outer surface of apical half. **Thorax:** Acrostichal setulae biserial; 7 dorsocentral bristles, 0 presutural intra-alar bristles, 1 presutural supra-alar (posthumeral) bristle, 3 postsutural supra-alar bristles, 2 notopleural bristles. Scutellum with 2 pairs of bristles. **Legs:** *Foreleg:* Dark grey to brownish grey, pale at knee and apex of tibia, tarsomeres 1–2 pale yellowish-brown, tarsomeres 3–5 pale brown to dark brown (darker apically). Coxa with moderately long stout pale setae, densely covering anterior surface. Femur with moderately long setae on posterior surface. Tibia with short setae and setulae. Tarsus with setulae, tarsomeres 2–4 each with dark stout apicoventral seta (stoutest on tarsomere 2); tarsomere 1 dilated, distinctly thicker than tarsomeres 3–5 (Figs 48–49); tarsomere 2 slightly expanded. *Midleg:* Dark grey, pale at knee and apex of tibia, tarsomeres 1–2 pale yellowish-brown, tarsomeres 3–5 pale brown to dark brown, darker apically. Femur with anterodorsal setae most prominent, short to moderately long. Tibia with 1 apicoventral bristle. Tarsomeres 1–4 each with a few dark spine-like apicoventral setae. *Hindleg:* Dark grey, femur dark brown posteriorly, pale at knee and extreme apex of tibia, tarsomere 1 and base of tarsomere 2 pale yellowish-brown, apex of tarsomere 2 and tarsomeres 3–5 brown to dark brown, darker apically. Femur with anteroventral row of setae most prominent, short or absent basally, longer apically. Tibia clothed with short setae. Tarsus longer than tibia with short setae and setulae; tarsomere 1 long, but shorter than combined length of tarsomeres 2–4; tarsomeres 1–4 lacking peg-like or thickened setae dorsally; tarsomere 2 long, longer than tarsomere 3; tarsomere 3 long, longer than tarsomere 4; tarsomere 4 slightly longer than tarsomere 5. **Wing** (cf. Fig. 60): Infusate apically, hyaline basally, with yellowish veins basally and dark brown veins apically. Cell dm produced apically (dm-m crossvein with aberrant stub vein on holotype). Vein CuA+CuP short, straight. **Abdomen:** Tergites 2–4 with setae well-developed. Sternite 5 without projecting pregenitalic process, posterior edge of sternite deeply emarginate. Sternite 8 subquadrate with setae longer along posterolateral margins. *Hypopygium* (Figs 85, 101–102, 126): Large. Left epandrial lamella with ventral portion elongate (about 2X longer than high); ventral epandrial process broadly bifurcate, dorsal arm elongate and strongly hooked ventrally, more or less evenly slender basally with apex slightly expanded, ventral arm thick with minute apicodorsal seta and minute distiventral seta, apex with expanded lamelliform concavity. Dorsal lobe of left surstylus subtriangular, with basiventral edge broadly rounded, apex

pointed, with long basidorsal seta, short lateral seta and long apical seta, medial surface with knob-like projection bearing lamelliform apical process. Ventral lobe of left surstylus shallowly bilobate in lateral view, dorsal lobe short with apex rounded, ventral lobe with rounded base bearing short lateral seta and complex upturned bifurcate projection arising medioventrally. Right epandrial lamella with ventral epandrial process very short and broad; basal portion of epandrial lamella narrowed and dorsally curved, with deep dorsal emargination bordering ventral margin of right cercus. Dorsal lobe of right surstylus with 3 lateral setae (lowermost seta weaker), apex rounded bearing thick apically-frayed preniseta on medial surface. Ventral lobe of right surstylus recurved at base with lateral seta near middle, with elongate finely-tipped process proximal to narrow apex. Hypandrium very large, elongate-reniform with convex anterior and posterior ends extending to or beyond margins of epandrial lamellae in lateral view, bare. Left postgonite lobe ovoid basally, constricted near middle, distal portion subrectangular and flat without claw-like apical process, base of lobe with broad curved apically-pointed medial projection. Right postgonite lobe with broad lateral protuberance pointed at apical margin and lamelliform medial projection, apex bifurcate with short digitiform process and rounded lamelliform process. Phallus relatively short and moderately curved, gradually tapering distally, apex straight. Ejaculatory apodeme broadly subtriangular. Hypoproct projected dorsally as pair of subtriangular lobes, each lobe with 3 preapical ventral setae, left lobe with piliferous flange lateral to lower seta. Cerci with anal setae well-developed and differentiated from surrounding hairs; right cercus much larger than left cercus with basal portion distended and rounded laterally, apex weakly deflected dorsally, truncate with pair of setae along apicolateral margin; left cercus oblong-subrectangular in dorsal view, apex even with apex of right cercus, weakly deflected dorsally, broadly truncate with pair of apical setae.

**Female:** Unknown.

**Distribution and seasonal occurrence.** *Parathalassius dilatus* is currently known only from two male specimens collected from El Segundo Dunes and adjacent Long Beach (Naples) in Los Angeles County in southern California (see Remarks) (Fig. 145) in April.

**Etymology.** The specific name refers to the expanded tarsomeres 1–2 of the male foreleg.

**Remarks.** The most recent specimen (paratype) of this species was collected by R. Mattoni and R. Rogers in 1986 during a survey of the El Segundo dune reserve located along the western edge of the Los Angeles International Airport. This approximately 80 hectare reserve is the largest remaining habitat in the historical coastal El Segundo dune system in southwestern Los Angeles (Mattoni 1990). The dune system supports several rare species of insects and plants, including the endangered El Segundo blue butterfly, *Euphilotes battoides allyni* (Shields), and the El Segundo giant flower-loving fly, *Rhaphiomidas terminatus terminatus* Cazier (Mydidae), which was until recently thought to be extinct (George & Mattoni 2006). The holotype of *P. dilatus* was collected in 1918 from Naples, likely at nearby Long Beach, which abuts the southern edge of the El Segundo dune system. *Parathalassius dilatus* probably represents another rare species of fly that is restricted to the El Segundo and historically adjacent dune systems.

### ***Parathalassius infuscatus* sp. nov.**

(Figs 7, 27, 41, 59, 87, 111–112, 119, 146)

**Type material. HOLOTYPE** ♂ labelled: “USA: CA: Santa Barbara Co.:/ Surf Beach, Vandenberg Air/ Force Base, 34.683801°N/ 120.605520°W, 21.iii.2016/ A.J. Abela, ex: sandy coastal/ foredune”; “HOLOTYPE/*Parathalassius infuscatus* / Brooks & Cumming [red label]” (CNC). **PARATYPES: USA: California:** same data as holotype (2♂, CNC); same data except, CNC588232, CNC588233 (2♂, barcoded, CNC); same data as holotype except, 21.iii.2016 (1♀, CNC); same data as holotype except, 11.ii.2017 (1♀, CNC).

**Other material examined. USA: California:** San Luis Obispo County: Dune Lakes, 3 mi. S Oceano [ca. 35°04'25"N 120°36'57"W], 27.iv.1973, J. Powell (1♂, 1♀, EMEC); Morro Bay, dunes [ca. 35°22'16.4"N 120°51'52.0"W], 12.iv.1981 (3♂, 1♀, EMEC); Oso Flaco Dunes, 35.032931°N 120.629882°W, 8.iii.2015, A. Abela (1♂, photograph, see Fig. 2C); same data except, 11.ii.2017 (20♂, 3♀, CNC).

**Diagnosis.** This small distinctive species is characterized by broadly infusate wings in both the male and female with the base of M<sub>2</sub> usually appearing indistinct, uniformly short male ommatrichia, 2 notopleural bristles, and male hypopygium with an unbranched left ventral epandrial process.





50 (*P. candidatus* ♂)



51 (*P. sinclairi* ♂)



52 (*P. susanae* ♂)



53 (*P. candidatus* ♂)

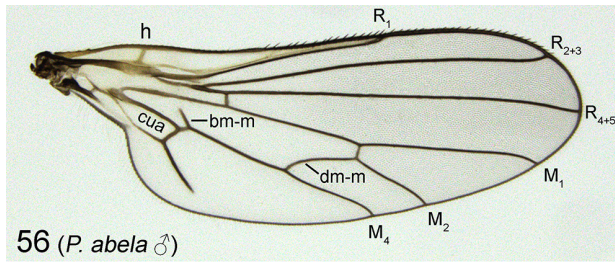


54 (*P. sinclairi* ♂)

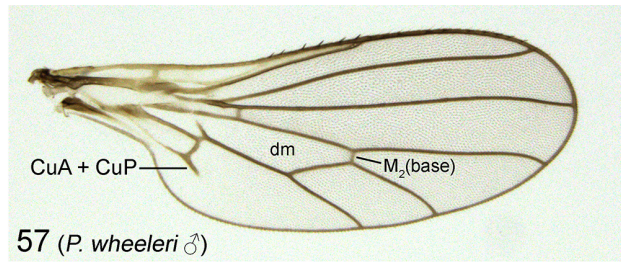


55 (*P. susanae* ♂)

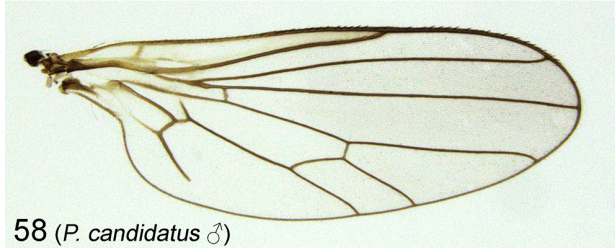
**FIGURES 50–55.** Male left hindlegs of Nearctic *Parathalassius*. **50.** *Parathalassius candidatus* Melander, hindleg, lateral view. **51.** *Parathalassius sinclairi* **sp. nov.**, hindleg, lateral view. **52.** *Parathalassius susanae* **sp. nov.**, hindleg, lateral view. **53.** *Parathalassius candidatus* Melander, apex of tibia and tarsus, dorsolateral view. **54.** *Parathalassius sinclairi* **sp. nov.**, apex of tibia and tarsus, dorsolateral view. **55.** *Parathalassius susanae* **sp. nov.**, apex of tibia and tarsus, dorsal view.



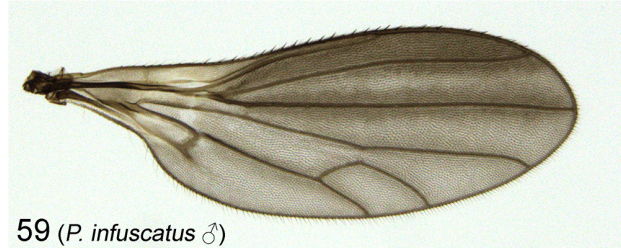
56 (*P. abela* ♂)



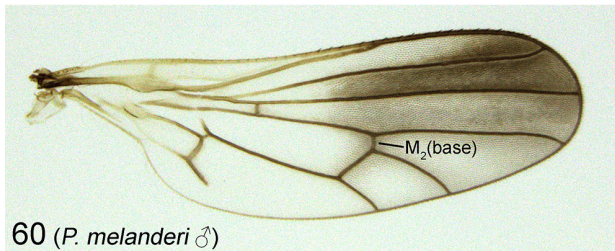
57 (*P. wheeleri* ♂)



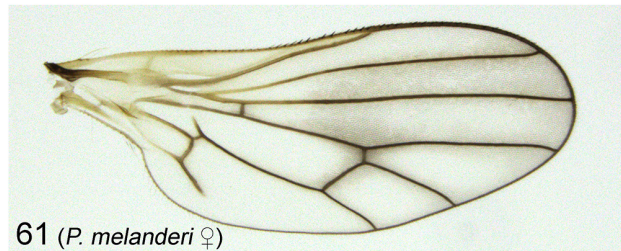
58 (*P. candidatus* ♂)



59 (*P. infuscatus* ♂)



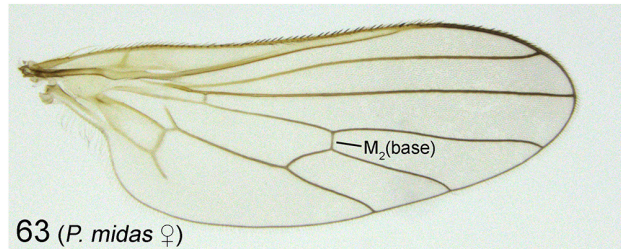
60 (*P. melanderi* ♂)



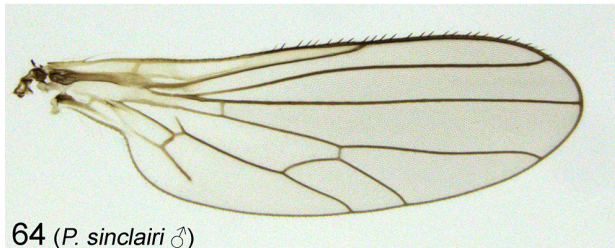
61 (*P. melanderi* ♀)



62 (*P. midas* ♂)



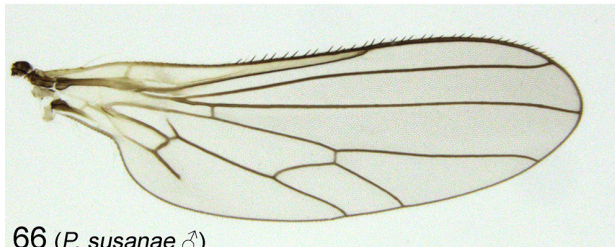
63 (*P. midas* ♀)



64 (*P. sinclairi* ♂)



65 (*P. socali* ♂)



66 (*P. susanae* ♂)



67 (*P. uniformus* ♂)

**FIGURES 56–67.** Wings of Nearctic *Parathalassius*. 56. *Parathalassius abela* sp. nov., male. 57. *Parathalassius wheeleri* sp. nov., male. 58. *Parathalassius candidatus* Melander, male. 59. *Parathalassius infuscatus* sp. nov., male. 60. *Parathalassius melanderi* Cole, male. 61. *Parathalassius melanderi* Cole, female. 62. *Parathalassius midas* sp. nov., male. 63. *Parathalassius midas* sp. nov., female. 64. *Parathalassius sinclairi* sp. nov., male. 65. *Parathalassius socali* sp. nov., male. 66. *Parathalassius susanae* sp. nov., male. 67. *Parathalassius uniformus* sp. nov., male. Abbreviations: bm-m—basal medial crossvein; cua— anterior cubital (=anal) cell; CuA— anterior branch of cubital vein; CuP— posterior branch of cubital vein; dm— discal medial cell; dm-m— discal medial crossvein; h— humeral crossvein; M<sub>1</sub>, M<sub>2</sub>, M<sub>4</sub>— medial veins; R<sub>1</sub>, R<sub>2+3</sub>, R<sub>4+5</sub>— radial veins.

**Description. Male** (Fig. 7): Body length 1.5–2.0 mm, wing length 1.4–1.5 mm. Dark brown ground colour covered mostly with dense brownish-grey pruinosity. Setae of body and legs yellowish-white. **Head** (Fig. 27): Eyes with ommatrichia of nearly uniform length, not distinctly longer on lower third. Face and clypeus covered with greyish-white pruinosity, not concolourous with brownish-grey frons and vertex. Face narrowest at middle, about 2.5X width of anterior ocellus. Gena without setae and postgena with moderately short sparse pale setae, not forming beard flanking mouthparts. Antenna (Fig. 41) including arista-like stylus, entirely dark brown; postpedicel subtriangular, 1.5–1.6X longer than wide; arista-like stylus of medium length, about 1.6X length of postpedicel. Palpus with 2–3 moderately long setae and several short setulae on outer surface of apical half. **Thorax:** Acrostichal setulae weakly developed, biserial; 5–6 dorsocentral bristles, 0 presutural intra-alar bristles, 1 presutural supra-alar (posthumeral) bristle, 2 postsutural supra-alar bristles, 2 notopleural bristles. Scutellum with 2–3 pairs of bristles. **Legs:** *Foreleg:* Dark brownish-grey, paler at knee and extreme apex of tibia, tarsus pale brown to brown. Coxa with short pale setae on anterior surface. Femur with short setae on posterior surface. Tibia with short setae and setulae. Tarsus with setulae; tarsomeres 1–2 not dilated. *Midleg:* Dark brownish-grey, paler at knee, tarsus pale brown to brown. Femur with short setae on anterior surface. Tibia with pair of dark apicoventral bristles. Tarsomeres 1–4 each with a few dark spine-like apicoventral setae. *Hindleg:* Dark brownish-grey, femur dark brown posteriorly, tarsus pale brown to brown. Femur with anteroventral row of setae most prominent, short basally, slightly longer apically. Tibia clothed with very short setae. Tarsus slightly longer than tibia with short setae and setulae; tarsomere 1 long, but shorter than combined length of tarsomeres 2–4; tarsomeres 1–4 lacking peg-like or thickened setae dorsally; tarsomere 2 long, longer than tarsomere 3; tarsomere 3 longer than either tarsomere 4 or 5; tarsomeres 4 and 5 subequal in length. **Wing** (Fig. 59): Infusate with dark brown veins, membrane lighter and more yellow basally. Vein  $M_2$  usually appearing indistinct basally. Cell dm produced apically, dm-m crossvein slightly concave to nearly straight. Vein CuA+CuP very short, straight. **Abdomen:** Tergites 2–4 with setae relatively weak and sparse. Sternite 5 with short digitiform pregenitalic process present, base with short acute anterior projection, apex blunt and covered with short microtrichia, posterior edge of sternite (behind process) not emarginate. Sternite 8 subquadrate with setae relatively sparse, longer laterally. *Hypopygium* (Figs 87, 111–112, 119): Large. Left epandrial lamella with ventral portion elongate (about 2X longer than high); ventral epandrial process unbranched (dorsal lobe absent), basal 3/4 broadly subrectangular in lateral view with stout apically frayed apicodorsal seta and pair of minute setae along distiventral margin, apex upturned with expanded, lamelliform concavity. Dorsal lobe of left surstylus subpyriform, with basiventral edge rounded and flap-like, apex broadly rounded, with short basidorsal seta, short lateral seta and long thick apical seta, medial surface with knob-like projection bearing thick, hook-like apical seta. Ventral lobe of left surstylus broad with curved seta on distiventral margin and complex upturned projection arising medioventrally. Right epandrial lamella with ventral epandrial process short broad and rounded apically; basal portion of epandrial lamella narrowed and dorsally curved, with deep dorsal emargination bordering ventral margin of right cercus. Dorsal lobe of right surstylus with 2 similar sized setae on dorsal margin, apex narrowed with squared-off tip bearing long seta on lower apical margin and thick apically frayed prensiseta on medial surface. Ventral lobe of right surstylus subtriangular with acute apex, with seta near middle of ventral margin. Hypandrium large, reniform, mainly bare except for two setae posteriorly on right side below ventral edge of right epandrial lamella. Left postgonite lobe ovoid basally, constricted medially, distal portion broadly lamelliform with claw-like apical process, base of lobe with slender medial projection. Right postgonite lobe broad basally with lateral protuberance, bifurcate, ventral arm tapered to acute tip, dorsal arm with rounded lamelliform apex. Phallus bifurcate with narrow curved ventral branch about half length of dorsal branch. Ejaculatory apodeme subrectangular. Hypoproct projected dorsally as pair of slender digitiform lobes. Cerci with anal setae relatively long, well-developed and differentiated from surrounding hairs; right cercus much larger than left cercus with basal portion distended and rounded laterally, apex weakly deflected dorsally, with broad flap-like medial expansion and stub-like tip, bearing 2 setae; left cercus Y-shaped in dorsal view, basal portion narrow, strap-like, distal portion with flap-like medial and apical lobes, apical lobe weakly deflected dorsally, bearing 2 setae.

**Female:** Body length 1.9–2.0 mm, wing length 1.8–2.0 mm. Wing infusate as in male (cf. Fig. 59), but usually slightly lighter. Similar to male except as follows: **Head:** Face and clypeus covered with brownish-grey pruinosity, concolourous with frons and vertex. Face wider, at middle about 3.5X width of anterior ocellus. **Abdomen:** Tergite 5 broadly subtriangular to semicircular in dorsal view with posterior margin rounded (cf. Fig. 131). Terminalia distinctly narrower than base of segment 5 (cf. Figs 131–132); sternite 8 trough-like, lacking basal

bulge, apical portion with longitudinal ridges, apex broadly rounded; tergite 10 with hemitergites subtriangular and short, each with 2 or 3 acanthoporphite spines; cercus short, pointed apically.

**Distribution and seasonal occurrence.** *Parathalassius infuscatus* is currently known only from coastal dunes in San Luis Obispo County and Santa Barbara County in southern California (Fig. 146). Adults have only been collected or photographed from February to late April. We were unable to locate specimens at the type locality (Figs 19–20), later in the season in early June, 2016.

**Etymology.** The specific name refers to the dark infuscated wing in both males and females.

**Remarks.** Adults of *P. infuscatus* were found on open sand between patches of beach bur (*Ambrosia chamissonis*) during the day (Fig. 19) and on the vegetation by late afternoon (Fig. 20).

### ***Parathalassius maritimus* Shamshev**

*Parathalassius maritimus* Shamshev, 1998: 6.

**Material examined. JAPAN:** Hokkaido, Shari, 3.viii.1967, T. Saigusa (2♂, 1♀, CNC); Kyushu, Fukuoka, Camp Hakata, 1–3.vi.1955, H. Lyman (1♂, EMEC).

**Diagnosis.** This medium sized Palaearctic species is characterized by a short-subtriangular antennal postpedicel, uniformly short male ommatrichia, white to pale yellow setae on the lower part of the head, 2 notopleural bristles, pale legs, hyaline wing, and left ventral epandrial process of the male hypopygium bifurcate with slender hook-shaped dorsal arm and sclerotized flattened serratulate apex on ventral arm.

**Distribution.** This eastern Palaearctic species is known from the Kuril Islands (Kunashir) in the Russian Far East (Shamshev 1998) and is here newly recorded from Japan, from Hokkaido and Kyushu.

**Remarks.** In his description of *P. maritimus* from the Kuril Islands, Shamshev (1998) indicated that the larger setae on the head and thorax of this species are brown compared with the smaller setae that are whitish. In contrast, the specimens from Japan have the larger setae on the head and thorax pale yellow, rather than brown.

### ***Parathalassius melanderi* Cole**

(Figs 28, 42, 60–61, 86, 99–100, 125, 136, 147)

*Parathalassius melanderi* Cole, 1912: 154.

**Type material examined. LECTOTYPE** (here designated in order to fix identity of the species), ♂, from Laguna Beach [ca. 33°32'24"N 117°47'04"W], Orange County, California, USA, labelled: “Laguna Bch/ Cal. Cole [1912]”; “8”; “*Parathalassius melanderi*/ n.sp. [red label]”; “LECTOTYPE/ *Parathalassius melanderi* Cole/ des. Brooks & Cumming 2016 [red label]” (USNM). **PARALECTOTYPE: USA: California:** same data as lectotype except, S. Cal. (1♂, EMEC). Our paralectotype label has additionally been attached to this specimen.

**Other material examined. MEXICO: Baja California:** Ensenada [ca. 31°50'06"N 116°36'39"W], 24.vi.1950, A.L. Melander (2♂, 1♀, USNM); 10 mi. N El Rosario, El Consuelo Dunes [ca. 30°11'N 115°47'W], 24.iii.1979, J.D. Pinto, UCRC ENT 461757 (1♀, UCRC). **USA: California:** Orange County: Corona Del Mar [ca. 33°35'33"N 117°52'26"W], 19.xi.1946, A.L. Melander (1♀, USNM); Crystal Cove State Park, 33°34'51.9"N 117°50'55.7"W, 6.vi.2016, swept sandy seacoast & beach vegetation, S.E. Brooks (40♂, 59♀, CNC; 2♂, 2♀, CSCA); same data except, CNC574905, CNC574937 (2♂, barcoded, CNC), CNC574932, CNC574943 (2♀, barcode-associated, CNC); same data except, J.M. Cumming (8♂, 22♀, CNC); same data except, CNC580763, CNC580778 (2♂, barcoded, CNC), CNC580779 (1♀, barcode-associated, CNC); same data except, S.H. Cumming (1♀, CNC); Crystal Cove State Park, Pelican Point, moist sand in tidal zone, 6.viii.1993, H. Ulrich (2♀, ZFMK); same data except, 7.viii.1993 (1♂, 4♀, ZFMK); same data except, 8.viii.1993 (43♂, 13♀, ZFMK); same data except, 20.vii.1994 (8♂, 8♀, ZFMK); same data except, 21.vii.1994 (56♂, 10♀, ZFMK); Crystal Cove, 33°34.8'N 117°50.7'W, beach, 6.iv.2005, W.N. & D. Mathis (9♂, 1♀, USNM); same data except, CNC478112 (1♀, barcode-associated); Laguna Beach [ca. 33°32'24"N 117°47'04"W], Cole (2♀, EMEC); Doheny Park [33°27'42"N 117°40'56"W], 22.v.1944, A.L. Melander (1♂, USNM); San Clemente State Beach, 33°24'18.7"N 117°36'22.8"W, 7.vi.2016, swept sandy seacoast, S.E. Brooks (4♂, CNC); same data except, J.M. Cumming (5♀, CNC); same data

except, S.H. Cumming (1♀, CNC); San Clemente, 23.v.1944, A.L. Melander (1♂, USNM); San Diego County: Carlsbad [ca. 33°09'27"N 117°21'12"W], 22.vi.1950, A.L. Melander (1♂, USNM); same data except, 24.vi.1954 (1♂, USNM); San Onofre State Beach, 33°22'29.3"N 117°34'04.7"W, 7.vi.2016, swept sandy seacoast, S.E. Brooks (1♀, CNC); Silver Strand State Beach (east shore), 32°37'49.9"N 117°08'24.9"W, 8.vi.2016, swept sandy shore & beach vegetation, S.E. Brooks (2♂, 2♀, CNC); Silver Strand State Beach, 4.viii.1993, H. Ulrich (1♀, ZFMK); Santa Barbara County: Carpinteria [ca. 34°23'35"N 119°31'29"W], 23.ix.1946, A.L. Melander (1♂, 1♀, USNM); Ventura County: San Nicolas Is., Dutch Harbor area [ca. 33°13'N 119°29'W], 6.v.1978, R. Coville (3♂, 1♀, EMEC); same data except, J. Powell (1♂, EMEC).

**Diagnosis.** This relatively small distinctive species is characterized by a short-subtriangular antennal postpedicel, longer lower male ommatrichia, 2 notopleural bristles, male with a wing darkened towards the apex, and female with slight infuscate shading along the wing veins near the apex of cell dm. *Parathalassius melanderi* is most similar to *P. dilatatus*, but does not have male foretarsomeres 1–2 dilated.

**Redescription. Male:** Body length 2.3–2.9 mm, wing length 2.0–2.2 mm. Dark brown ground colour covered mostly with dense greyish-white pruinosity. Setae of body and legs white. **Head** (Fig. 28): Eyes with ommatrichia of lower third distinctly longer and slightly flattened, forming dense reflective mat of whitish coloured hair. Face and clypeus concolourous with greyish-white frons and vertex. Face narrowest at middle, about 2.0–2.5X width of anterior ocellus. Gena and postgena with long white setae, forming distinct beard flanking mouthparts. Antenna (Fig. 42) including arista-like stylus, entirely dark brown; postpedicel short-subtriangular, 1.35–1.45X longer than wide; arista-like stylus of medium length, about 1.5X length of postpedicel. Palpus with dense brush of 10–12 setae on outer surface of apical half. **Thorax:** Acrostichal setulae biserial; 6 dorsocentral bristles, 0 presutural intra-alar bristles, 1 presutural supra-alar (posthumeral) bristle, 2–3 postsutural supra-alar bristles, 2 notopleural bristles. Scutellum with 2–3 pairs of bristles. **Legs:** *Foreleg:* Dark grey, pale at knee and apex of tibia, tarsomeres 1–2 pale yellowish-brown, tarsomeres 3–5 brown to greyish-brown. Coxa with moderately long stout pale setae, densely covering anterior surface. Femur with moderately long setae on posterior surface, posteroventral rows prominent. Tibia with short setae and setulae. Tarsus with setulae; tarsomeres 1–2 not dilated. *Midleg:* Dark grey, pale at knee and apex of tibia, tarsomeres 1–2 pale yellowish-brown, tarsomeres 3–5 brown to greyish-brown, darker apically. Femur with anterodorsal setae most prominent, short. Tibia with pair of apicoventral bristles. Tarsomeres 1–4 each with several dark spine-like apicoventral setae. *Hindleg:* Dark grey, femur dark brown posteriorly, pale at knee and apex of tibia, tarsomeres 1–2 and base of tarsomere 3 pale yellowish-brown, apex of tarsomere 3 and tarsomeres 4–5 brown to greyish-brown, darker apically. Femur with anteroventral row of setae most prominent, short basally, longer apically. Tibia clothed with short setae. Tarsus longer than tibia with short setae and setulae; tarsomere 1 long, but shorter than combined length of tarsomeres 2–4; tarsomeres 1–4 lacking peg-like or thickened setae dorsally; tarsomere 2 long, longer than tarsomere 3; tarsomere 3 long, longer than tarsomere 4; tarsomere 4 longer than tarsomere 5. **Wing** (Fig. 60): Lightly infuscate apically, hyaline basally, with yellowish veins basally and dark brown veins apically. Cell dm slightly produced apically, dm-m crossvein nearly straight. Vein CuA+CuP short to medium length, straight. **Abdomen:** Tergites 2–4 with setae well-developed. Sternite 5 without projecting pregenitalic process, posterior edge of sternite deeply emarginate. Sternite 8 subquadrate with setae longer along posterolateral margins. *Hypopygium* (Figs 86, 99–100, 125): Large. Left epandrial lamella with ventral portion elongate (about 2X longer than high); ventral epandrial process broadly bifurcate, dorsal arm elongate and strongly curved ventrally, more or less evenly slender, apex slightly expanded dorsally and prominently hook-like, ventral arm thick with minute apicodorsal seta and pair of minute setae along distiventral margin, apex with expanded lamelliform concavity. Dorsal lobe of left surstylus subtriangular, with basiventral edge broadly rounded, apex pointed, with long basidorsal seta, short lateral seta and long apical seta, medial surface with knob-like projection bearing lamelliform apical process. Ventral lobe of left surstylus shallowly bilobate in lateral view, dorsal lobe short with apex rounded, ventral lobe with rounded base bearing short lateral seta and complex upturned bifurcate projection arising medioventrally. Right epandrial lamella with ventral epandrial process spur-like; basal portion of epandrial lamella narrowed and dorsally curved, with deep dorsal emargination bordering ventral margin of right cercus. Dorsal lobe of right surstylus with 3 lateral setae (lowermost seta weaker), apex narrowed with rounded tip bearing thick apically-frayed preniseta on medial surface. Ventral lobe of right surstylus recurved at base with lateral seta near middle, with elongate finely-tipped process proximal to narrow apex. Hypandrium very large, elongate-reniform with convex anterior and posterior ends extending to or beyond margins of epandrial lamellae in lateral view, bare. Left postgonite lobe ovoid basally, constricted near middle, distal portion subrectangular and flat

without claw-like apical process, base of lobe with broad curved apically-pointed medial projection. Right postgonite lobe with broad lateral protuberance pointed at apical margin and lamelliform medial projection, apex bifurcate with short digitiform process and rounded lamelliform process. Phallus short and weakly curved, basal portion broad with ventral flange, gradually tapering distally, lacking dorsal flange and left lateral protuberance at 2/3 length. Ejaculatory apodeme broadly subtriangular. Hypoproct strongly projected dorsally as pair of acutely pointed subtriangular lobes, each lobe with 3 preapical ventral setae, lower seta strong, left lobe with piliferous flange lateral to lower seta. Cerci with anal setae well-developed and differentiated from surrounding hairs; right cercus much larger than left cercus with basal portion distended and rounded laterally, apex weakly deflected dorsally, truncate with pair of setae along apicolateral margin; left cercus oblong-subrectangular in dorsal view, apex even with apex of right cercus, weakly deflected dorsally, broadly pointed with pair of apical setae.

**Female:** Body length 2.4–3.0 mm, wing length 2.1–2.4 mm. Similar to male except as follows: **Head:** Eyes with ommatrichia of nearly uniform length, not distinctly longer on lower third. Face wider, at middle about 4.0–4.5X width of anterior ocellus. Palpus less densely setose. **Legs:** *Foreleg:* Coxa with slightly shorter more slender setae on anterior surface. **Wing** (Fig. 61): Hyaline, with (in most specimens) slight infuscate shading along veins near apex of cell dm. **Abdomen:** Tergite 5 broadly subtriangular to semicircular in dorsal view with posterior margin rounded (cf. Fig. 131). Terminalia distinctly narrower than base of segment 5 (cf. Figs 131–132); sternite 8 trough-like, lacking basal bulge, not narrowed apically, apical half without longitudinal ridges, apex emarginate (Fig. 136); sternite 9 reduced to narrow weakly-developed transverse sclerotized band; tergite 10 with hemitergites subtriangular and short, each with 2 acanthophorite spines; cercus short, blunt-tipped.

**Distribution and seasonal occurrence.** *Parathalassius melanderi* is currently known to occur on sandy seashores from Carpinteria in Southern California, south to El Consuelo Dunes, near El Rosario in Baja California (Fig. 147). Adults have been collected from late March to mid November.

**Remarks.** A large series of *P. melanderi* collected at Crystal Cove State Park in southern California (Fig. 21) exhibited a behavioural change depending on the time of day. Early in the day, from morning through to mid afternoon, a few adult flies (both males and females) were collected on open dry or wet sand near the ocean, but apparently nowhere else. After 6:30 pm however, flies were no longer found on this part of the beach, but numerous individuals (both males and females) were taken further away from the ocean, on vegetation bordering the beach (Fig. 22).

### ***Parathalassius midas* sp. nov.**

(Figs 29–32, 43, 62–63, 76–77, 88, 113–114, 120, 127–129, 134, 148)

**Type material. HOLOTYPE** ♂ labelled: “USA: WA: Pacific Co., Cape/ Disappointment, nr. Ilwaco,/ Benson Beach, N46°16'20.4"/ W124°04'25.4", 1.vii.2014, swp [swept]/ dunes & beach grass (*Ammophila*)/ S.E. Brooks”; CNC/ 588234; “HOLOTYPE/ *Parathalassius midas*/ Brooks & Cumming [red label]”; “Legs removed/ for DNA/ analysis [green label]” (CNC). **PARATYPES: MEXICO: Baja California:** 3.2 mi. S Colonia Guerrero [ca. 30°41'N 116°01'W], 27.iv.1963, P.H. Arnaud Jr. (2♂, USNM). **USA: California:** Orange County: Corona Del Mar [ca. 33°35'33"N 117°52'26"W], 19.xi.1946, A.L. Melander (1♂, USNM); Laguna Beach [ca. 33°32'24"N 117°47'04"W], Baker (1♀, EMEC); same data except, 20.x.1951, A.L. Melander (1♀, USNM); San Diego County: Cardiff State Beach, 33°00'53.4"N 117°16'51.0"W, 8.vi.2016, swept sandy seacoast, S.E. Brooks (2♀, CNC); same data except, CNC574847 (1♀, barcode-associated, CNC); same data except, J.M. Cumming, CNC576883 (1♀, barcode-associated, CNC); same data except, S.H. Cumming (2♀, CNC); Carlsbad [ca. 33°09'27"N 117°21'12"W], 22.vi.1950, A.L. Melander (3♂, USNM); Santa Barbara County: Carpinteria [ca. 34°23'35"N 119°31'29"W], 12.vi.1953, A.L. Melander (6♀, USNM); same data except, 17.vi.1953 (4♀, USNM); U.C., Goleta [ca. 34°25'02"N 119°49'33"W], 27.vi.1965, D. Bragg (1♀, UCDC). **Oregon:** Lane County: Florence, 44°01'N 124°08.2'W, beach, 1.viii.2005, D. & W.N. Mathis (2♂, USNM).

**Other material examined. USA: WA:** Pacific County: Ilwaco, Cape Disappointment, Waikiki Beach, on wet sand, 23.vii.1993, H. Ulrich (1♀, ZFMK).

**Diagnosis.** This relatively large distinctive species is characterized by 2 notopleural bristles, pale legs, males with golden pruinosity and golden-yellow setae on the lower part of the head, uniformly short male ommatrichia, male wing with dark anteroapical spot, left ventral epandrial process of the male hypopygium bifurcate with broad

hook-shaped dorsal arm and sclerotized flattened serratulate apex on ventral arm, and prominent unique female terminalia.

**Description. Male:** Body length 2.6–3.3 mm, wing length 2.7–3.0 mm. Dark brown ground colour covered mostly with dense greyish-white to brownish-grey pruinosity. Setae of body and legs pale yellow to golden-yellow. **Head** (Figs 29–30): Eyes with ommatrichia of nearly uniform length, not distinctly longer on lower third. Face, clypeus and lower frons covered with golden pruinosity, not concolourous with greyish-white to brownish-grey upper frons and vertex. Face narrowest at middle, about 1.75X width of anterior ocellus. Gena and postgena with moderately long golden-yellow setae, forming beard flanking mouthparts. Antenna (cf. Fig. 43) including arista-like stylus, entirely dark brown; postpedicel subquadrate, with expanded anteroventral margin, 1.4–1.5X longer than wide; arista-like stylus long, about 2.0X length of postpedicel. Palpus with 7–8 golden-yellow setae on outer surface of apical half. **Thorax:** Acrostichal setulae primarily biserial; 6–8 dorsocentral bristles, 0–1 presutural intra-alar bristles, 1 presutural supra-alar (posthumeral) bristle, 3–4 postsutural supra-alar bristles, 2 notopleural bristles. Scutellum with 3 pairs of bristles. **Legs:** *Foreleg:* Dark grey basally, pale yellow from knee to apex of tibia, tarsus pale yellow, tarsomeres 2–5 or 3–5 pale brown to dark brown in some specimens. Coxa with moderately long pale yellow to golden-yellow setae on anterior surface. Femur with numerous long pale yellow to golden-yellow setae on posterior surface, posterodorsal and posteroventral rows prominent. Tibia with short pale yellow setae and setulae. Tarsus with pale yellow setulae; tarsomeres 1–2 not dilated. *Midleg:* Dark grey basally, pale yellow from knee to apex of tibia, tarsus pale yellow, tarsomeres 2–5 or 3–5 pale brown to dark brown in some specimens. Femur with pale yellow to golden-yellow setae on anterior surface, anteroventral rows long and prominent. Tibia with 1 apicoventral bristle. Tarsomeres 1–4 each with several dark spine-like apicoventral setae. *Hindleg:* Dark grey basally, pale yellow from knee to apex of tibia, femur brown posteriorly, tarsus pale yellow, tarsomeres 2–5 or 3–5 pale brown to dark brown in some specimens. Femur with pale yellow to golden-yellow setae on anterior surface, anteroventral row long and prominent. Tibia clothed with short pale yellow setae. Tarsus slightly shorter than tibia with mostly short pale yellow setae and setulae; tarsomere 1 shorter than combined length of tarsomeres 2–4; tarsomeres 1–4 lacking peg-like or thickened setae dorsally; tarsomere 2 longer than tarsomere 3; tarsomere 3 longer than tarsomere 4; tarsomere 5 subequal in length to tarsomere 3. **Wing** (Fig. 62): Hyaline with dark brown veins and infusate anteroapical spot. Cell dm produced apically, dm-m crossvein concave. Vein CuA+CuP short to medium length, slightly curved to straight. **Abdomen:** Tergites 2–4 with setae well-developed and relatively long. Sternite 5 with slender anteriorly curved hook-like pregenitalic process present, base with short blunt anterior projection, apex pointed and lacking distinct microtrichia, posterior edge of sternite 5 (behind process) deeply emarginate. Sternite 8 subrectangular with setae relatively sparse, elongate on posterolateral margins. **Hypopygium** (Figs 76–77, 88, 113–114, 120): Large. Left epandrial lamella with ventral portion short, about as long as high; ventral epandrial process with short stem-like base proximal to broad bifurcation, dorsal arm elongate hook-shaped and strongly curved ventrally, ventral arm thick in basal part with minute preapical dorsal seta and pair of minute setae along distiventral margin, sclerotized apex flattened and slightly narrowed, ventral edge and medial surface serratulate. Dorsal lobe of left surstylus with basiventral edge produced as a subquadrate flap-like lobe, apex with broad bifurcate asymmetrical process arising from short tubular base, dorsal margin with 2 long setae (distal-most seta shorter), medial surface lacking knob- or stalk-like projection. Ventral lobe of left surstylus broadly subtriangular with narrow base, with complex upturned projection arising medioventrally. Right epandrial lamella bluntly pointed below articulation with ventral lobe of surstylus, ventral epandrial process not developed; basal portion of epandrial lamella narrowed and straight, with shallow dorsal emargination bordering ventral margin of right cercus. Dorsal lobe of right surstylus very broad with 2 long lateral setae (lower seta thickened), apex narrowed with blunt bilobate tip without apically-frayed prensiseta on medial surface. Ventral lobe of right surstylus broad, basally articulated, with preapical ventral ridge bearing short seta, apex flap-like and ventrally curved. Hypandrium small, reniform, bare, interior surface with weak longitudinal carina extending from base of posterior notch. Left postgonite lobe large with anteriorly curved dorsal projection and shorter ventral projection basally, markedly broadened preapically, apex deflected medially and tapered to acute tip, middle of lobe with broad lamelliform medial projection. Right postgonite lobe trifurcate, with slender upturned ventral projection, basally broad medial projection with elongate digitiform apex, and narrowly pointed dorsal projection. Phallus elongate and broadly curved, dorsoventrally flattened in basal half with serratulate process on right side near mid-length, apical half narrower with bifurcate tip. Ejaculatory apodeme subrectangular and relatively small. Hypoproct projected dorsally as pair of apically tapering, asymmetrical lobes, left lobe digitiform in distal part with

blunt tip, right lobe broader with dentiform ventral process proximal to acute tip. Cerci with anal setae well-developed and differentiated from surrounding hairs; right cercus slightly larger than left cercus, subrectangular, apex not deflected dorsally, truncate and shallowly excavated with long thick submarginal seta; left cercus suboval in dorsal view, apex not deflected dorsally, acute with pair of long thick marginal setae.

**Female:** Body length 3.0–4.3 mm, wing length 2.9–3.6 mm. Similar to male except as follows: Body covered with greyish-white pruinosity. Setae of body and legs lighter, white to pale yellow. **Head** (Figs 31–32, 43): Face, clypeus and lower frons without golden pruinosity, concolourous with greyish-white frons and vertex. Face wider, at middle about 3.0–3.5X width of anterior ocellus. **Legs:** *Foreleg:* Coxa with paler slightly shorter more slender setae on anterior surface. **Wing** (Fig. 63): Entirely hyaline with yellowish veins basally, brown veins apically. **Abdomen:** Tergite 5 subrectangular in dorsal view with posterior margin truncate (Fig. 128). Terminalia large, nearly as broad as base of segment 5 (Figs 128–129); sternite 7 with a few setae along posterior margin; sternite 8, plate-like, lacking basal bulge, widened beyond base and narrowed apically, apical half without longitudinal ridges, apex bifurcate (Figs 129, 134); sternite 9 with trough-like transverse sclerite posteriorly and concave oval sclerite anteriorly; tergite 10 with hemitergites subtriangular and long, each with elongate apical projection bearing 2 acanthophorite spines at tip (Figs 127–128); cercus relatively long, blunt-tipped, with well-differentiated ventral lobe.

**Distribution and seasonal occurrence.** *Parathalassius midas* is currently known to occur on sandy seashores from Cape Disappointment, Washington, south to Colonia Guerrero, Baja California, including localities in Oregon and California (Fig. 148). Adults have been collected from late April to mid November.

**Etymology.** The specific name is derived from *Midas*, the Greek mythical king with a golden touch, in reference to the gold face and setae of males of this new species.

**Remarks.** The COI barcoded Washington male holotype shows a significant degree of genetic divergence (at minimally 4.1%) from the two female southern California COI barcoded specimens (Fig. 154), possibly indicating the presence of an additional cryptic species within the current concept of *P. midas*. Despite this degree of genetic divergence, the northern populations of *P. midas* from Washington and Oregon, appear morphologically identical to the southern populations from California and Baja California.

This species is rarely collected and does not appear to be abundant on the beaches it has colonized.

### ***Parathalassius sinclairi* sp. nov.**

(Figs 33, 44, 51, 54, 64, 68–71, 78–79, 82, 97–98, 118, 130–132, 137, 149)

**Type material. HOLOTYPE** ♂ labelled: “USA: OR: Tillamook Co./ Manzanita, N45°42'54.9"/ W123°56'25.4", 3.vii.2014/ swp [swept] dunes & beach grass (*Ammophila*), J.M. Cumming”; “HOLOTYPE/ *Parathalassius sinclairi*/ Brooks & Cumming [red label]” (CNC). **PARATYPES: USA: Oregon:** same data as holotype (12♂, 11♀, CNC); same data as holotype except, CNC487121, CNC487160 (2♂, barcoded, CNC); same data as holotype except, S.E. Brooks (8♂, 12♀, CNC), same data except, CNC487161 (1♂, barcoded, CNC), CNC487162, CNC487163 (2♀, barcode-associated, CNC); same data as holotype except, S.H. Cumming (3♀, CNC).

**Other material examined. CANADA: British Columbia:** Haida Gwaii, Graham Is., 3km N Tlell [ca. 53°33'37"N 131°55'39"W], 13.vii.1988, meadow behind dunes, T.A. Wheeler (2♂, 1♀, CNC); same data except, CNC487131 (1♂, barcoded, CNC); Vancouver Island: Sannich Pen., Island View Beach, 48°34'37.56"N 123°22'5.09"W, 22.viii.2008, sandy beach with logs, S.E. Brooks (1♂, 1♀, CNC); same data except, J.M. Cumming (1♀, CNC); 6km SE Sidney, ex: beach, 25.vi–4.vii.1999, J.M. Cumming (1♂, 1♀, CNC); Sidney Is., 48°38'28.06"N 123°19'50.05"W, 6.vii.1994, ex: veg along sandy beach, J.M. Cumming (1♂, 2♀, CNC). **USA: Alaska:** Aleutians East Borough: Cold Bay [ca. 55°11'49"N 162°41'55"W], 163°W, 21.viii.1952, W.R. Mason (1♀, CNC); Wosnesenski Island, 55.21688°N 161.36708°W, near shore, 11.vii.2009, H. Goulet & C. Boudreault (1♂, CNC); same data except, 11 m, YPT (1♂, CNC); same data except, A. Renaud (1♀, CNC); Aleutians West Census Area: Adak Island, 51.90201°N 176.61880°W, 9 m, swept, 15.vii.2009, A. Renaud (5♂, 2♀, CNC); Katmai [ca. 58°32'11"N 153°55'49"W], vii.1917, J.S. Hine (4♀, USNM). **Oregon:** Lane County: dunes behind Baker Beach, 44°04'39"N 124°06'44"W, 27.vi.2012, J.D. Pinto, UCRC ENT 431380 (1♂, UCRC); Heceta Beach, 44°02'14.7"N 124°07'57.2"W, 7.vii.2014, swept dunes & beach grass (*Ammophila*), J.M. Cumming (3♂, 5♂, CNC); same data except, CNC487168, CNC487169 (2♂, barcoded, CNC), CNC487170, CNC487171 (2♀, barcode-associated, CNC); Suislaw North Jetty, nr. Florence, 44°01'07.0"N 124°08'12.6"W, 7.vii.2014, swept



dunes & beach grass (*Ammophila*), S.E. Brooks (8♂, 2♀, CNC); same data except, CNC487125, CNC487126, CNC487127 (3♀, barcode-associated, CNC); same data except, J.M. Cumming (1♂, 4♀, CNC); same data except, CNC487172, CNC487173 (2♂, barcoded, CNC); same data except, 8.vii.2014, S.E. Brooks (4♂, 11♀, CNC); same data except, J.M. Cumming (6♂, 6♀, CNC); same data except, CNC487174, CNC487175 (2♀, barcode-associated, CNC); Lincoln County: South Beach State Park, 44°36'05.6"N 124°03'54.0"W, 3.vii.2014, swept dunes & beach grass (*Ammophila*), S.E. Brooks (27♂, 25♀, CNC); same data except, CNC487122 (1♂, barcoded, CNC); same data except, J.M. Cumming (71♂, 89♀, CNC); same data except, CNC487164, (1♂, barcoded, CNC), CNC487123, CNC487166, CNC487167 (3♀, barcode-associated, CNC); same data except, S.H. Cumming (6♂, 3♀, CNC); 2.5mi. N Waldport [ca. 44°27'28"N 124°04'56"W], 1.vii.1971, Oman (1♂, 1♀, UGIC); Tillamook County: Cape Kiwanda, 45°12.9'N 123°58.3'W, beach, 3.viii.2005, D. & W.N. Mathis (1♂, USNM). **Washington:** Grays Harbor County: Copalis [ca. 47°06'37"N 124°11'06"W], 5.ix.1934, A.L. Melander (11♂, 8♀, USNM); Ocean City [ca. 47°04'15"N 124°10'37"W], 19.vii.1975, T.L. Whitworth (4♂, 3♀, LACM); Pacific County: Cape Disappointment State Park nr. Ilwaco, Benson Beach, 46°16'20.4"N 124°04'25.4"W, 1.vii.2014, swept dunes & beach grass (*Ammophila*) S.E. Brooks (204♂, 160♀, CNC; 2♂, 2♀, CSCA); same data except, CNC487133–CNC487137, CNC487141, CNC487142 (7♂, barcoded, CNC), CNC487143–CNC487150, CNC487152–CNC487157, CNC487184, CNC487186, CNC487194, CNC487195 (18♀, barcode-associated, CNC); same data except, 2.vii.2014 (20♂, 13♀, CNC); same data except, CNC487119, CNC487120, CNC487158 (3♀, barcode-associated, CNC); same data except, 1.vii.2014, J.M. Cumming (180♂, 148♀, CNC); same data except, CNC487138–CNC487140 (3♂, barcoded, CNC), CNC487116, CNC487117, CNC487159 (3♀, barcode-associated, CNC); same data except, 2.vii.2014 (20♂, 27♀, CNC); same data except, 1.vii.2014, swept dunes & beach vegetation, S.H. Cumming (32♂, 24♀, CNC); same data except, CNC487109, CNC487182 (2♀, barcode-associated, CNC); same data except, 2.vii.2014 (37♂, 44♀, CNC); same data except, CNC487151 (1♀, barcode-associated, CNC); Ilwaco, Cape Disappointment, 23.vii.1993, H. Ulrich (130♂, 76♀, ZFMK); same data except, 24.vii.1993 (76♂, 73♀, ZFMK); same data except, Benson Beach, dunes, 24.vii.1993 (34♂, 19♀, ZFMK); same data except, 25.vii.1993 (18♂, 10♀, ZFMK); same data except, 5.viii.1994 (173♂, 157♀, ZFMK); same data except, 9.viii.1994 (231♂, 118♀, ZFMK); same data except, sandy beach, 5.viii.1994 (2♀, ZFMK); same data except, 8.viii.1994 (10♂, 2♀, ZFMK); same data except, 9.viii.1994 (13♂, 18♀, ZFMK); same data except, 10.viii.1994 (18♂, 8♀, ZFMK); same data except, Waikiki Beach, on sand, 15.vii.1988 (2♂, ZFMK); same data except, dunes, 22.vii.1993 (15♂, 10♀, ZFMK); same data except, on wet sand, 25.vii.1993 (2♀, ZFMK); same data except, 26.vii.1993 (1♀, ZFMK); Ft. Canby State Park [=Cape Disappointment State Park], 29.vi.1988, W.N. & D. Mathis (4♂, USNM); Ilwaco [ca. 46°16'20"N 124°04'25"W], vii.1917, A.L. Melander (3♂, 1♀, USNM); same data except, 28.vi.1925 (1♀, USNM); same data except, 19.vii.1960, F.C. Harmston (1♂, USNM); Klipsan Beach [ca. 46°27'38"N 124°03'35"W], 14.vi.1975, W.J. Turner (1♂, 1♀, LACM); same data except, dunes (1♂, 1♀, USNM); Willapa Nat. Wildlife Ref., Willapa Bay, ca. 2 mi. N Oysterville [ca. 46°34'36"N 124°01'44"W], 22.vi.1989, R.S. Zack (1♂, 5♀, WSU).

**Diagnosis.** This medium sized species is characterized by an elongate-conical antennal postpedicel, longer lower male ommatrichia, 3 notopleural bristles, hyaline wing, and relatively dark legs with hind tarsomere 2 distinctly longer than tarsomere 3. Males have the face tinged with faint golden pruinosity, a comb-like anterodorsal row of short erect setae on the hind tibia, hind tarsomeres 2–4 bearing short thick perpendicular peg-like setae dorsally, and distinctive cerci, while females possess apical rugosity on sternite 8.

**Description. Male:** Body length 2.3–3.2 mm, wing length 2.4–3.0 mm. Dark brown ground colour covered mostly with dense greyish-white pruinosity. Setae of body and legs white. **Head** (Fig. 33): Eyes with ommatrichia of lower third distinctly longer and slightly flattened, forming dense reflective mat of whitish coloured hair. Face tinged with faint golden pruinosity in most specimens, clypeus concolourous with greyish-white frons and vertex. Face narrowest at middle, about 2.0X width of anterior ocellus. Gena and postgena with moderately long white setae, forming short beard flanking mouthparts. Antenna (Fig. 44) including arista-like stylus, entirely dark brown; postpedicel elongate-conical, 1.75–1.8X longer than wide; arista-like stylus of medium length, about 1.4X length of postpedicel. Palpus with 7–8 setae on outer surface of apical half. **Thorax:** Mesoscutum with some brownish-grey pruinosity on dorsum. Acrostichal setulae quadriserial; 7–8 dorsocentral bristles, 0 presutural intra-alar bristles, 1–2 presutural supra-alar (posthumeral) bristles, 3–4 postsutural supra-alar bristles, 3 notopleural bristles. Scutellum with 3 pairs of bristles. **Legs:** *Foreleg:* Dark grey, pale at knee and apex of tibia, tarsomeres 1–2 pale yellowish-brown to brown, tarsomeres 3–5 brown to greyish-brown. Coxa with moderately long pale setae on

anterior surface. Femur with numerous long setae on posterior surface, posterodorsal and posteroventral rows prominent. Tibia with short setae and setulae. Tarsus with setulae; tarsomeres 1–2 not dilated. *Midleg*: Dark grey, pale at knee and apex of tibia, tarsomere 1 pale yellowish-brown, tarsomeres 2–5 brown to greyish-brown. Femur with anteroventral rows of setae prominent. Tibia with pair of apicoventral bristles. Tarsomeres 1–4 each with pair of dark spine-like apicoventral setae. *Hindleg* (Figs 51, 54): Dark grey, femur dark brown posteriorly, pale at knee, tarsomere 1 and base of tarsomere 2 pale yellowish-brown, apex of tarsomere 2 and tarsomeres 3–5 brown to greyish-brown. Femur with ventral row of setae prominent. Tibia with anterodorsal and anteroventral rows of setae short to moderate length, shorter or subequal to width of tibia; anterodorsal row short, erect and comb-like. Tarsus slightly shorter than tibia with short setae and setulae; tarsomere 1 slightly shorter than combined length of tarsomeres 2–4; tarsomeres 1–4 with several short thick perpendicular peg-like setae dorsally, shortest on tarsomere 1; tarsomere 2 distinctly longer than tarsomere 3; tarsomere 3 longer than tarsomere 4; tarsomere 5 subequal in length to tarsomere 3. **Wing** (Fig. 64): Hyaline with dark brown veins. Cell dm produced apically, dm-m crossvein concave. Vein CuA+CuP of medium length, straight. **Abdomen** (Figs 68–71): Tergites 2–4 with setae well-developed and relatively long. Sternite 5 with slender anteriorly curved digitiform pregenitalic process present, base with tiny anterior projection, apex blunt and covered with microtrichia, posterior edge of sternite 5 (behind process) deeply emarginate. Sternite 8 subquadrate with prominent elongate setae on posterolateral margins. *Hypopygium* (Figs 68–71, 78–79, 82, 97–98, 118): Large. Left epandrial lamella with ventral portion elongate (about 2X longer than high); ventral epandrial process broadly bifurcate, dorsal arm curved ventrally, narrow in middle portion, apex expanded and hook-like, ventral arm thick with minute apicodorsal seta 1–2 minute setae along distiventral margin, apex with expanded lamelliform concavity. Dorsal lobe of left surstylus with basiventral edge broadly rounded, apex narrow and pointed, with long basidorsal seta, shorter basilateral seta and long apical seta, medial surface with knob-like projection bearing lamelliform apical process. Ventral lobe of left surstylus shallowly bilobate in lateral view, dorsal lobe short with apex subquadrate, ventral lobe with rounded base bearing short lateral seta and complex upturned multilobate projection arising medioventrally. Right epandrial lamella with ventral epandrial process not developed; basal portion of epandrial lamella narrowed and dorsally curved, with deep dorsal emargination bordering ventral margin of right cercus. Dorsal lobe of right surstylus with 3 lateral setae (middle/lowermost seta weaker), apex narrowed with rounded tip bearing thick apically-frayed prensiseta on medial surface. Ventral lobe of right surstylus with lateral seta near middle, distal half recurved and tapered with tubercle bearing strong seta proximal to narrow medially pointed apex. Hypandrium very large, elongate-reniform with convex anterior and posterior ends extending to or beyond margins of epandrial lamellae in lateral view, bare. Left postgonite lobe rounded basally, constricted near middle, distal portion broadly lamelliform usually with claw-like apical process, base of lobe with slender medial projection. Right postgonite lobe with broad lateral protuberance and bump-like medial projection, apex bifurcate with short digitiform process and rounded lamelliform process. Phallus short and weakly curved, broad in basal 2/3 with apical 1/3 narrower (in lateral view), dorsal flange and left lateral dentiform projection present at 2/3 length. Ejaculatory apodeme broadly subtriangular. Hypoproct strongly projected dorsally as pair of slender blade-like lobes, right lobe with preapical ventral flange and piliferous region basally. Cerci with anal setae relatively short and not well-differentiated from surrounding well-developed hairs, medial margin of each cercus strongly produced dorsally; right cercus much larger than left cercus with basal portion distended and rounded laterally, apex strongly deflected dorsally at right angle, elongate, narrow and pointed, with 2 short apical setae present along lateral margin; left cercus oblong in dorsal view, apex strongly deflected dorsally at right angle, short and acute, with 2 long preapical setae on lateral margin.

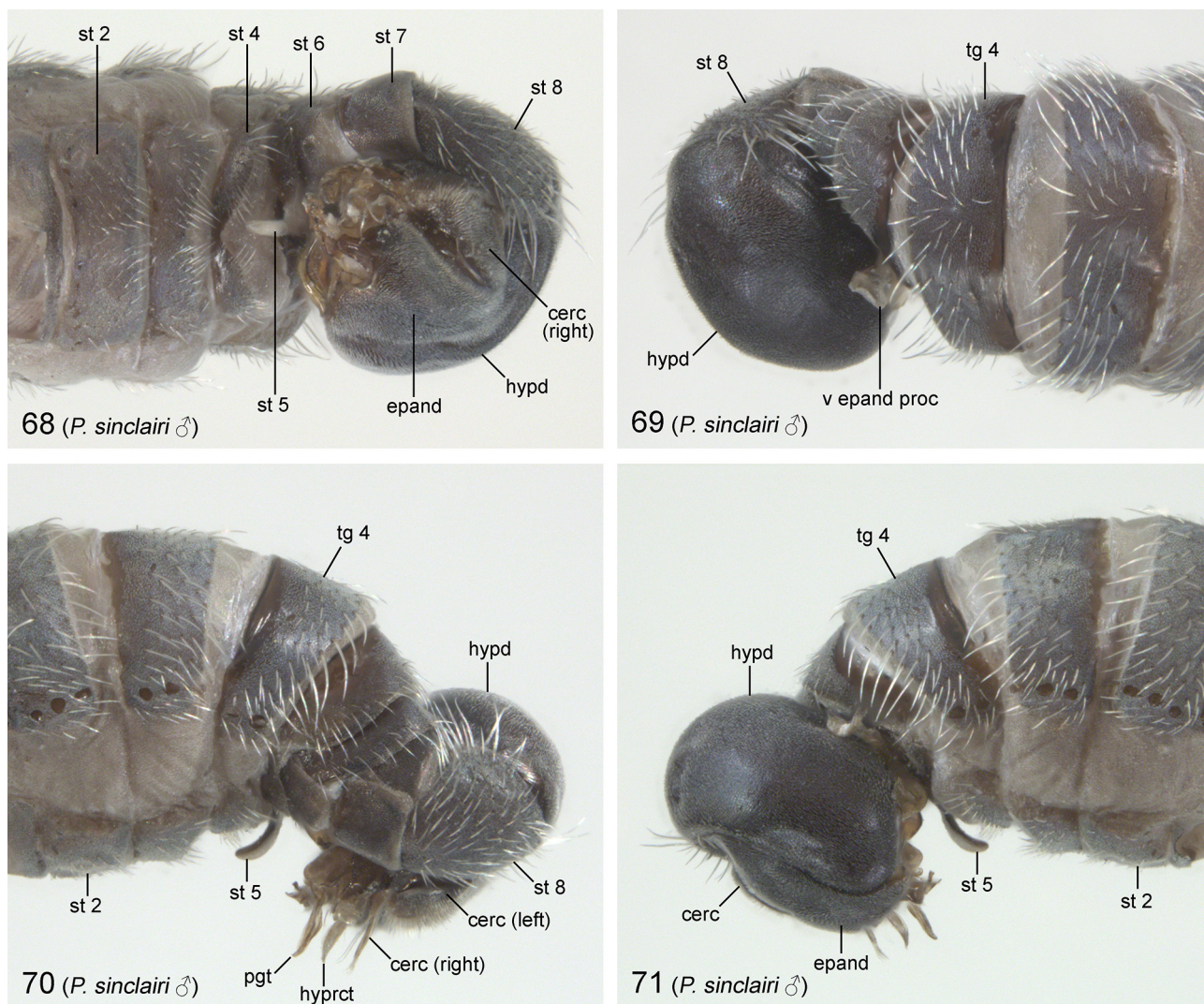
**Female:** Body length 2.3–3.6 mm, wing length 2.2–3.2 mm. Similar to male except as follows: **Head:** Eyes with ommatrichia of nearly uniform length, not distinctly longer on lower third. Face not tinged with faint golden pruinosity, concolourous with greyish-white frons and vertex. Face wider, at middle about 3.5–4.0X width of anterior ocellus. **Legs:** *Foreleg:* Coxa with shorter more slender pale setae on anterior surface. Femur with posteroventral row of setae only prominent apically. *Hindleg:* Tibia with anterodorsal row slightly longer and less comb-like. Tarsomeres 1–4 without short thick peg-like setae dorsally. **Abdomen:** Tergite 5 broadly subtriangular to semicircular in dorsal view with posterior margin rounded (Fig. 131). Terminalia distinctly narrower than base of segment 5 (Figs 131–132); sternite 8 trough-like, lacking basal bulge, not distinctly narrowed apically, apical quarter rugose, apex truncate with margin somewhat irregular (Figs 130, 132, 137); sternite 9 reduced to narrow transverse sclerotized band; tergite 10 with hemitergites subtriangular and short, each with 2 acanthophorite spines; cercus short, pointed apically.

**Distribution and seasonal occurrence.** *Parathalassius sinclairi* is currently known to occur on sandy seashores of the Aleutian Islands and mainland Alaska, south along the coast of British Columbia, Washington and Oregon to the dunes near Florence in Lane County (Fig. 149). Adults have been collected from mid June to early September.

**Etymology.** This species is named in honour of our esteemed colleague and friend, Dr. Bradley J. Sinclair, who has contributed significantly to the systematic study of Empidoidea.

**Remarks.** The considerable COI barcode sequence data obtained from specimens of *P. sinclairi* from British Columbia, Washington and Oregon (Fig. 154) show very little genetic divergence (<1.1%), suggesting that there has been considerable gene exchange and possible movement between populations of this widely distributed species.

*Parathalassius sinclairi* has been taken in large numbers in several localities in both fore and back dune habitats (Figs 11–14).



**FIGURES 68–71.** Male terminalia of *Parathalassius sinclairi* sp. nov. **68.** Ventral view. **69.** Dorsal view. **70.** Left lateral view. **71.** Right lateral view. Abbreviations: cerc—cercus; epand—epandrium; hypd—hypandrium; hyprct—hypoproct; pgt—postgonite; st—sternite; tg—tergite; v epand proc—left ventral epandrial process.

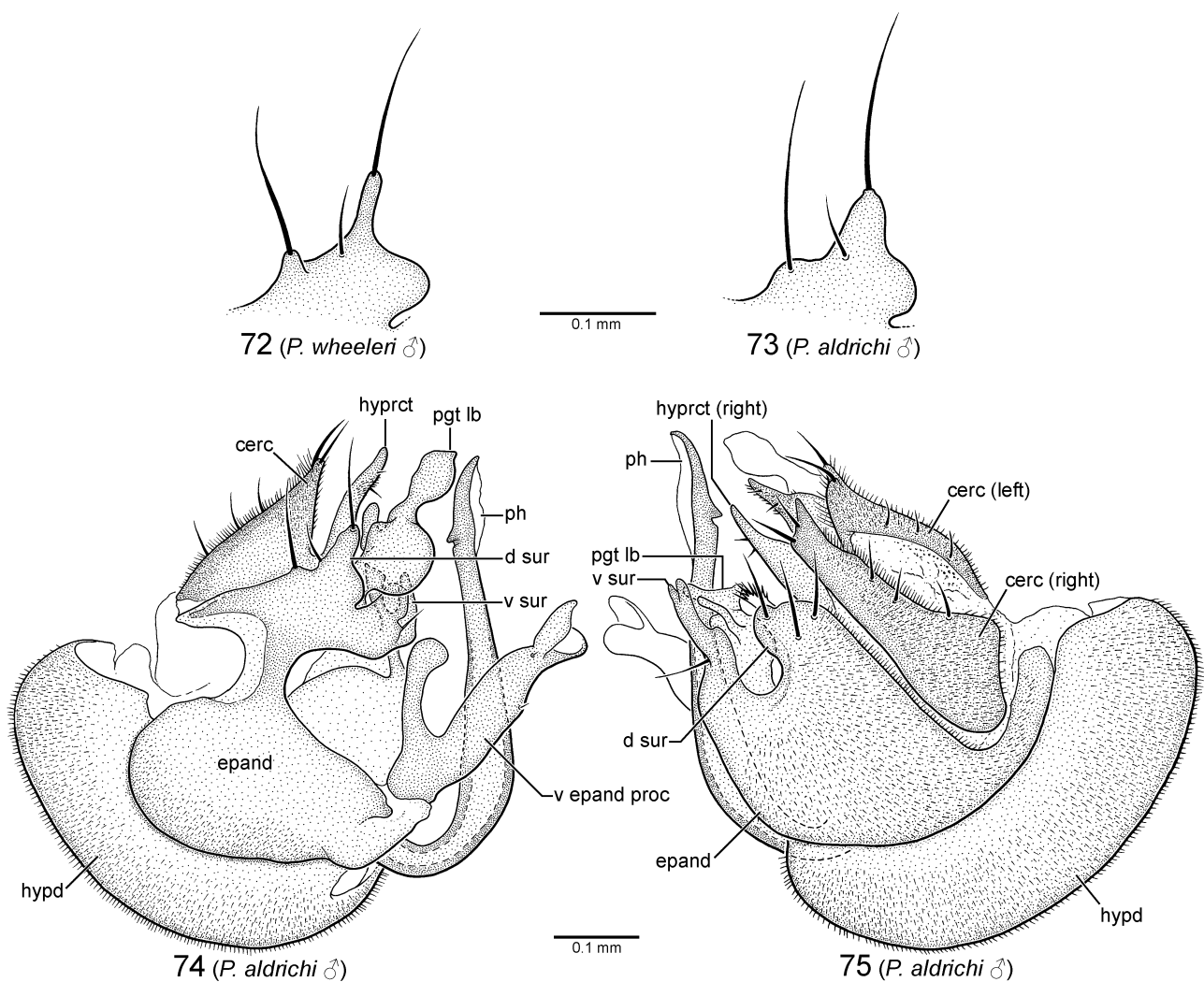
***Parathalassius socali* sp. nov.**

(Figs 34, 45, 65, 89–90, 107–108, 123, 139, 150)

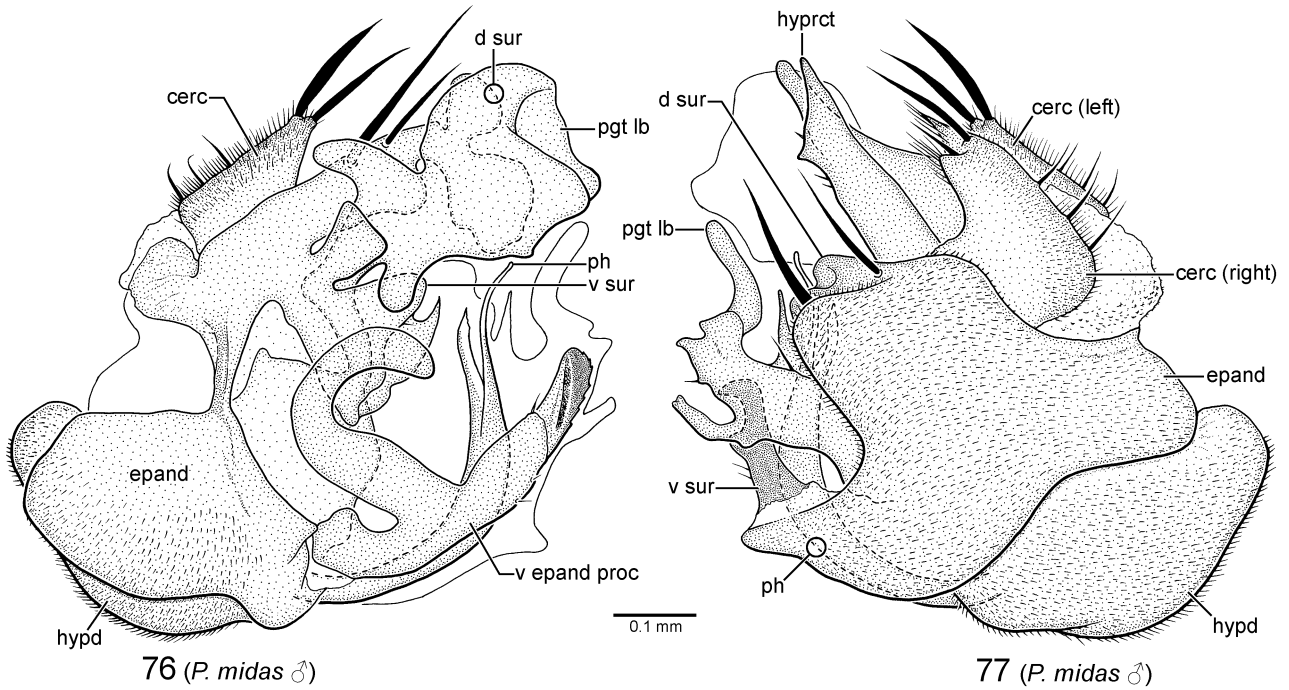
**Type material.** HOLOTYPE ♂ labelled “USA: CA: Orange Co., San/ Clemente SB [State Beach], 33°24'18.7"N/

117°36'22.8"W, 7.vi.2016, swp [swept] sandy seacoast, J.M./ Cumming, CNC577380"; "HOLOTYPE/*Parathalassius socali*/ Brooks & Cumming [red label]" (CNC)

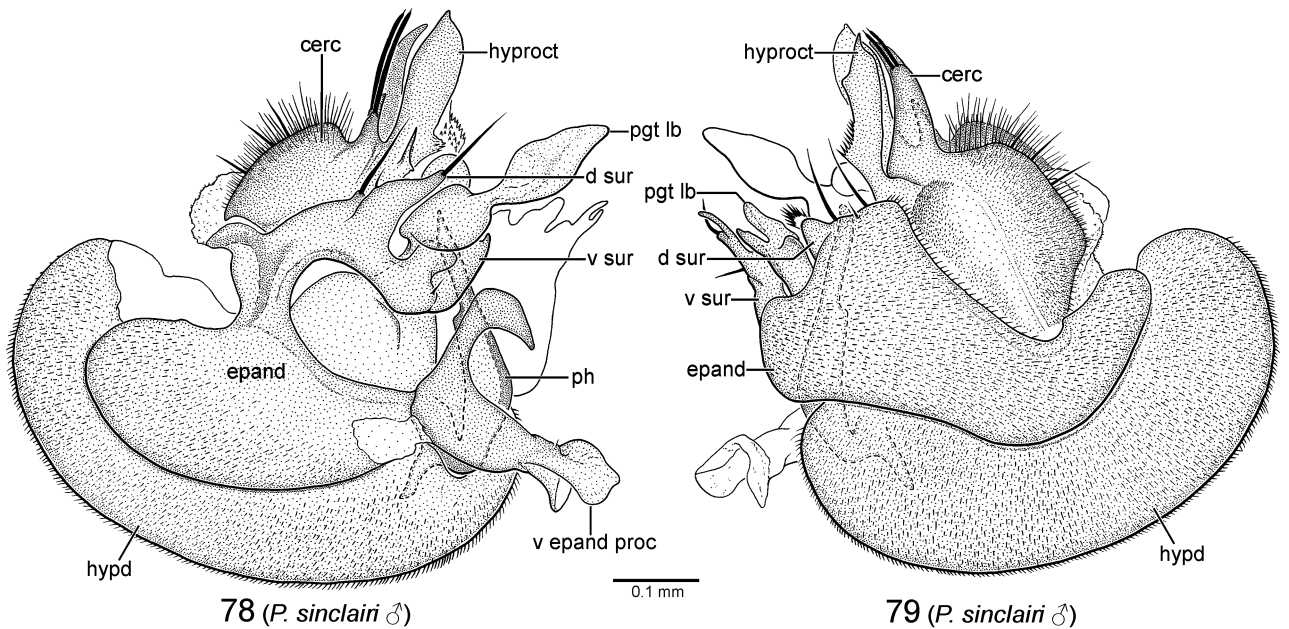
**PARATYPES: USA: California:** same data as holotype except, CNC577343, CNC577346, CNC577347, CNC577348, CNC577354–CNC577356, CNC577362, CNC577366, CNC577377, CNC577383, CNC577396, CNC577398, (13♂, CNC); same data as holotype except, CNC577376, CNC577390 (2♂, barcoded, CNC); same data as holotype except, CNC577331, CNC577337, CNC577340, CNC577345, CNC577349, CNC577350–CNC577353, CNC577357–CNC577361, CNC577363, CNC577364, CNC577367–CNC577369, CNC577371–CNC577379, CNC577381, CNC577382, CNC577384, CNC577386, CNC577391–CNC577395, CNC577397, CNC577399, CNC577401, CNC580706 (39♀, CNC); same data as holotype except, CNC577344, CNC577385, CNC577389 (3♀, barcode-associated, CNC); same data as holotype except, S.E. Brooks, CNC574853, CNC574856, CNC574858, CNC574863 (4♂, CNC); same data except, CNC574860 (1♂, barcoded, CNC); same data except, CNC574855, CNC574857, CNC574859, CNC574861, CNC574864, CNC574865, CNC574868–CNC574871 (10♀, CNC); same data as holotype except, S.H. Cumming, CNC577405 (1♂, CNC), CNC577402, CNC577404 (2♀, CNC).



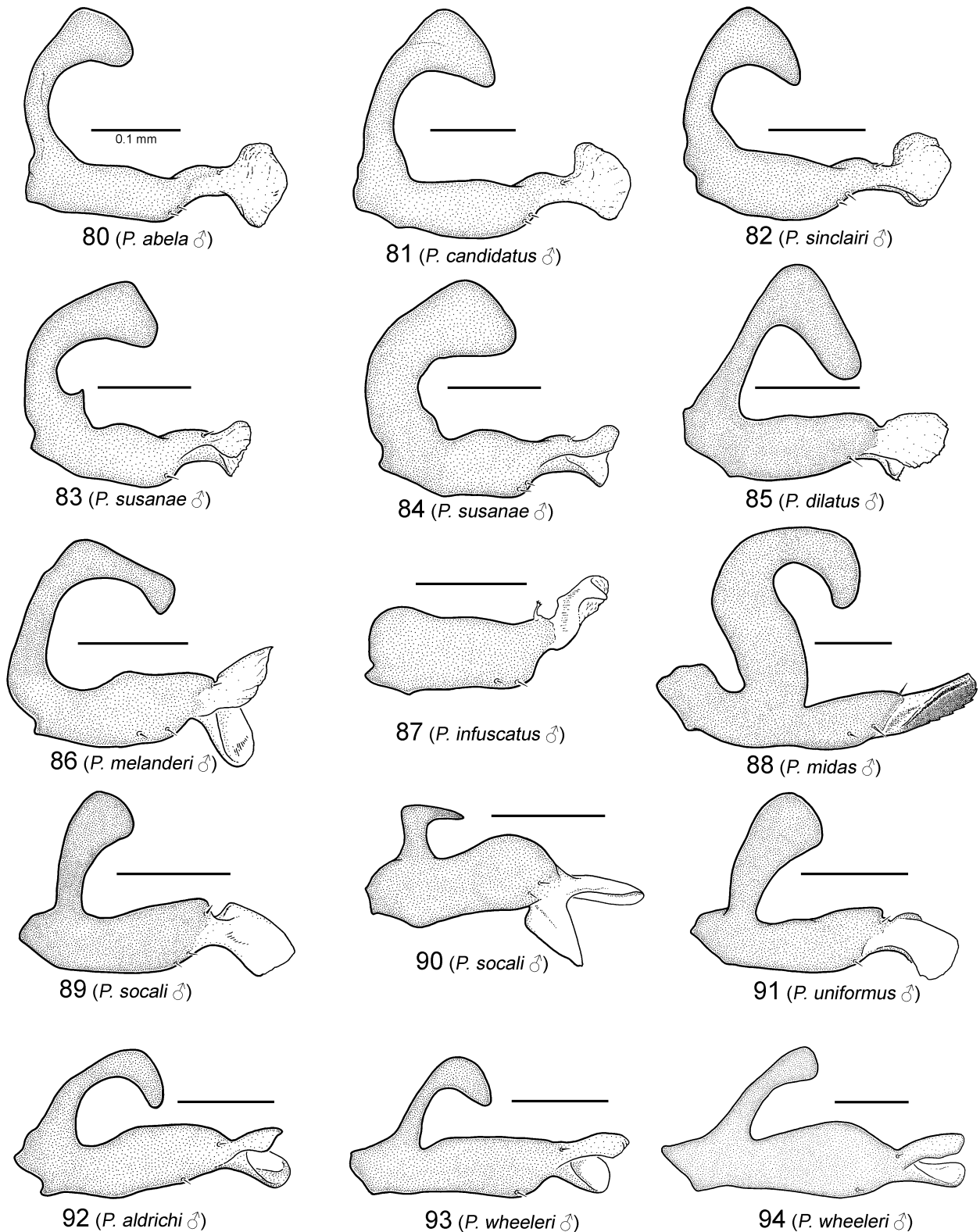
**FIGURES 72–75.** Dorsal lobe of left surstyli and hypopygia of Nearctic *Parathalassius*. **72.** *Parathalassius wheeleri* **sp. nov.**, apex of dorsal lobe of left surstylus, lateral view. **73.** *Parathalassius aldrichi* Melander, apex of dorsal lobe of left surstylus, lateral view. **74.** *Parathalassius aldrichi* Melander, hypopygium, left lateral view. **75.** *Parathalassius aldrichi* Melander, hypopygium, right lateral view. Abbreviations: cerc—cercus; d sur—dorsal lobe of surstylus; epand—epandrium; hypd—hypandrium; hyprct—hypoproct; pgt lb—postgonite lobe; ph—phallus; v epand proc—left ventral epandrial process; v sur—ventral lobe of surstylus. Scale bars = 0.1 mm.



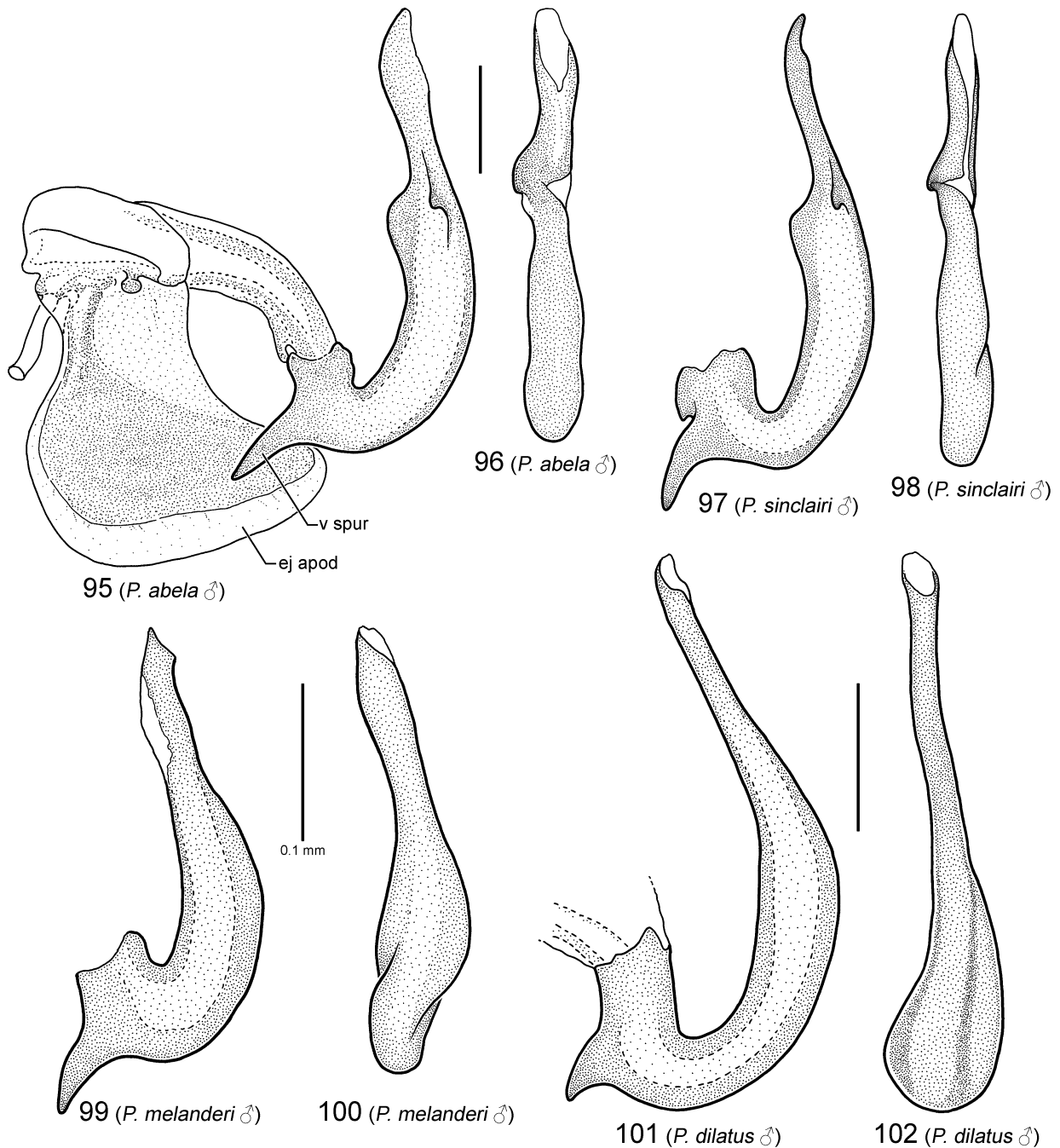
**FIGURES 76–77.** Hypopygium of *Parathalassius midas* sp. nov. **76.** Left lateral view. **77.** Right lateral view. Abbreviations: cerc—cercus; d sur—dorsal lobe of surstylus; epand—epandrium; hypd—hypandrium; hyprct—hypoproct; pgd lb—postgonite lobe; ph—phallus; v epand proc—left ventral epandrial process; v sur—ventral lobe of surstylus. Scale bar = 0.1 mm.



**FIGURES 78–79.** Hypopygium of *Parathalassius sinclairi* sp. nov. **78.** Left lateral view. **79.** Right lateral view. Abbreviations: cerc—cercus; d sur—dorsal lobe of surstylus; epand—epandrium; hypd—hypandrium; hyproct—hypoproct; pgd lb—postgonite lobe; ph—phallus; v epand proc—left ventral epandrial process; v sur—ventral lobe of surstylus. Scale bar = 0.1 mm.



**FIGURES 80–94.** Left ventral epandrial processes of Nearctic *Parathalassius*, lateral view (unless otherwise noted). **80.** *Parathalassius abela* sp. nov. **81.** *Parathalassius candidatus* Melander. **82.** *Parathalassius sinclairi* sp. nov. **83.** *Parathalassius susanae* sp. nov. **84.** *Parathalassius susanae* sp. nov. **85.** *Parathalassius dilatus* sp. nov. **86.** *Parathalassius melanderi* Cole. **87.** *Parathalassius infuscatus* sp. nov. **88.** *Parathalassius midas* sp. nov. **89.** *Parathalassius socali* sp. nov. **90.** *Parathalassius socali* sp. nov., ventrolateral view. **91.** *Parathalassius uniformus* sp. nov. **92.** *Parathalassius aldrichi* Melander. **93.** *Parathalassius wheeleri* sp. nov. **94.** *Parathalassius wheeleri* sp. nov. Scale bars = 0.1 mm.



**FIGURES 95–102.** Phallus of Nearctic *Parathalassius* species. **95.** *Parathalassius abela* **sp. nov.**, entire phallus, left lateral view. **96. *Parathalassius abela* **sp. nov.**, distal portion, posterior view. **97. *Parathalassius sinclairi* **sp. nov.**, distal portion, left lateral view. **98. *Parathalassius sinclairi* **sp. nov.**, distal portion, posterior view. **99. *Parathalassius melanderi* Cole, distal portion, left lateral view. **100. *Parathalassius melanderi* Cole, distal portion, posterior view. **101. *Parathalassius dilatus* **sp. nov.**, distal portion, left lateral view. **102. *Parathalassius dilatus* **sp. nov.**, distal portion, posterior view. Abbreviations: ej apod—ejaculatory apodeme; v spur—ventral spur-like projection. Scale bars = 0.1 mm.**************

**Other material examined. USA: California:** Monterey County: Salinas River State Beach [ca. 36°46'33"N 121°47'50"W], 26.vii.1994, dunes, H. Ulrich (16♂, 2♀, ZFMK); same data except, 27.vii.1994 (13♂, 26♀, ZFMK); Orange County: Huntington Beach [ca. 33°39'27"N 118°00'25"W], 4.vi.1945, A.L. Melander (1♂, USNM); San Clemente, 5.vi.1945, A.L. Melander (8♂, 1♀, USNM); Santa Barbara County: Carpinteria [ca. 34°23'35"N 119°31'29"W], 15.vi.1947, A.L. Melander (2♂, 2♀, USNM); same data except, 12.vi.1953 (9♂, 1♀, USNM); same data except, 17.vi.1953 (3♂, 1♀, USNM); Surf Beach, Vandenberg Air Force Base, 34.683801°N

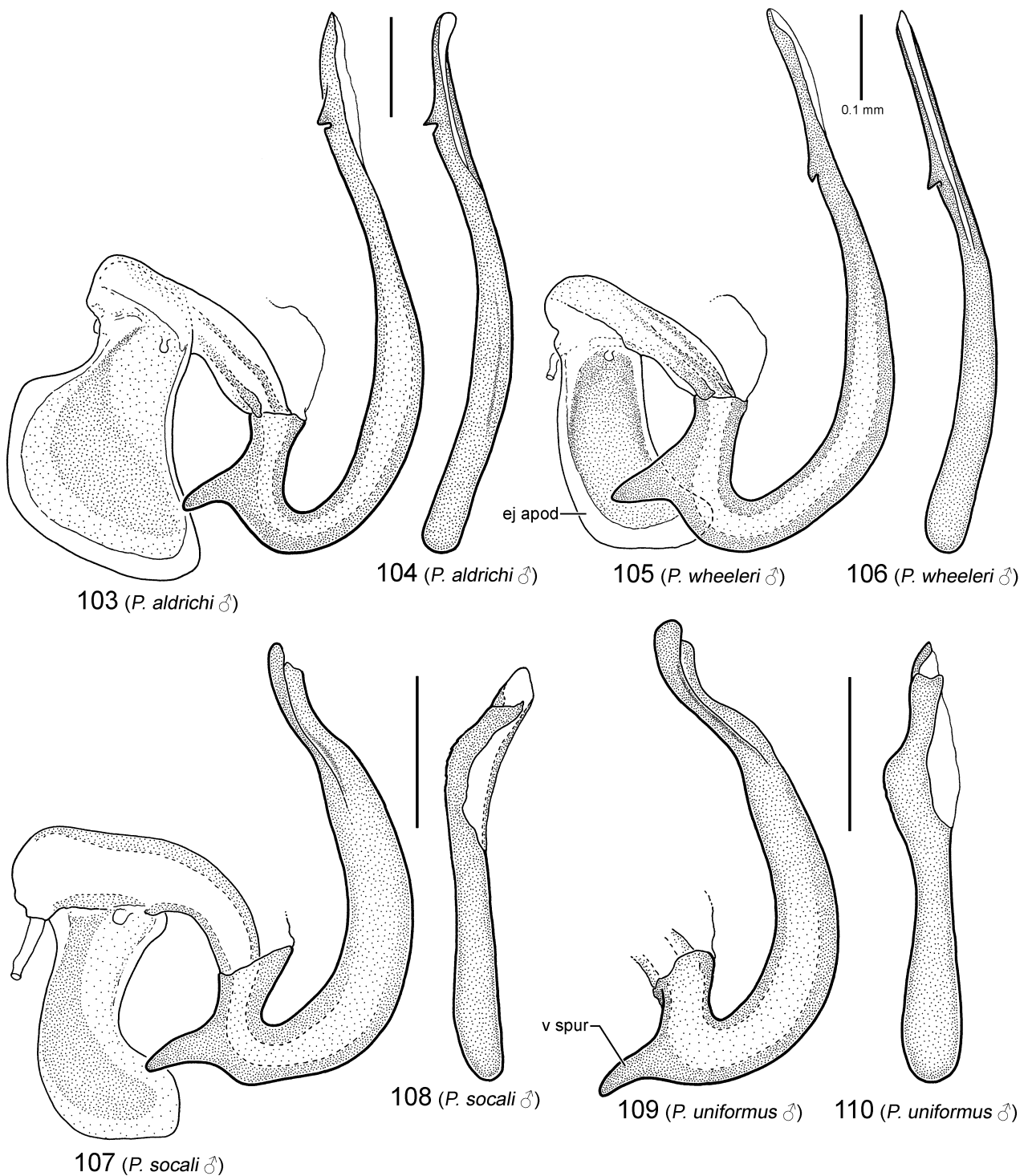
120.605520°W, 4.vi.2016, J.M. Cumming, ex: *Ambrosia chamissionis* & coastal dunes (1♀, CNC); same data except CNC582795, CNC582813 (2♀, barcode-associated, CNC).

**Diagnosis.** This relatively small species is characterized by a short-subtriangular antennal postpedicel, longer lower male ommatrichia, 2 notopleural bristles, hyaline wing, relatively dark legs, male hind tarsomere 1 with long erect setae dorsally, male hypopygium compact, and female sternite 8 with apical longitudinal ridges at most barely developed laterally.

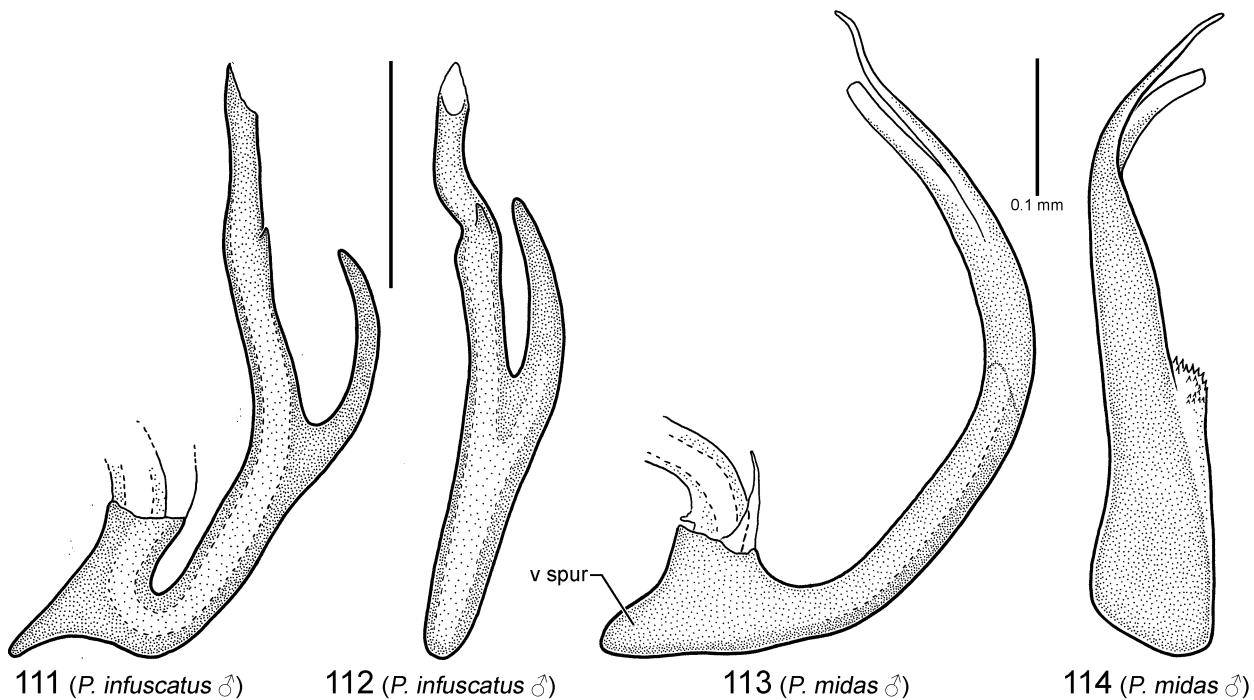
**Description. Male:** Body length 1.9–2.3 mm, wing length 1.6–1.7 mm. Dark brown ground colour covered mostly with dense greyish-white pruinosity. Setae of body and legs white. **Head** (Fig. 34): Eyes with ommatrichia of lower third distinctly longer and slightly flattened, forming dense reflective mat of whitish coloured hair. Face and clypeus concolourous with greyish-white frons and vertex. Face narrowest at middle, about 2.0–2.75X width of anterior ocellus. Gena and postgena with moderately long white setae, forming short beard flanking mouthparts. Antenna (Fig. 45) brown to dark brown, arista-like stylus lighter in colour in most specimens; postpedicel short-subtriangular, 1.25–1.4X longer than wide; arista-like stylus of medium length, about 1.6X length of postpedicel. Palpus with 7–8 setae on outer surface of apical half. **Thorax:** Acrostichal setulae primarily biserial; 6–7 dorsocentral bristles, 0 presutural intra-alar bristles, 1 presutural supra-alar (posthumeral) bristle, 2–3 postsutural supra-alar bristles, 2 notopleural bristles. Scutellum with 2 pairs of bristles. **Legs:** *Foreleg:* Dark grey, pale at knee and apex of tibia, tarsomere 1 pale yellow basally, apex of tarsomere 1 and tarsomeres 2–5 greyish-brown. Coxa with moderately long pale setae on anterior surface. Femur with mostly short setae on posterior surface, posterodorsal row long. Tibia with short setae and setulae. Tarsus with setulae; tarsomeres 1–2 not dilated. *Midleg:* Dark grey, pale at knee and extreme apex of tibia, tarsomere 1 pale yellowish-brown, tarsomeres 2–5 brown to greyish-brown. Femur with anterodorsal setae most prominent, short. Tibia with 1 apicoventral bristle. Tarsomeres 1–4 each with several dark spine-like apicoventral setae. *Hindleg:* Dark grey, femur dark brown posteriorly, pale at knee, tarsomere 1 pale yellowish-brown (apex brown in some specimens), tarsomeres 2–5 brown to greyish-brown. Femur with anteroventral row of setae most prominent, short basally, longer apically. Tibia with anterodorsal and anteroventral rows of setae long, mostly longer than width of tibia, anterodorsal row longest. Tarsus slightly longer than tibia with mostly short setae and setulae; tarsomere 1 shorter than combined length of tarsomeres 2–4, bearing long erect setae dorsally; tarsomeres 1–4 lacking peg-like or thickened setae dorsally; tarsomere 2 distinctly longer than tarsomere 3; tarsomere 3 longer than tarsomere 4; tarsomere 5 subequal in length to tarsomere 3. **Wing** (Fig. 65): Hyaline with yellowish brown veins. Cell dm produced apically, dm-m crossvein slightly concave. Vein CuA+CuP short to medium length, slightly curved to straight. **Abdomen:** Tergites 2–4 with setae well-developed. Sternite 5 with small nub-like pregenitalic process present, posterior edge of sternite 5 (behind process) weakly emarginate. Sternite 8 subquadrate with setae longer along posterolateral margins. *Hypopygium* (Figs 89–90, 107–108, 123): Relatively compact. Left epandrial lamella with ventral portion elongate (about 2X longer than high); ventral epandrial process broadly bifurcate, dorsal arm with weak ventral curve, apex expanded and blunt, ventral arm thick with minute apicodorsal seta and pair of minute setae along distiventral margin, apex with expanded lamelliform concavity. Dorsal lobe of left surstylus with basiventral edge rounded and flap-like, apex broadly rounded, with long basidorsal seta on bump-like protuberance, short lateral seta and long apical seta, medial surface with stalk-like projection bearing lamelliform apical seta. Ventral lobe of left surstylus bilobate, dorsal lobe short with apex subquadrate, ventral lobe with basal pointed process bearing apical seta and complex upturned bifurcate projection arising medioventrally. Right epandrial lamella with ventral epandrial process barely developed as short angular projection; basal portion of epandrial lamella narrowed and dorsally curved, with deep dorsal emargination bordering ventral margin of right cercus. Dorsal lobe of right surstylus with 3 lateral setae (distal-most seta stronger), apex narrowed with subtriangular tip bearing thick apically-frayed preniseta on medial surface. Ventral lobe of right surstylus with lateral seta at basal third and 2 slightly shorter setae below, distal 2/3 recurved, slender with narrow apically pointed lamelliform seta proximal to rounded lamelliform apex. Hypandrium large, reniform and bare. Left postgonite lobe ovoid basally, constricted near middle, distal portion subrectangular and flat without claw-like apical process, base of lobe with broad curved apically-pointed medial projection. Right postgonite lobe with broad lateral protuberance and lamelliform medial projection, apex bifurcate with well-developed digitiform ventral process and lamellate dorsal process. Phallus relatively short and moderately curved, flattened preapically with membranous region on right side, apex bent laterally. Ejaculatory apodeme subtriangular with apex slightly curved ventrally. Hypoproct projected dorsally as pair of slender pointed lobes, each lobe with ventral cluster of 3–4 minute setae proximal to apex. Cerci with anal setae well-developed



and differentiated from surrounding hairs; right cercus much larger than left cercus with basal portion distended and rounded laterally, apex slightly widened, not dorsally deflected, truncate with pair of setae at apicolateral margin; left cercus oblong-subrectangular in dorsal view, apex even with apex of right cercus, not dorsally deflected, acute with pair of thickened apical setae.



**FIGURES 103–110.** Phallus of Nearctic *Parathalassius* species. **103.** *Parathalassius aldrichi* Melander, entire phallus, left lateral view. **104.** *Parathalassius aldrichi* Melander, distal portion, posterior view. **105.** *Parathalassius wheeleri* **sp. nov.**, entire phallus, left lateral view. **106.** *Parathalassius wheeleri* **sp. nov.**, distal portion, posterior view. **107.** *Parathalassius socali* **sp. nov.**, entire phallus, left lateral view. **108.** *Parathalassius socali* **sp. nov.**, distal portion, posterior view. **109.** *Parathalassius uniformus* **sp. nov.**, distal portion, left lateral view. **110.** *Parathalassius uniformus* **sp. nov.**, distal portion, posterior view. Abbreviations: ej apod—ejaculatory apodeme; v spur—ventral spur-like projection. Scale bars = 0.1 mm.



**FIGURES 111–114.** Phallus of Nearctic *Parathalassius* species. **111.** *Parathalassius infuscatus* sp. nov., distal portion, left lateral view. **112.** *Parathalassius infuscatus* sp. nov., distal portion, posterior view. **113.** *Parathalassius midas* sp. nov., distal portion, left lateral view. **114.** *Parathalassius midas* sp. nov., distal portion, posterior view. Abbreviation: v spur—ventral spur-like projection. Scale bars = 0.1 mm.

**Female:** Body length 2.3–3.0 mm, wing length 2.0–2.2 mm. Similar to male except as follows: **Head:** Eyes with ommatrichia of nearly uniform length, not distinctly longer on lower third. Face wider, at middle about 4.0–4.25X width of anterior ocellus. **Legs:** *Hindleg:* Tibia with anterodorsal and anteroventral rows of setae slightly shorter. Tarsomere 1 without erect setae dorsally. **Abdomen:** Tergite 5 broadly subtriangular to semicircular in dorsal view with posterior margin rounded (cf. Fig. 131). Terminalia distinctly narrower than base of segment 5 (cf. Figs 131–132); sternite 8 trough-like, with weak basal bulge, not narrowed apically, apical half with longitudinal ridges absent to barely apparent, at most slightly developed laterally along apical margin and not present medially, apex emarginate (Fig. 139); sternite 9 unsclerotized and indistinct; tergite 10 with hemitergites subtriangular and short, each with 2 acanthophorite spines; cercus short, pointed apically.

**Distribution and seasonal occurrence.** *Parathalassius sociali* is currently known only from sandy seashores in southern California, from Salinas River State Beach in Monterey County, south to San Clemente in Orange County (Fig. 150). Adults have been collected from early June to late July.

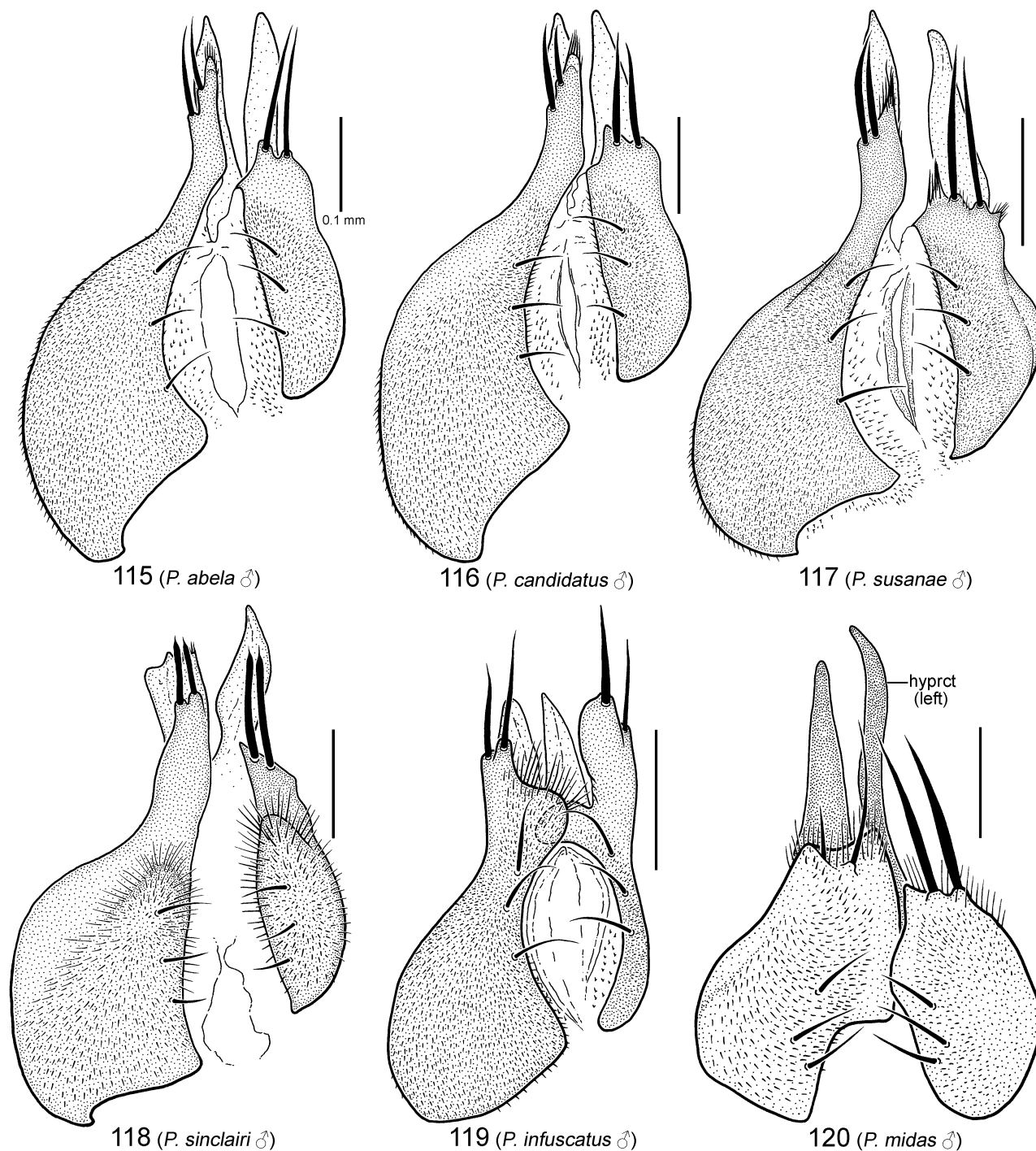
**Etymology.** The specific name refers to the southern Californian distribution of this species and is derived from the commonly used abbreviation, SoCal.

**Remarks.** The COI barcode sequence data obtained from specimens of *P. sociali* (Fig. 154) indicate a significant degree of genetic divergence (at minimally 3.5%) between populations at Surf Beach, Santa Barbara County (represented only by females) and San Clemente, Orange County. This suggests considerable isolation of populations of this species on these two geographically distant beaches (380 km apart).

***Parathalassius susanae* sp. nov.**

(Figs 35, 46, 52, 55, 66, 83–84, 117, 141, 151)

**Type material. HOLOTYPE** ♂ labelled: “USA: OR: Lane Co., Suislaw/ North Jetty, nr. Florence,/ 44°01'07.0"N 124°08'12.6"W/ 8.vii.2014, swp [swept] dunes &/ beach grass (*Ammophila*)/ S.E. Brooks”; “HOLOTYPE/*Parathalassius susanae*/ Brooks & Cumming [red label]” (CNC). **PARATYPES: USA: Oregon:** same data as holotype (1♂, CNC); same data as holotype except, J.M. Cumming (3♂, CNC); same data except, CNC487190 (1♂, barcoded, CNC), CNC487191 (1♀, barcode-associated, CNC); same data except, 7.vii.2014 (2♂, CNC).



**FIGURES 115–120.** Male cerci of Nearctic *Parathalassius*, dorsal view. **115.** *Parathalassius abela* sp. nov. **116.** *Parathalassius candidatus* Melander. **117.** *Parathalassius susanae* sp. nov. **118.** *Parathalassius sinclairi* sp. nov. **119.** *Parathalassius infuscatus* sp. nov. **120.** *Parathalassius midas* sp. nov. Abbreviation: hyprct—hypoproct. Scale bars = 0.1 mm.

**Other material examined. CANADA: British Columbia:** Haida Gwaii, Graham Island: Tlell, Naikoon Prov. Park [ca. 53°33'37"N 131°55'39"W], intertidal, 14.vii.1988, S.A. Marshall (3♂, 11♀, CNC); 3 km N Tlell [ca. 53°33'37"N 131°55'39"W], 13.vii.1988, meadow behind dunes, T.A. Wheeler (1♂, 2♀, CNC); Queen Charlotte City [ca. 53°15'14.68"N 132° 05'14.01"W], 14.viii.1957, E.E. MacDougall (1♀, CNC). **USA: California:** Humboldt County: Clam Beach [ca. 40°59'40"N 124°06'58"W], 21.vi.1935, A.L. Melander (1♂, 1♀, USNM); Clam Beach Co. Park N of Eureka [ca. 40°59'40"N 124°06'58"W], 15.v.1978, D.D. Wilder (7♀, CAS); same data except, 16.v.1978 (1♀, CAS); Samoa Peninsula, Samoa Dunes Recreation Area, 40°45'41"N 124°13'37"W,

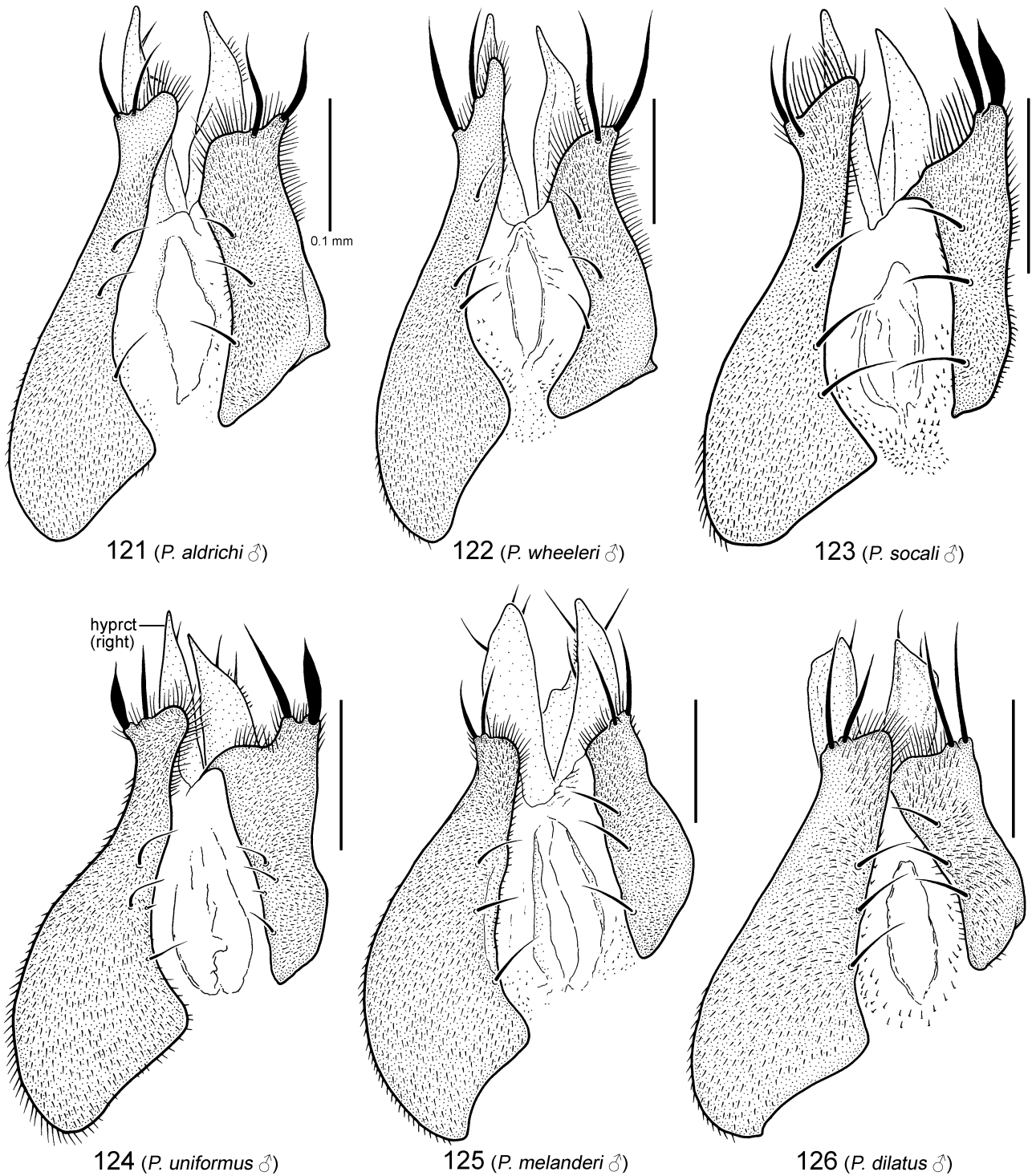
21.v.2009, S.E. Brooks (2♂, 2♀, CNC); same data except, CNC487193 (1♂, barcoded, CNC). **Georgia:** McIntosh County: Sapelo Island [ca. 31°27'21"N 81°13'16"W], 20.vi.1987, open sand dunes, BRC HYM TEAM (1♂, CNC); same data except, CNC DIPTERA #103903 (1♀, barcode-associated, CNC). **Oregon:** Coos County: Bandon, Bullards Beach, 43°08'44"N 124°24'56"W, 29.v.2009, swept beach-grass, S.E. Brooks (4♂, 3♀, CNC); same data except, CNC DIPTERA #103911 (1♂, barcoded, CNC); same data except, J.M. Cumming (3♂, CNC); same data except, CNC487189 (1♀, barcode-associated, CNC); Curry County: Gold Beach [ca. 42°24'N 124°25'W], dunes, 28.vii.1993, H. Ulrich (1♂, 1♀, ZFMK); 3mi. SE Pistol River [ca. 42°13'59"N 124°23'27"W], 28.vi.1972, G. Steyskal (2♂, 1♀, USNM); Lincoln County: South Beach State Park, 44°36'05.6"N 124°03'54.0"W, 3.vii.2014, swept dunes & beach grass (*Ammophila*), S.E. Brooks (2♂, 2♀, CNC); same data except, J.M. Cumming (1♀, CNC); Tillamook County: Manzanita, 45°42'54.9"N 123°56'25.4"W, 3.vii.2014, swept dunes & beach grass (*Ammophila*), J.M. Cumming (2♂, 1♀, CNC); same data except, CNC487188 (1♂, barcoded, CNC); same data except, S.E. Brooks, CNC487187 (1♀, barcode-associated, CNC). **Washington:** Jefferson County: Olympic National Park, along Kalaloch Beach [ca. 47°36'19"N 124°22'29"W], 22.vii.1978, D.D. Wilder (16♂, 11♀, CAS); Pacific County: Cape Disappointment State Park nr. Ilwaco, Benson Beach, 46°16'20.4"N 124°04'25.4"W, 1.vii.2014, swept dunes & beach grass (*Ammophila*), S.E. Brooks (13♂, 6♀, CNC; 2♂, 2♀, CSCA); same data except, CNC487180, CNC487181 (2♂, barcoded, CNC), CNC487185 (1♀, barcode-associated, CNC); same data except, 2.vii.2014 (1♂, 4♀, CNC); same data except, 1.vii.2014, J.M. Cumming (2♂, 2♀, CNC); same data except, 2.vii.2014 (2♂, 3♀, CNC); same data except, 1.vii.2014, swept dunes & beach vegetation, S.H. Cumming (3♂, 3♀, CNC); Ilwaco, Cape Disappointment, 23.vii.1993, H. Ulrich (8♂, 6♀, ZFMK); same data except, 24.vii.1993 (19♂, 9♀, ZFMK); same data except, 25.vii.1993 (2♀, ZFMK); same data except, Benson Beach, dunes, 24.vii.1993 (2♂, ZFMK); same data except, 25.vii.1993 (5♀, ZFMK); same data except, 5.viii.1994 (1♂, 2♀, ZFMK); same data except, 9.viii.1994 (4♂, 2♀, ZFMK); same data except, on wet sand, 27.vii.1993 (11♂, 11♀, ZFMK); same data except, sandy beach, 3.viii.1994 (11♂, 9♀, ZFMK); same data except, 5.viii.1994 (1♂, 2♀, ZFMK); same data except, 8.viii.1994 (13♂, 14♀, ZFMK); same data except, 9.viii.1994 (15♂, 7♀, ZFMK); same data except, 10.viii.1994 (44♂, 26♀, ZFMK); same data except, Waikiki Beach, on sand, 15.vii.1988 (51♂, 30♀, ZFMK); same data except, on rock, 16.vii.1988 (2♂, 4♀, ZFMK); same data except, 17.vii.1988 (2♂, ZFMK); same data except, dunes, 22.vii.1993 (1♂, 2♀, ZFMK); same data except, on wet sand, 25.vii.1993 (7♂, 8♀, ZFMK); same data except, 26.vii.1993 (17♂, 23♀, ZFMK); same data except, sandy beach, 22.vii.1993 (4♂, 2♀, ZFMK); same data except, 9.viii.1994 (10♂, 4♀, ZFMK); Ft. Canby State Park [=Cape Disappointment State Park], 29.vi.1988, W.N. & D. Mathis (3♂, 1♀, USNM); Ilwaco [ca. 46°16'20"N 124°04'25"W], vii.1917, A.L. Melander (32♂, 35♀, USNM); same data (3♂, 1♀, CUCI); same data except, 27.viii.1917 (5♂, 3♀, USNM); same data except, 12.vii.1922 (1♀, USNM); same data except, 28.vi.1925 (3♀, USNM); same data except, Beach, vii.1917 (2♂, EMEC); Seaview [ca. 46°20'05"N 124°4'02"W], 1.ix.1920, O.E. Miner (1♂, USNM).

**Diagnosis.** This medium sized to relatively large species is characterized by an elongate-conical antennal postpedicel, 3–4 notopleural bristles, relatively dark legs, hind tarsomeres 2 and 3 nearly subequal in length, males with greyish-white pruinosity on the face and clypeus, and longer lower male ommatrichia. *Parathalassius susanae* is similar to *P. candidatus* and *P. sinclairi*, but males and females are most easily distinguished from the latter two species by hind tarsomere 2 being nearly subequal in length to tarsomere 3. Males of *P. susanae* are further distinguished from those of *P. sinclairi* by the longer anterodorsal setae on the hind tibia and by the hind tarsus, which lacks dorsal peg-like setae on tarsomeres 2–4.

**Description. Male:** Body length 2.7–3.4 mm, wing length 2.8–3.0 mm. Dark brown ground colour covered mostly with dense greyish-white pruinosity. Setae of body and legs white. **Head** (Fig. 35): Eyes with ommatrichia of lower third distinctly longer and slightly flattened, forming dense reflective mat of whitish coloured hair. Face and clypeus concolourous with greyish-white frons and vertex. Face narrowest at middle, about 2.0X width of anterior ocellus. Gena and postgena with moderately long white setae, forming short beard flanking mouthparts. Antenna (Fig. 46) including arista-like stylus, entirely dark brown; postpedicel elongate-conical, 1.65–1.75X longer than wide; arista-like stylus of medium length, about 1.6X length of postpedicel. Palpus with 7–8 setae on outer surface of apical half. **Thorax:** Mesoscutum with some brownish-grey pruinosity on dorsum. Acrostichal setulae quadriserial; 7–8 dorsocentral bristles, 0 presutural intra-alar bristles, 1–2 presutural supra-alar (posthumeral) bristles, 3–4 postsutural supra-alar bristles, 3 notopleural bristles. Scutellum with 3 pairs of bristles. **Legs:** *Foreleg:* Dark grey, pale at knee and apex of tibia, tarsomeres 1–2 pale yellowish-brown to brown, tarsomeres 3–5 brown to greyish-brown. Coxa with moderately long pale setae on anterior surface. Femur with

numerous long setae on posterior surface, posterodorsal and posteroventral rows prominent. Tibia and tarsus with mostly short setae and setulae, tarsus with some longer setae dorsally; tarsomeres 1–2 not dilated. *Midleg*: Dark grey, pale at knee and extreme apex of tibia, tarsomere 1 pale yellowish-brown, tarsomeres 2–5 brown to greyish-brown. Femur with anteroventral and ventral rows of setae prominent. Tibia with pair of apicoventral bristles. Tarsus with some longer setae dorsally; tarsomeres 1–4 each with pair of dark spine-like apicoventral setae. *Hindleg* (Figs 52, 55): Dark grey, femur dark brown posteriorly, slightly paler at knee and extreme apex of tibia, tarsomere 1 pale yellowish-brown basally, apex of tarsomere 1 and tarsomeres 2–5 brown to greyish-brown. Femur with anteroventral and posteroventral rows of setae prominent. Tibia with anterodorsal and anteroventral rows of setae of moderate length, subequal or slightly longer than width of tibia. Tarsus slightly shorter than tibia with mostly short setae and setulae, longer setae dorsally; tarsomere 1 shorter than combined length of tarsomeres 2–4; tarsomeres 1–4 lacking peg-like or distinctively thickened setae dorsally; tarsomeres 3–5 widened apically and slightly flattened; tarsomeres 2, 3 and 5 nearly subequal in length, tarsomere 4 slightly shorter. **Wing** (Fig. 66): Hyaline with brown to dark brown veins. Cell dm produced apically, dm-m crossvein concave. Vein CuA+CuP of medium length, straight. **Abdomen**: Tergites 2–4 with setae well-developed and relatively long. Sternite 5 with slender anteriorly curved digitiform pregenitalic process present, base lacking anterior projection, apex blunt and covered with microtrichia, posterior edge of sternite 5 (behind process) deeply emarginate. Sternite 8 subquadrate with prominent elongate setae on posterolateral edges. *Hypopygium* (Figs 83–84, 117): Large. Left epandrial lamella with ventral portion elongate (about 2X longer than high); ventral epandrial process broadly bifurcate, dorsal arm curved ventrally, narrowed in middle section, apex expanded, blunt or hook-like, ventral arm thick with minute apicodorsal seta and 1–2 minute setae along distiventral margin, apex with expanded lamelliform concavity. Dorsal lobe of left surstylus with basiventral edge weakly rounded, apex thumb-like, with long basidorsal seta, short lateral seta and long apical seta, medial surface with knob-like projection bearing lamelliform apical process. Ventral lobe of left surstylus shallowly bilobate in lateral view, dorsal lobe short with apex rounded or bluntly pointed, ventral lobe with rounded base bearing short lateral seta and complex upturned multilobate projection arising medioventrally. Right epandrial lamella with ventral epandrial process not developed; basal portion of epandrial lamella narrowed and dorsally curved, with deep dorsal emargination bordering ventral margin of right cercus. Dorsal lobe of right surstylus with 3 lateral setae (lowermost seta weaker), apex narrowed with squared-off tip bearing thick apically-frayed preniseta on medial surface. Ventral lobe of right surstylus with 1–2 lateral setae near middle, distal half weakly recurved with broad lateral edge, tapered with tubercle bearing strong seta proximal to rounded apex. Hypandrium very large, elongate-reniform with convex anterior and posterior ends extending to or beyond margins of epandrial lamellae in lateral view, bare. Left postgonite lobe ovoid basally, constricted near middle, distal portion broadly lamelliform with claw-like apical process, base of lobe with narrow slender projection. Right postgonite lobe with broad lateral protuberance and indistinct medial projection, apex bifurcate with short digitiform process and broad rounded lamelliform process. Phallus (cf. Figs 97–98) short and weakly curved, broad in basal 2/3 with apical 1/3 narrower (in lateral view), left lateral dentiform projection present at 2/3 length, dorsal flange not developed. Ejaculatory apodeme broadly subtriangular. Hypoproct strongly projected dorsally as pair of slender lobes. Cerci with anal setae well-developed and differentiated from surrounding hairs; right cercus much larger than left cercus with basal portion distended and rounded laterally, apex strongly deflected, elongate, narrow and pointed, with 2 short preapical setae present along lateral margin; left cercus oblong-subrectangular in dorsal view, apex strongly deflected dorsally, short and subrectangular, with medial and lateral corners weakly pointed, with 2 long setae on posterior margin.

**Female**: Body length 2.9–3.3 mm, wing length 2.9–3.5 mm. Similar to male except as follows: **Head**: Eyes with ommatrichia of nearly uniform length, not distinctly longer on lower third. Face wider, at middle about 3.75–4.5X width of anterior ocellus. **Legs**: *Foreleg*: Coxa with shorter more slender pale setae on anterior surface. Femur with posteroventral row of setae only prominent apically. Tarsus with slightly shorter setae dorsally. *Midleg*: Tarsus with slightly shorter setae dorsally. *Hindleg*: Tibia with anterodorsal and anteroventral rows slightly shorter. Tarsus with slightly shorter setae dorsally. **Abdomen**: Tergite 5 broadly subtriangular to semicircular in dorsal view with posterior margin rounded (cf. Fig. 131). Terminalia distinctly narrower than base of segment 5 (cf. Figs 131–132); sternite 8 trough-like, lacking basal bulge, not distinctly narrowed apically, apical half with longitudinal ridges, apex truncate (Fig. 141); sternite 9 a narrow transverse sclerotized band; tergite 10 with hemitergites subtriangular and short, each with 2 acanthophorite spines; cercus short, pointed apically.



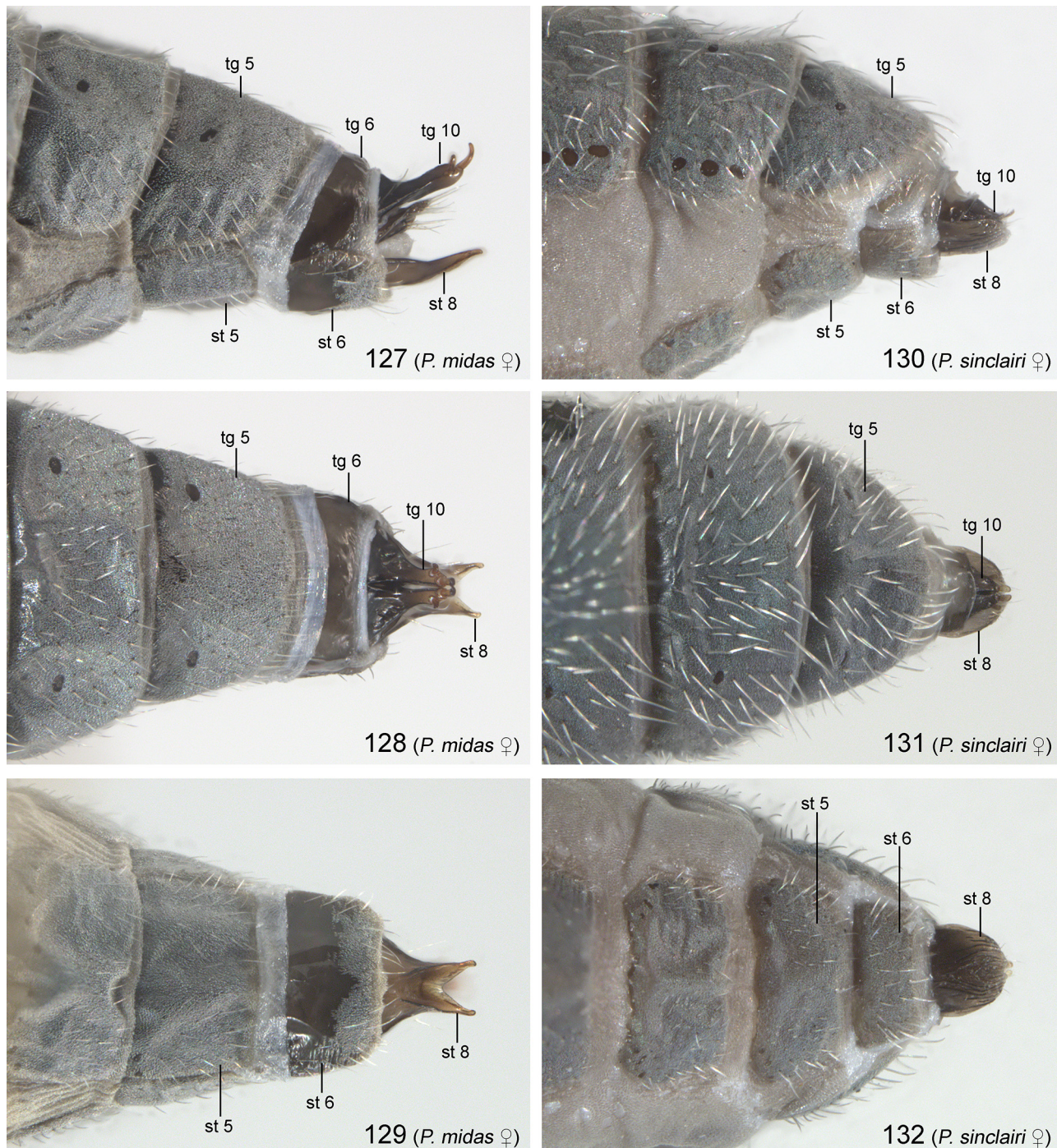
**FIGURES 121–126.** Male cerci of Nearctic *Parathalassius*, dorsal view. **121.** *Parathalassius aldrichi* Melander. **122.** *Parathalassius wheeleri* sp. nov. **123.** *Parathalassius socali* sp. nov. **124.** *Parathalassius uniformus* sp. nov. **125.** *Parathalassius melanderi* Cole. **126.** *Parathalassius dilatus* sp. nov. Abbreviation: hyprct—hypoproct. Scale bars = 0.1 mm.

**Distribution and seasonal occurrence.** *Parathalassius susanae* is currently known to occur on sandy seashores from Haida Gwaii, British Columbia, south along the coast of Washington, Oregon and northern California. There is also a reliable record of this species from a sandy seashore location on Sapelo Island, Georgia along the Atlantic coast, which is presumably the result of a recent introduction (see Remarks) (Fig. 151). Adults have been collected from mid May to early September.

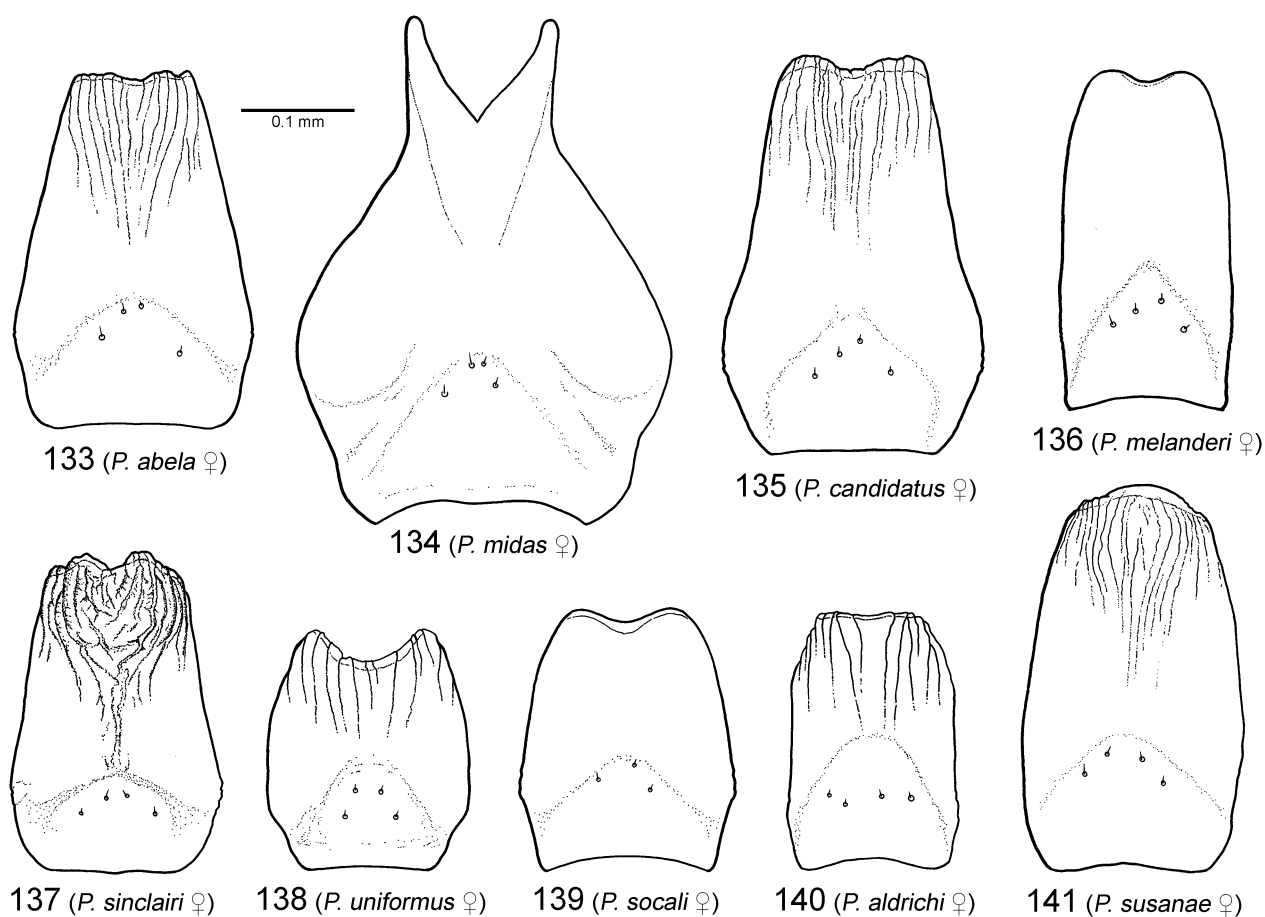
**Etymology.** This species is named in recognition of the second author's wife, Susan Cumming, who has

extensively supported his various research endeavours, including collecting many specimens of *Parathalassius* used in this study.

**Remarks.** The COI barcode sequence data obtained from specimens of *P. susanae* (Fig. 154) from Washington, Oregon, northern California, and even Georgia (see below), show very little genetic divergence (<1.1%), suggesting that there has been considerable gene exchange and possible movement between populations of this widely distributed species.



**FIGURES 127–132.** Female terminalia of Nearctic *Parathalassius*. **127.** *Parathalassius midas* sp. nov., lateral view. **128.** Same, dorsal view. **129.** Same, ventral view. **130.** *Parathalassius sinclairi* sp. nov., lateral view. **131.** Same, dorsal view. **132.** Same, ventral view. Abbreviations: st—sternite; tg—tergite.



**FIGURES 133–141.** Female sternite 8 of Nearctic *Parathalassius*, ventral view. **133.** *Parathalassius abela* sp. nov. **134.** *Parathalassius midas* sp. nov. **135.** *Parathalassius candidatus* Melander. **136.** *Parathalassius melanderi* Cole. **137.** *Parathalassius sinclairi* sp. nov. **138.** *Parathalassius uniformus* sp. nov. **139.** *Parathalassius socali* sp. nov. **140.** *Parathalassius aldrichi* Melander. **141.** *Parathalassius susanae* sp. nov. Scale bar = 0.1 mm.

A male and female specimen of *P. susanae* were collected in 1987 from the sandy shoreline of Sapelo Island in Georgia (Fig. 151). The species identity was also confirmed through comparison of a DNA barcode (COI) sequence taken from the female specimen (Fig. 154, CNC DIPTERA #103903). This is the only record of the genus from the Atlantic coast of North America and is presumably the result of a recent introduction. This may have occurred through human-assisted movement of plants such as beach grass (*Ammophila*) from the Pacific coast. These plants are routinely used to counter coastal erosion and stabilize dune habitats, although currently there is no evidence that this procedure was employed on Sapelo Island.

### ***Parathalassius ulrichi* Shamshev**

*Parathalassius ulrichi* Shamshev 1998: 4.

**Material examined. JAPAN: Hokkaido:** Wakkasakanai, zone A~C, Sarobetsu, 1.vii.1967, T. Saigusa (3♂, 3♀, CNC); Wakkasakanai, 26.vi.1986, T. Saigusa (11♂, 3♀, ZFMK); Wakkanai, Sakanoshita Beach, 20.viii.1993, M. Satô (11♂, 14♀, ZFMK).

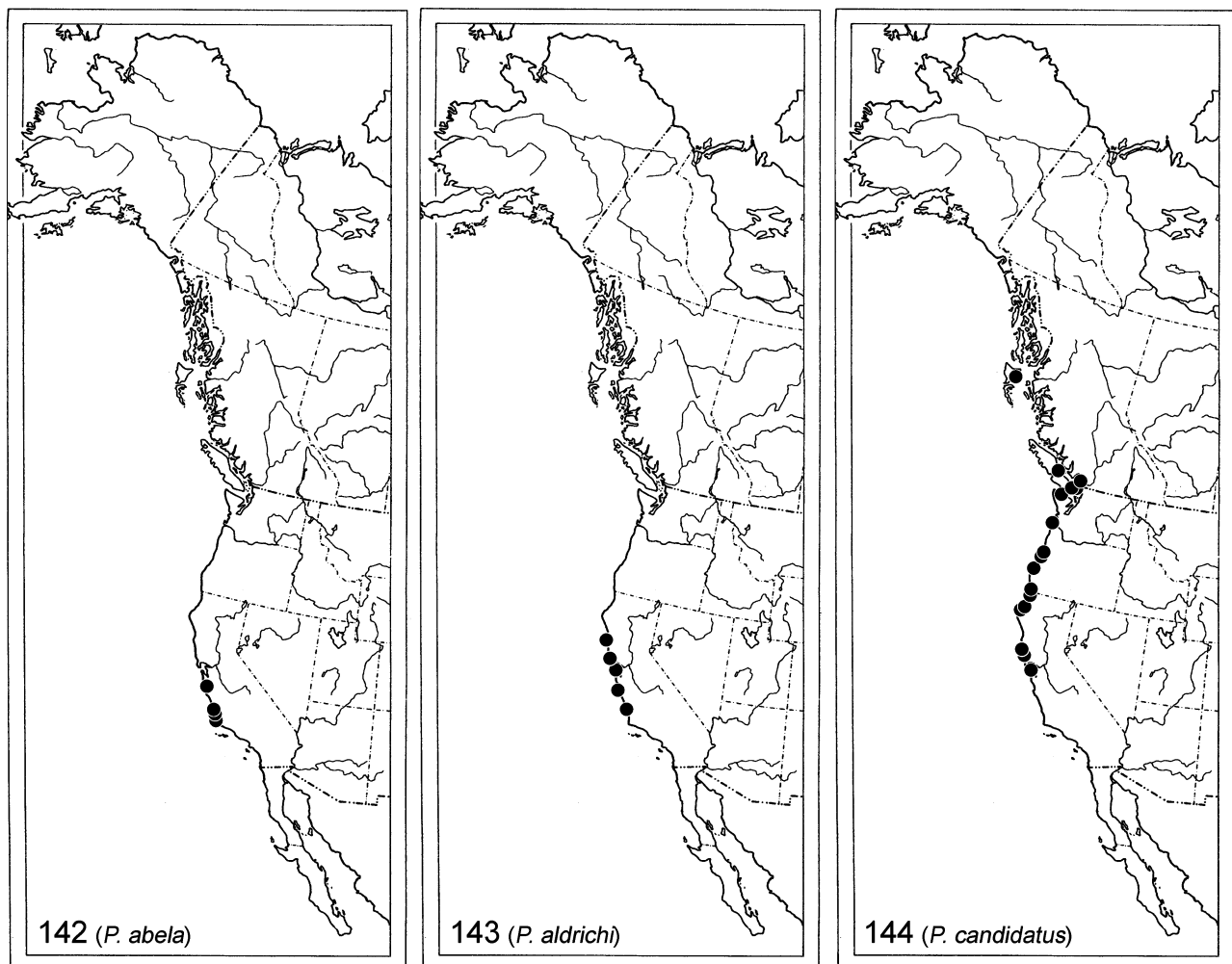
**Diagnosis.** This relatively small to medium sized Palearctic species is characterized by a head and thorax with dark setae, a subtriangular antennal postpedicel, longer lower male ommatrichia, 3 notopleural bristles (see Remarks), hyaline slightly brown-tinted wing, and dark legs with hind tarsomere 2 distinctly longer than tarsomere 3. *Parathalassius ulrichi* is very similar to the Nearctic *P. sinclairi*, but males have longer anterodorsal setae on the



hind tibia, and possess thickened angled setae dorsally on the hind tarsus, rather than perpendicular peg-like setae. In addition, females of *P. ulrichi* have longitudinal ridges on the apex of sternite 8, unlike *P. sinclairi* with female sternite 8 rugose apically.

**Distribution.** This eastern Palaearctic species is known from the Kuril Islands (Chirinktotan, Kunashir and Shikotan) in the Russian Far East (Shamshev 1998) and is here newly recorded from Hokkaido, Japan.

**Remarks.** In his description of *P. ulrichi* Shamshev (1998) indicated that this species has 2 notopleural bristles. The specimens from Hokkaido all have 3 notopleural bristles and I. Shamshev (pers. comm.) has confirmed that additional material collected from the type locality on the Kuril Islands also have 3 (or apparently very rarely 2) notopleural bristles.



**FIGURES 142–144.** Known geographical distributions of Nearctic *Parathalassius*. **142.** *Parathalassius abela* sp. nov. **143.** *Parathalassius aldrichi* Melander. **144.** *Parathalassius candidatus* Melander.

***Parathalassius uniformus* sp. nov.**

(Figs 8–10, 36–37, 47, 67, 91, 109–110, 124, 138, 152)

**Type material.** **HOLOTYPE** ♂ labelled: “USA: CA: Santa Barbara Co.:/ Surf Beach, Vandenberg Air/ Force Base, 34.683801°N/ 120.605520°W, 5.iv.2016/ A.J. Abela, ex: sandy coastal/ foredune”; “HOLOTYPE/ *Parathalassius uniformus*/ Brooks & Cumming [red label]” (CNC). **PARATYPES:** **USA: California:** same data as holotype (37♂, 3♀, CNC); same data as holotype except, 6.iv.2016 (10♂, 6♀, CNC).

**Other material examined.** **USA: California:** same data as holotype except, 4.vi.2016, ex: *Ambrosia chamissionis* & coastal dunes (14♂, 34♀, CNC); same data except, CNC573801, CNC573803 (2♂, barcoded, CNC), CNC573765 (1♀, barcode-associated); same data except, S.E. Brooks (25♂, 30♀, CNC; 2♂, 2♀, CSCA);

same data except, CNC573332 (1♂, barcoded, CNC), CNC573254, CNC573337 (2♀, barcode-associated, CNC); same data except, J.M. Cumming (4♂, 13♀, CNC); same data except, CNC582777 (1♂, barcoded, CNC), CNC582785 (1♀, barcode-associated, CNC); same data except, S.H. Cumming (1♂, 4♀, CNC).

**Diagnosis.** This relatively small species is characterized by a subtriangular antennal postpedicel, uniformly short male ommatrichia, 2 notopleural bristles, hyaline wing, relatively dark legs, male hypopygium compact, and female sternite 8 with longitudinal ridges extended across apical third.

**Description. Male** (Figs 8–10): Body length 1.7–2.1 mm, wing length 1.5–1.7 mm. Dark brown ground colour mostly covered with dense greyish-white pruinosity. Setae of body and legs white. **Head** (Fig. 36): Eyes with ommatrichia of nearly uniform length, not distinctly longer on lower third. Face and clypeus concolourous with greyish-white frons and vertex. Face narrowest at middle, about 2.5X width of anterior ocellus. Gena without setae and postgena with moderately short sparse setae, not forming beard flanking mouthparts. Antenna (Fig. 47) including arista-like stylus, entirely dark brown; postpedicel subtriangular, 1.4–1.5X longer than wide; arista-like stylus of medium length, about 1.7X length of postpedicel. Palpus with 2–3 moderately long setae and several short setulae on outer surface of apical half. **Thorax:** Acrostichal setulae biserial; 6–7 dorsocentral bristles, 0 presutural intra-alar bristles, 1 presutural supra-alar (posthumeral) bristle, 2–3 postsutural supra-alar bristles, 2 notopleural bristles. Scutellum with 2–3 pairs of bristles. **Legs:** *Foreleg:* Dark grey, pale at knee and apex of tibia, tarsomere 1 pale yellow basally, apex of tarsomere 1 and tarsomeres 2–5 brown. Coxa with short pale setae on anterior surface. Femur with short setae on posterior surface. Tibia with short setae and setulae. Tarsus with setulae; tarsomeres 1–2 not dilated. *Midleg:* Dark grey, pale at knee and extreme apex of tibia, tarsomere 1 pale yellow basally, apex of tarsomere 1 and tarsomeres 2–5 brown. Femur with apical anterodorsal setae most prominent, relatively short. Tibia with 1 apicoventral bristle. Tarsomeres 1–4 each with several dark spine-like apicoventral setae. *Hindleg:* Dark grey, femur dark brown posteriorly, pale at knee and extreme apex of tibia, tarsomere 1 pale yellow, tarsomeres 2–5 pale brown to brown. Femur with anteroventral row of setae prominent, short basally, longer apically. Tibia with anterodorsal and anteroventral rows of setae short to moderate length, shorter or subequal to width of tibia. Tarsus slightly longer than tibia with short setae and setulae; tarsomere 1 shorter than combined length of tarsomeres 2–4; tarsomeres 1–4 lacking peg-like or thickened setae dorsally; tarsomere 2 longer than tarsomere 3; tarsomere 3 longer than tarsomere 4; tarsomere 5 subequal in length to tarsomere 3. **Wing** (Fig. 67): Hyaline with brown veins. Cell dm produced apically, dm-m crossvein slightly concave. Vein CuA+CuP short to medium length, nearly straight. **Abdomen:** Tergites 2–4 with setae relatively short and weak. Sternite 5 with short straight digitiform pregenitalic process present, base lacking anterior projection, apex blunt and covered with microtrichia, posterior edge of sternite 5 (behind process) emarginate. Sternite 8 subquadrate with setae longer along posterolateral margins. *Hypopygium* (Figs 91, 109–110, 124): Relatively compact. Left epandrial lamella with ventral portion elongate (about 2X longer than high); ventral epandrial process broadly bifurcate, dorsal arm with weak ventral curve, apex expanded and blunt, ventral arm thick with minute apicodorsal seta and minute distiventral seta, apex with expanded lamelliform concavity. Dorsal lobe of left surstylus with basiventral edge rounded and flap-like, apex broadly rounded, with long basidorsal seta on bump-like protuberance, short lateral seta and long apical seta, medial surface with stalk-like projection bearing lamelliform apical seta. Ventral lobe of left surstylus shallowly bilobate in lateral view, dorsal lobe short with apex subquadrate, ventral lobe with basal pointed process bearing apical seta and complex upturned bifurcate projection arising medioventrally. Right epandrial lamella with ventral epandrial process barely developed as a short angular projection; basal portion of epandrial lamella narrowed and dorsally curved, with deep dorsal emargination bordering ventral margin of right cercus. Dorsal lobe of right surstylus with 3 lateral setae (distal-most seta strongest, middle seta weakest), apex narrowed with subtriangular tip bearing thick apically-frayed preniseta on medial surface. Ventral lobe of right surstylus with lateral seta at basal third, distal 2/3 recurved, slender with narrow apically pointed lamelliform seta proximal to rounded lamelliform apex. Hypandrium large, reniform and bare. Left postgonite lobe subquadrate basally, constricted near middle, distal portion subrectangular and flat with claw-like apicodorsal process, base of lobe with broad curved apically-pointed medial projection. Right postgonite lobe with broad lateral protuberance and lamelliform medial projection, apex bifurcate with well-developed digitiform ventral process and lamellate dorsal process. Phallus relatively short and moderately curved, flattened preapically with membranous region on right side, apex straight. Ejaculatory apodeme subtriangular with apex slightly curved ventrally. Hypoproct projected dorsally as pair of slender pointed lobes, each lobe with ventral cluster of 3–4 minute setae proximal to apex, left lobe also with piliferous region apicoventrally. Cerci with anal setae well-developed and differentiated

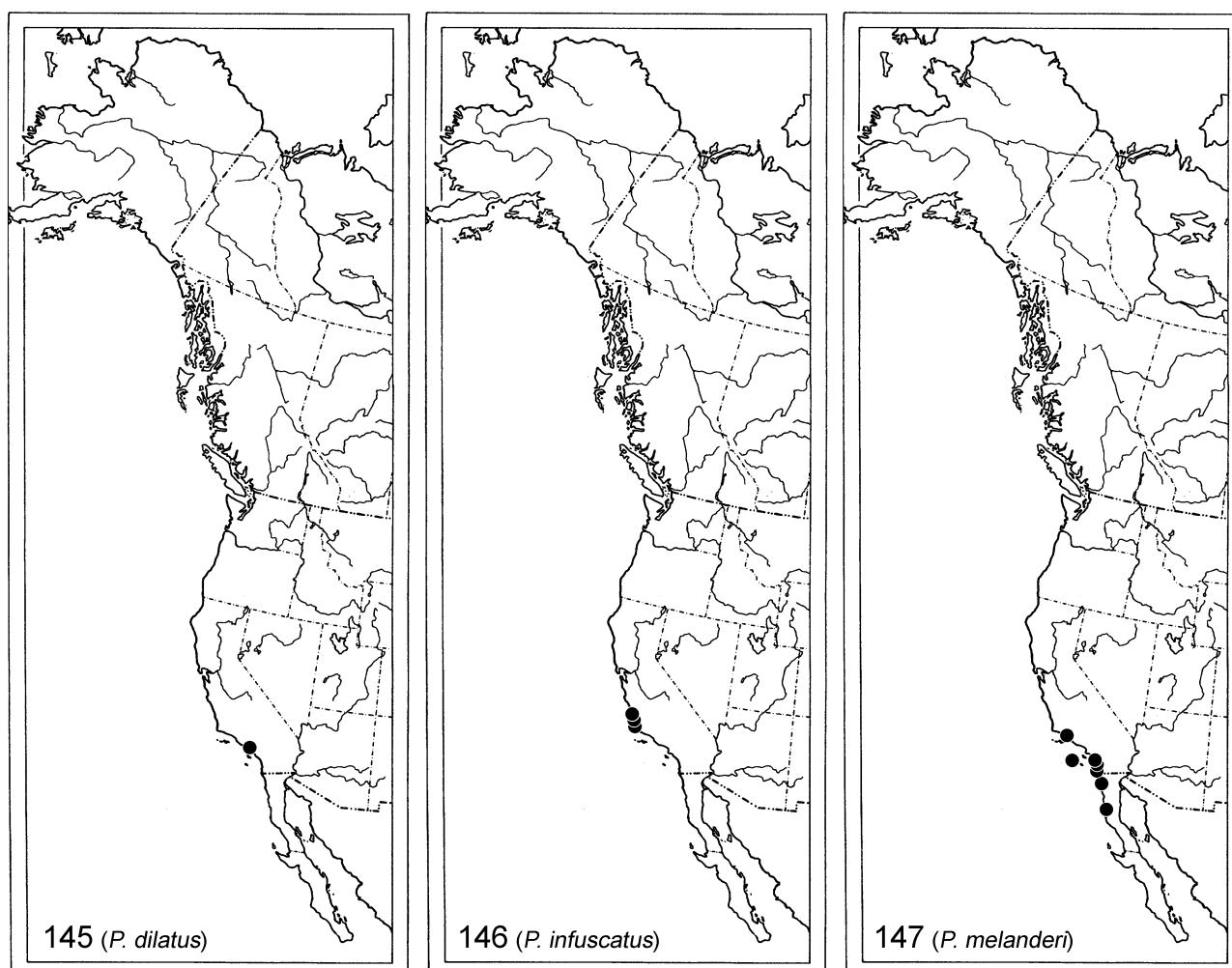
from surrounding hairs; right cercus much larger than left cercus with basal portion distended and rounded laterally, apex slightly widened, not dorsally deflected, truncate with pair of setae at apicolateral margin; left cercus oblong in dorsal view, apex broad, even with apex of right cercus, not dorsally deflected, with stub-like apicolateral projection bearing pair of thickened setae.

**Female** (Fig. 10): Body length 1.9–2.8 mm, wing length 1.5–2.1 mm. Similar to male except as follows: **Head** (Fig. 37): Face wider, at middle about 4.0–4.25X width of anterior ocellus. **Legs:** *Hindleg:* Femur with anteroventral row of setae shorter. Tibia with anterodorsal and anteroventral rows of setae shorter. **Abdomen:** Tergites 2–4 with setae slightly longer. Tergite 5 broadly subtriangular to semicircular in dorsal view with posterior margin rounded (cf. Fig. 131). Terminalia distinctly narrower than base of segment 5 (cf. Figs 131–132); sternite 8 trough-like, with weak basal bulge, not narrowed apically, apical third with longitudinal ridges extended across sternite including medial margin, apex emarginate (Fig. 138); sternite 9 unsclerotized and indistinct; tergite 10 with hemitergites subtriangular and short, each with 2 acanthophorite spines; cercus short, pointed apically.

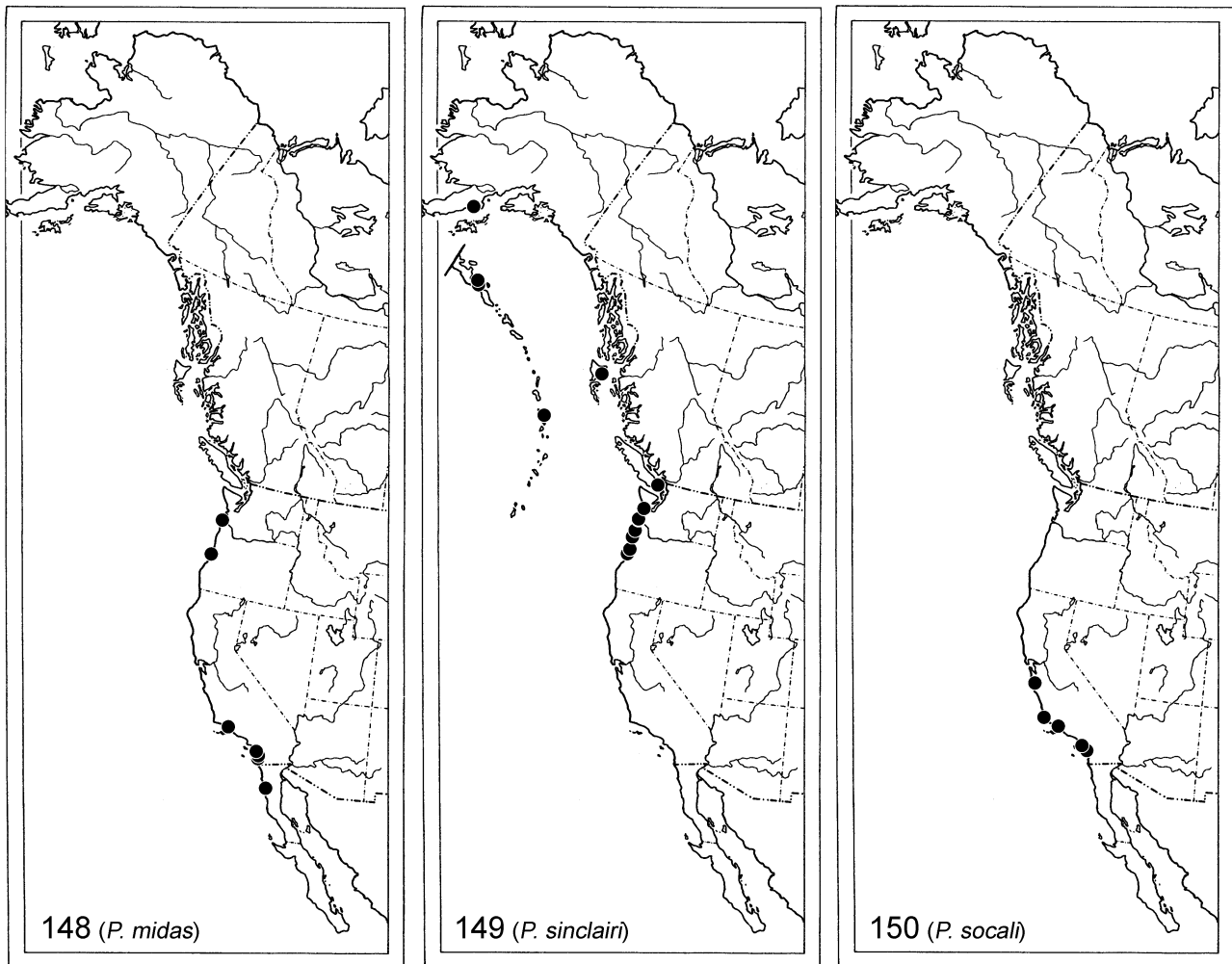
**Distribution and seasonal occurrence.** *Parathalassius uniformus* is currently known only from the coastal dunes at Surf Beach, Santa Barbara County, California (Fig. 152). Adults have been collected from early April to early June.

**Etymology.** The specific name refers to the uniform length of the ommatrichia on the male eyes (Fig. 36).

**Remarks.** Adults were frequently found on open sand between patches of beach bur (*Ambrosia chamissonis*) (Figs 10, 19).



**FIGURES 145–147.** Known geographical distributions of Nearctic *Parathalassius*. **145.** *Parathalassius dilatus* sp. nov. **146.** *Parathalassius infuscatus* sp. nov. **147.** *Parathalassius melanderi* Cole.



**FIGURES 148–150.** Known geographical distributions of Nearctic *Parathalassius*. **148.** *Parathalassius midas* sp. nov. **149.** *Parathalassius sinclairi* sp. nov. **150.** *Parathalassius sociali* sp. nov.

***Parathalassius wheeleri* sp. nov.**

(Figs 25, 39, 57, 72, 93–94, 105–106, 122, 153)

**Type material.** **HOLOTYPE** ♂ labelled: “USA: OR: Lane Co., Suislaw/ North Jetty, nr. Florence, / 44°01′07.0″N 124°08′12.6″W/ 7.vii.2014, swept dunes &/ beach grass (*Ammophila*) / S.E. Brooks”; “HOLOTYPE/*Parathalassius wheeleri*/ Brooks & Cumming [red label]” (CNC). **PARATYPES:** **USA: Oregon:** same data as holotype (4♂, 3♀, CNC); same data as holotype except, CNC487199 (1♂, barcoded, CNC); same data as holotype except, J.M. Cumming (3♂, 2♀, CNC); same data except, CNC487200 (1♀, barcode-associated, CNC); same data except, 8.vii.2014 (2♂, 5♀, CNC).

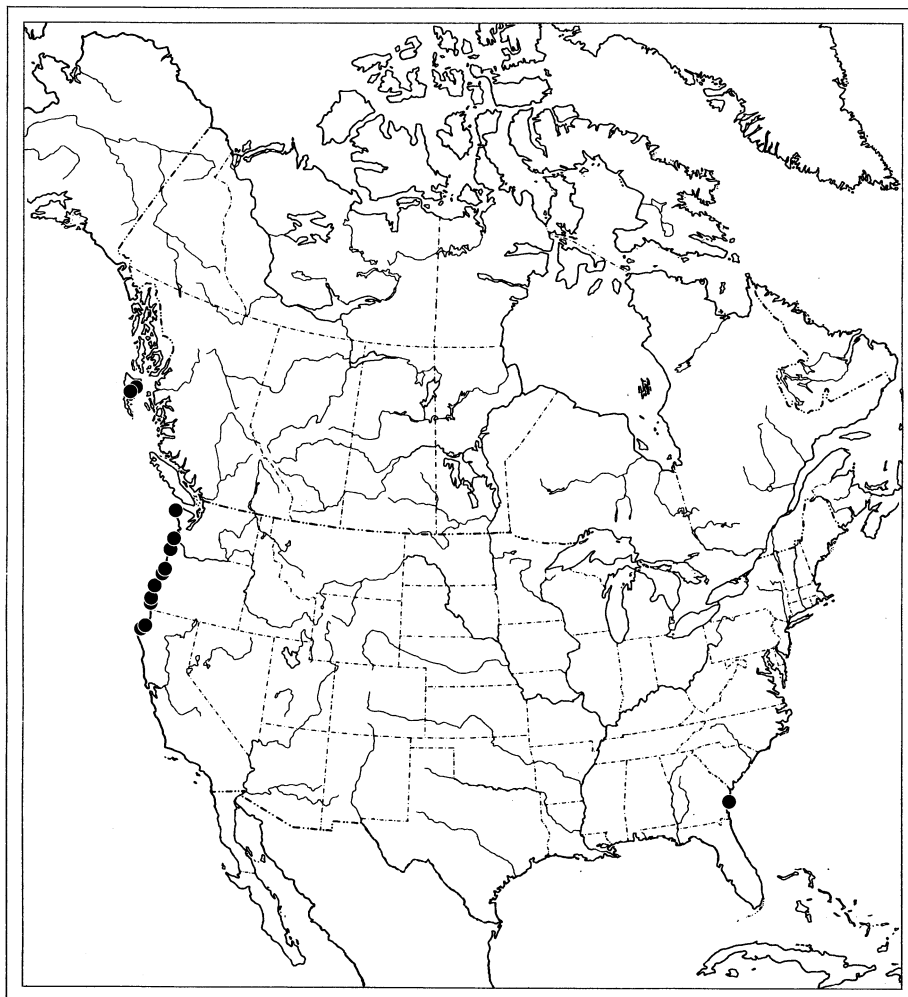
**Other material examined.** **CANADA: British Columbia:** Haida Gwaii, Graham Is., 3km N Tlell [ca. 53°33′37″N 131°55′39″W], 13.vii.1988, meadow behind dunes, T.A. Wheeler, (1♀, CNC); Vancouver Is., Brooks Peninsula, Cape Cook Lagoon, 50°12′N 127°48′W, 2.viii.1981, fall trap sand dunes (4♂, 6♀, UBCZ); same data except, 5.viii.1981 (8♂, 1♀, UBCZ); same data except, 7.viii.1981 (3♂, UBCZ); same data except, 2.viii.1981, CNC DIPTERA #103908 (1♂, UBCZ). **USA: California:** Del Norte County: Smith River Dunes [ca. 41°55′03″N 124°12′17″W], 15.vi.1981 (7♂, 8♀, EMEC); Humboldt County: Clam Beach [ca. 40°59′40″N 124°06′58″W], 21.vi.1935, A.L. Melander (1♂, 1♀, USNM); Clam Beach Co. Park N of Eureka, 15.v.1978, D.D. Wilder (8♂, 8♀, CAS); Fieldbrook [ca. 40°57′32″N 124°07′32″W], 31.v.1903, H.S. Barber (1♀, USNM); Lanphere-Christensen Dunes [ca. 40°53′09″N 124°08′47″W], 16.vi.1981, M.E. Buegler (10♂, 14♀, EMEC); same data except, 4 mi. W

Arcata, 26.vii.1975, M.E. Buegler & E.I. Schlinger (8♂, 7♀, EMEC); Samoa Peninsula, Samoa Dunes Recreation Area, 40°45'41"N 124°13'37"W, 21.v.2009, J.M. Cumming (13♂, 23♀, CNC; 2♂, 2♀, CSCA); same data except, swept dune vegetation (11♂, 9♀, CNC); same data except, S.E. Brooks (30♂, 28♀, CNC); same data except, CNC DIPTERA #'s 103904, 103905, 103913 (2♂, 1♀, respectively, barcoded, CNC); Samoa dunes, 25.vi.1969, D. Levin, LACM ENT 337200 (1♂, LACM). **Oregon:** Lane County: Heceta Beach, 44°02'14.7"N 124°07'57.2"W, 7.vii.2014, swept dunes & beach grass (*Ammophila*), J.M. Cumming (1♂, CNC); same data except, CNC588229 (1♂, barcoded, CNC); Lincoln County: South Beach State Park, 44°36'05.6"N 124°03'54.0"W, 3.vii.2014, swept dunes & beach grass (*Ammophila*), J.M. Cumming (2♂, 2♀, CNC); same data except, CNC487198 (1♀, barcode-associated, CNC). **Washington:** Grays Harbor County: Copalis [ca. 47°06'37"N 124°11'6"W], 14.viii.1921, A.L. Melander (1♀, USNM); Pacific County: Tokeland [ca. 46°42'21"N 124°00'08"W], 18.vii.1917, A.L. Melander (1♀, USNM); Cape Disappointment State Park nr. Ilwaco, Benson Beach, 46°16'20.4"N 124°04'25.4"W, 1.vii.2014, swept dunes & beach grass (*Ammophila*), S.E. Brooks (1♂, 1♀, CNC); same data except, CNC487108 (1♀, barcode-associated, CNC); same data except, 2.vii.2014, CNC588230 (1♂, barcoded, CNC); same data except, 1.vii.2014, J.M. Cumming (1♀, CNC); same data except, CNC588231 (1♀, barcode-associated, CNC); Ilwaco, Cape Disappointment, 23.vii.1993, H. Ulrich (3♂, 6♀, ZFMK); same data except, 24.vii.1993 (3♂, ZFMK); same data except, 25.vii.1993 (1♀, ZFMK); same data except, Benson Beach, dunes, 5.viii.1994 (10♂, 16♀, ZFMK); same data except, 9.viii.1994 (29♂, 18♀, ZFMK); same data except, 10.viii.1994, sandy beach, (5♀, ZFMK); Ilwaco, vii.1917, A.L. Melander (1♂, USNM).

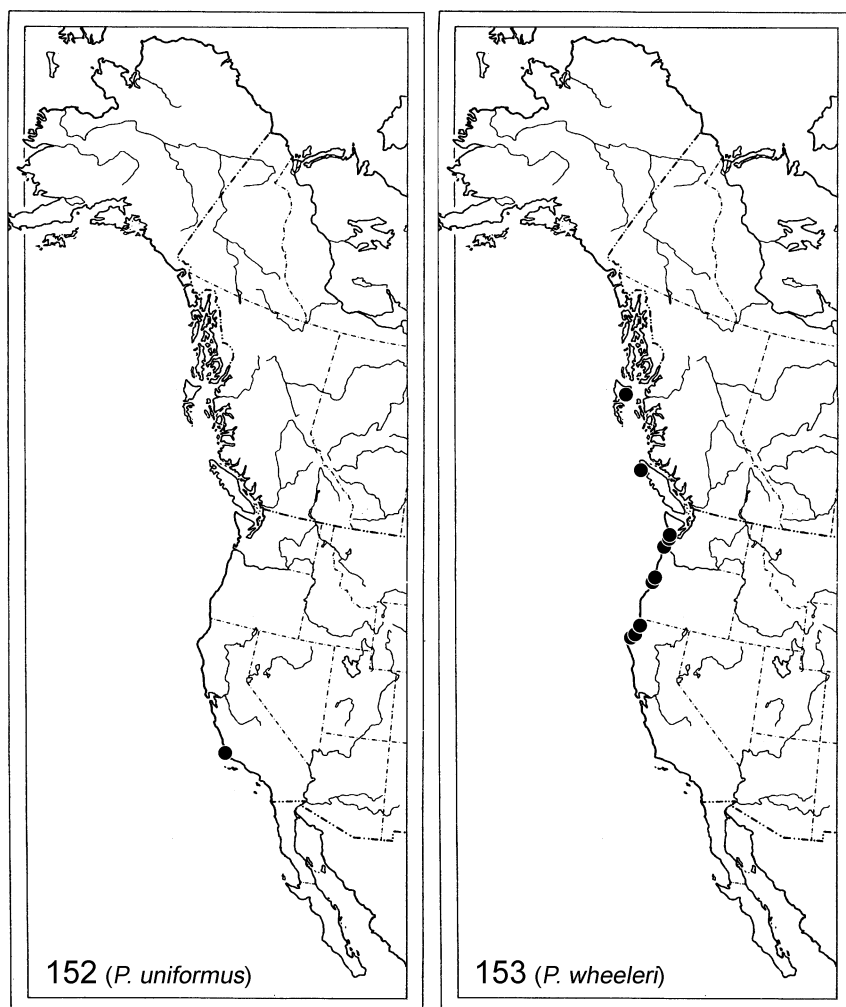
**Diagnosis.** This relatively small species is characterized by a subtriangular antennal postpedicel, longer lower male ommatrichia, 2 notopleural bristles, hyaline wing, and relatively dark legs. *Parathalassius wheeleri* is very similar to *P. aldrichi*, but males can be distinguished from this more southern species by the shape of the apex of the right cercus and dorsal lobe of the left surstylus, as well as the more basal position of the dentiform process of the phallus.

**Description. Male:** Body length 1.7–2.1 mm, wing length 1.7–1.9 mm. Dark brown ground colour covered mostly with dense greyish-white pruinosity. Setae of body and legs white. **Head** (Fig. 25): Eyes with ommatrichia of lower third distinctly longer and slightly flattened, forming dense reflective mat of whitish coloured hair. Face and clypeus concolourous with greyish-white frons and vertex. Face narrowest at middle, about 2.5X width of anterior ocellus. Gena and postgena with moderately long white setae, forming short beard flanking mouthparts. Antenna (Fig. 39) including arista-like stylus, entirely dark brown; postpedicel subtriangular, 1.5–1.6X longer than wide; arista-like stylus of medium length, about 1.5X length of postpedicel. Palpus with 7–8 setae on outer surface of apical half. **Thorax:** Acrostichal setulae primarily biserial; 6–7 dorsocentral bristles, 0 presutural intra-alar bristles, 1 presutural supra-alar (posthumeral) bristle, 2–3 postsutural supra-alar bristles, 2 notopleural bristles. Scutellum with 2–3 pairs of bristles. **Legs:** *Foreleg:* Dark grey, pale at knee and extreme apex of tibia, tarsus pale brown. Coxa with short pale setae on anterior surface. Femur with moderately long setae on posterior surface. Tibia and tarsus with setulae; tarsomeres 1–2 not dilated. *Midleg:* Dark grey, pale only at knee, tarsus greyish-brown. Femur with anterodorsal setae most prominent. Tibia with pair of apicoventral bristles. Tarsomeres 1–4 each with several dark spine-like apicoventral setae. *Hindleg:* Dark grey, femur dark brown posteriorly, pale at knee, tarsus pale brown to greyish-brown. Femur with anteroventral row of setae prominent. Tibia with anterodorsal and anteroventral rows of setae of moderate length, subequal or slightly longer than width of tibia. Tarsus subequal in length to tibia with short setae and setulae; tarsomere 1 shorter than combined length of tarsomeres 2–4; tarsomeres 1–4 lacking peg-like or thickened setae dorsally; tarsomere 2 longer than tarsomere 3; tarsomere 3 longer than tarsomere 4; tarsomere 5 subequal in length to tarsomere 3. **Wing** (Fig. 57): Hyaline with dark brown veins. Cell dm produced apically, dm-m crossvein nearly straight. Vein CuA+CuP short, straight. **Abdomen:** Tergites 2–4 with setae well-developed and relatively long. Sternite 5 without projecting pregenitalic process, with desclerotized region medially. Sternite 8 subquadrate with setae longer along posterolateral margins. *Hypopygium* (Figs 72, 93–94, 105–106, 122): Large. Left epandrial lamella with ventral portion elongate (about 2X longer than high); ventral epandrial process narrowly bifurcate, dorsal arm with apex expanded, blunt or hook-like, ventral arm thick and long with minute apicodorsal seta and minute distiventral seta, apex with expanded lamelliform concavity. Dorsal lobe of left surstylus with basiventral edge rounded and flap-like, apex narrow and digitiform, with long basidorsal seta (sometimes on bump-like protuberance or tubercle), short lateral seta and long apical seta, medial surface with stalk-like projection bearing lamelliform apical seta. Ventral lobe of left surstylus shallowly bilobate in lateral view, dorsal lobe short with apex subquadrate or broadly rounded, ventral lobe broadly rounded with short

marginal seta (sometimes on short tubercle) and complex upturned bifurcate projection arising medioventrally. Right epandrial lamella with ventral epandrial process not developed; basal portion of epandrial lamella narrowed and dorsally curved, with deep dorsal emargination bordering ventral margin of right cercus. Dorsal lobe of right surstylus with 3 lateral setae of similar size, apex narrowed with rounded to subtriangular tip bearing thick apically-frayed prensiseta on medial surface. Ventral lobe of right surstylus with lateral seta near basal third, distal 2/3 recurved, slender with narrow apically pointed lamelliform process proximal to lamelliform apex. Hypandrium large, reniform and bare. Left postgonite lobe ovoid basally, constricted near middle, distal portion subquadrate to subrectangular and flat without claw-like apicodorsal process, base of lobe with curved medial projection. Right postgonite lobe with broad lateral protuberance present or indistinct and continuous with apex, with rounded medial projection, apex bifurcate with well-developed digitiform ventral process and lamellate dorsal process. Phallus elongate with prominently projecting narrow curve and pointed dentiform process at 3/4 length. Ejaculatory apodeme subrectangular to subtriangular. Hypoproct projected dorsally as pair of slender pointed lobes, each lobe with 1–2 ventral seta proximal to apex, left lobe also with piliferous region ventrally. Cerci with anal setae well-developed and differentiated from surrounding hairs; right cercus much larger than left cercus with basal portion distended and rounded laterally, apex weakly dorsally deflected, pointed with narrow apicomедial projection, with 2 marginal setae; left cercus oblong in dorsal view, apex truncate, not dorsally deflected, with pair of thickened setae at apicolateral margin, outermost seta sometimes on short tubercle.



**FIGURE 151.** Known geographical distribution of *Parathalassius susanae* sp. nov.



**FIGURES 152–153.** Known geographical distributions of Nearctic *Parathalassius*. **152.** *Parathalassius uniformus* sp. nov. **153.** *Parathalassius wheeleri* sp. nov.

**Female:** Body length 1.9–2.5 mm, wing length 1.7–2.1 mm. Similar to male except as follows: **Head:** Eyes with ommatrichia of nearly uniform length, not distinctly longer on lower third. Face wider, at middle about 4.0X width of anterior ocellus. **Abdomen:** Tergite 5 broadly subtriangular to semicircular in dorsal view with posterior margin rounded (cf. Fig. 131). Terminalia distinctly narrower than base of segment 5 (cf. Figs 131–132); sternite 8 trough-like, with distinct basal bulge, not narrowed apically, apical half with longitudinal ridges, apex truncate (cf. Fig. 140); sternite 9 unsclerotized and indistinct; tergite 10 with hemitergites subtriangular and short, each with 2 acanthophorite spines; cercus short, pointed apically.

**Distribution and seasonal occurrence.** *Parathalassius wheeleri* is currently known to occur on sandy seashores from Haida Gwaii and Vancouver Island in British Columbia, south along the Washington, Oregon and northern California coast to the dunes of the Samoa Peninsula, Humboldt County (Fig. 153). Adults have been collected from mid May to mid August.

**Etymology.** This species is named in honour of fellow dipterist, Dr. Terry A. Wheeler, who collected a significant northern specimen of this species, plus other *Parathalassius*, from Haida Gwaii, British Columbia.

**Remarks.** COI barcode sequences (Fig. 154) and morphology confirm separation of *P. wheeleri* from the similar allopatric *P. aldrichi* (with minimally 8.2% genetic divergence). In addition, barcode sequence data obtained from specimens of *P. wheeleri* indicate a significant degree of genetic divergence (averaging 2.0%) between populations from Washington, Oregon and northern California, suggesting considerable isolation of populations of this species throughout its geographic range (British Columbia populations not sequenced).

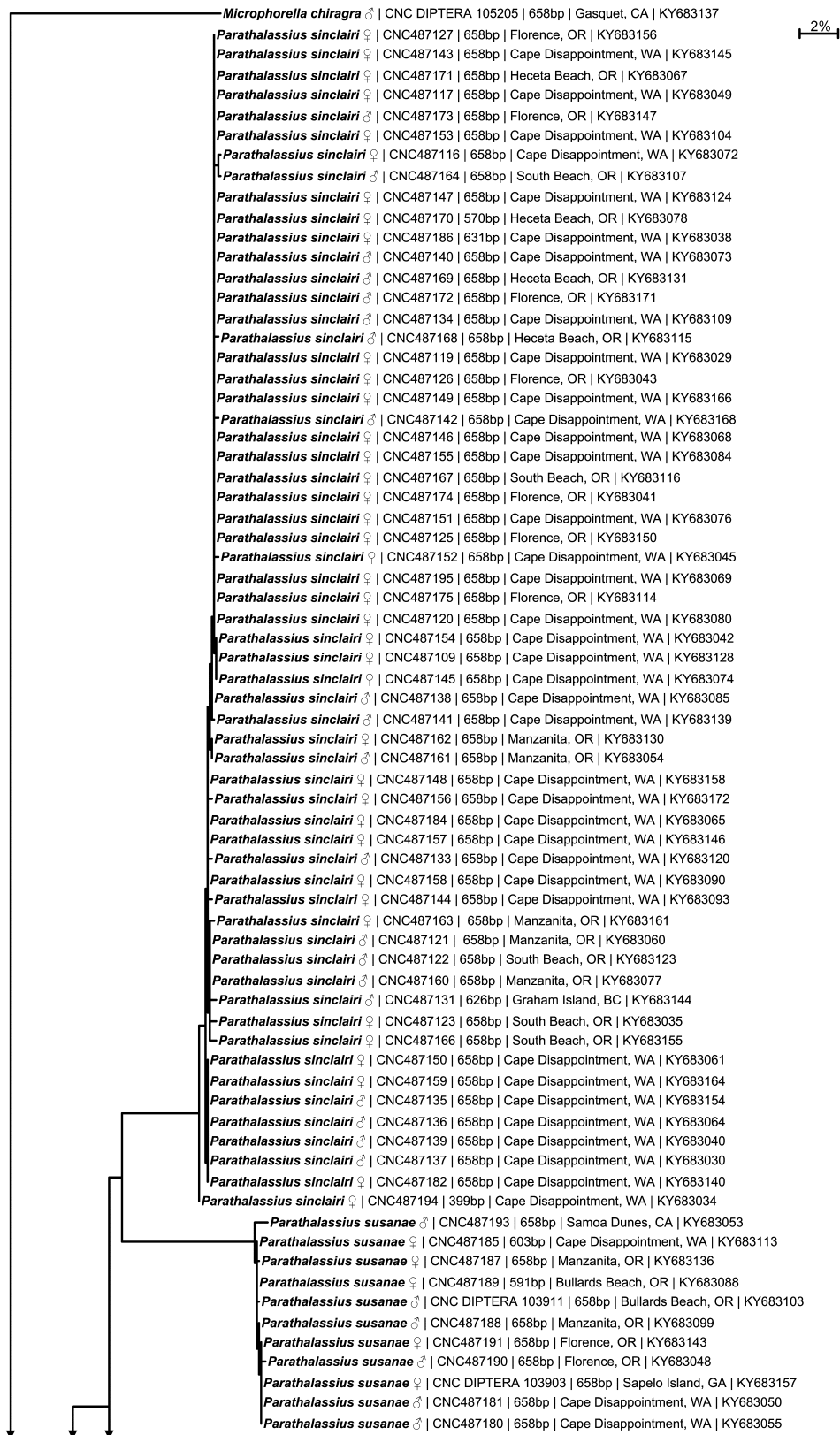
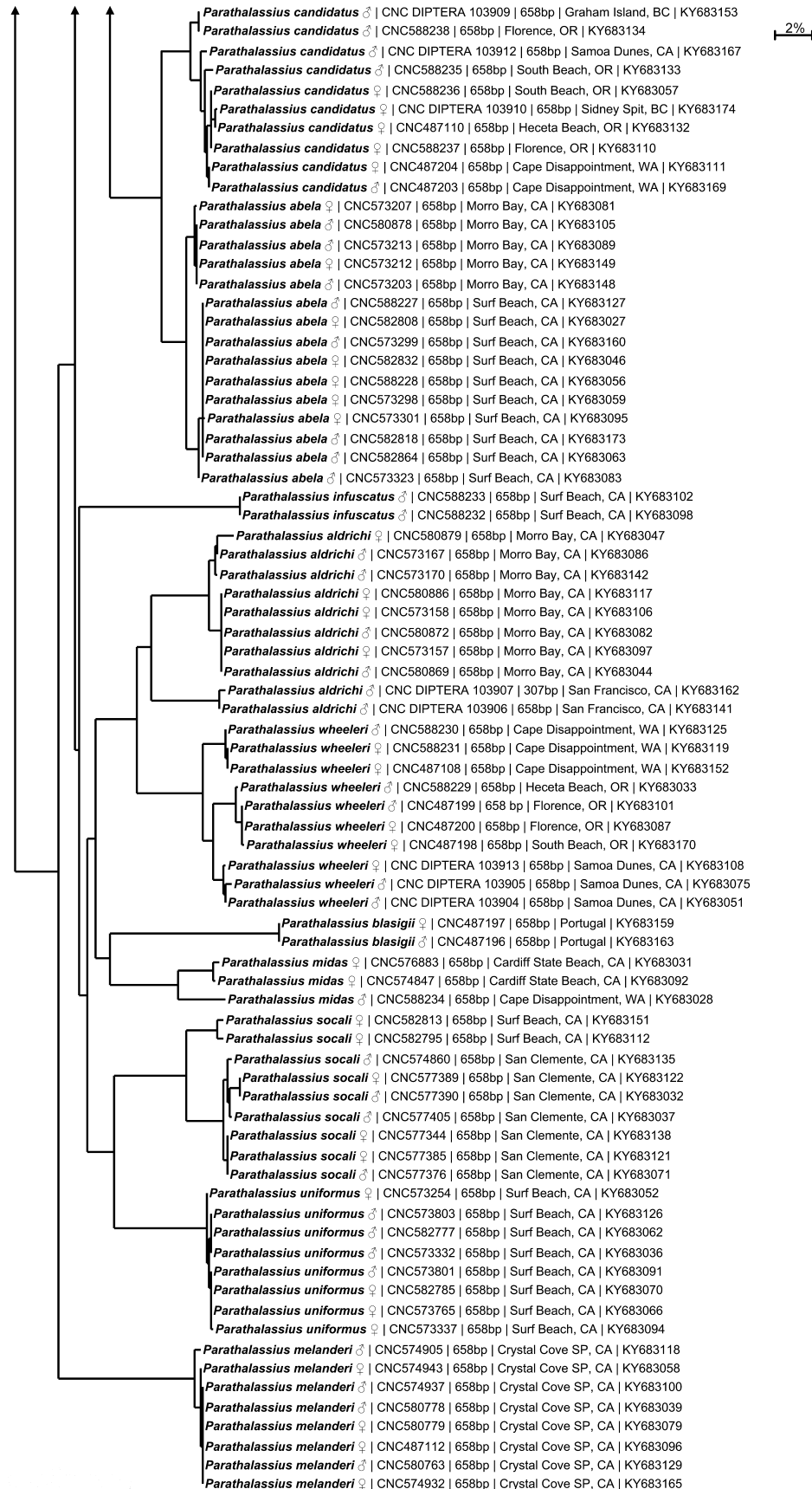


FIGURE 154. Neighbour-joining tree of 147 *Parathalassius* specimens and one outgroup specimen with COI sequences >300 base pairs (bp), including unique voucher number, sequence length, geographic locality, and GenBank number.





**FIGURE 154.** (continued). Neighbour-joining tree of 147 *Parathalassius* specimens and one outgroup specimen with COI sequences >300 base pairs (bp), including unique voucher number, sequence length, geographic locality, and GenBank number.

One male specimen of *P. wheeleri* collected at Lanphere-Christensen Dunes in Humboldt County, California by M.E. Buegler and E.I. Schlinger, was pinned with an aphid mounted below it, suggesting that the fly was taken with an aphid prey.

### Phylogenetic analysis of *Parathalassius* species relationships

The phylogenetic analysis was based on all world species of *Parathalassius*, including the new species described herein, as well as four outgroup taxa (Figs 155–156). The characters and character state codings used in the analysis are listed below and appear in the character matrix (see Table 1).

#### Head

1. *Male eye contiguity*. Holoptic (0); dichoptic (1).
2. *Eye*. Bare (0); with ommatrichia (1).
3. *Male ommatrichia*. Uniformly short (0); lower ommatrichia longer (1).
4. *Male face*. Subequal to width of female face (0); narrower than female face (1).
5. *Postpedicel shape*. Short-subtriangular (0); subtriangular (1); subquadrate (2); elongate-conical (3).
6. *Stylus*. Two articles (0); one article (1).
7. *Stylus length*. Shorter than postpedicel (0); longer than postpedicel (1).
8. *Male palpus length*. Long (0); short (1).
9. *Male palpus vestiture*. Palpus with scattered setae and setulae (0); palpus with dense brush of setae.

#### Head + Thorax

10. *Vestiture colour*. Dark (0); pale, with some darker setae (1); pale, without dark setae (2).
11. *Microtrichia*. Not covered with dense greyish pruinosity (0); covered with dense greyish pruinosity.

#### Thorax

12. *Prosternum*. Isolated from proepisternum (0); broadly fused to proepisternum forming precoxal bridge (1).
13. *Strong postpronotal setae*. Present (0); absent (1).
14. *Acrostichal setae*. Present (0); reduced to single pair (1).
15. *Acrostichal setae*. Quadriserial (0); biserial (1).
16. *Notopleural setae*. Two setae (0); three or four setae (1).
17. *Scutellar setae*. One pair (0); two or more pairs (1).

#### Legs

18. *Leg colour*. Primarily dark (0); tibiae and tarsi pale (1).
19. *Male hind tibia*. With short anterodorsal setae (0); with long anterodorsal setae (1).
20. *Male hind tarsomeres*. Dorsal setae not thickened (0); some dorsal setae thickened or peg-like (1).

#### Wing

21. *Male wing colour*. Entirely hyaline (0); infusate wing apex (1); broadly infusate (2).
22. *Shape of CuA*. Straight (0); recurved (1).
23. *CuA+CuP termination*. Long beyond cell cua (0); short to medium length beyond cell cua (1); absent beyond cell cua (2).
24. *Anal lobe*. Lobe slightly acute to obtuse, from alular incision to lobe apex (0); lobe partially developed, slightly convex beyond cell cua (1); lobe very weakly to barely developed (2).

#### Abdomen

25. *Male sternite 5*. Without ventrally projecting pregenitalic process (0); with short ventrally projecting pregenitalic process (1); with long ventrally projecting pregenitalic process (2).
26. *Male sternite 5 posterior edge*. Straight to weakly emarginate (0); deeply emarginate (1); medially desclerotized (2).
27. *Male tergite 8*. Rectangular (0); slender (1); greatly reduced (2).

28. *Apical female abdominal segments*. Retracted into segment 6 (0); retracted into segment 5 (1).  
29. *Female tergite 6*. With row of robust marginal setae (0); without robust marginal setae (1).

### Hypopygium

30. *Epandrial lamellae*. With basal connection (0); widely separated (1).  
31. *Left epandrial lamellae*. Without ventral process (0); with unarticulated ventral process (1) with articulated ventral process (2).  
32. *Left ventral epandrial process*. Unbranched, without dorsal arm (0); bifurcate, with dorsal and ventral arms (1).  
33. *Dorsal arm of left ventral epandrial process*. Nearly straight to slightly curved ventrally (0); strongly curved to hooked-shaped ventrally (1).  
34. *Ventral arm of left ventral epandrial process*. Apex simple (0); apex an expanded lamelliform concavity (1); apex flattened and serratulate (2).  
35. *Left ventral surstylar lobe*. Without complex upturned bifurcate projection (0); with complex upturned bifurcate projection (1).  
36. *Right epandrial lamella*. Not emarginate dorsally (0); shallowly emarginate dorsally (1); deeply emarginate dorsally (2).  
37. *Right ventral epandrial process*. Not developed (0); slightly to well developed (1).  
38. *Right dorsal surstylar lobe*. Without apically-flayed preniseta on medial surface (0); with apically-flayed preniseta on medial surface (1).  
39. *Hypandrium shape*. Small and subtriangular (0); small and reniform (1); large and reniform (2); very large and elongate-reniform (3).  
40. *Left postgonite lobe distal portion*. Subrectangular and simple apically (0); broad and bifurcate apically (1); broadly lamelliform usually with claw-like apex (2); broadened preapically with apex deflected medially and tapered (3).  
41. *Right postgonite lobe apex*. Simple or unifurcate (0); bifurcate (1); trifurcate (2).  
42. *Phallus*. Simple (0); bifurcate (1).  
43. *Shape of phallus*. Short and nearly straight (0); short and directed upwardly (1); elongate and broadly curved upwardly (2); elongate and J-shaped (3).  
44. *Inner dorsal surface of phallus*. Without flange (0); with flange (1).  
45. *Internal basal portion of phallus*. Without ventral spur-like projection (0); with small ventral spur-like projection (1); with large ventral spur-like projection (2).  
46. *Right side of phallus*. Without short process (0); with short process (1).  
47. *Apical portion of phallus*. Without pointed dentiform process (0); with pointed dentiform process (1).  
48. *Apex of phallus*. Simple (0); broadly membranous on right side (1); bifid (2).  
49. *Ejaculatory apodeme*. Small and subrectangular (0); large and subrectangular to subtriangular (1); large and disciform (2).  
50. *Hypoproct apex*. Straight to weakly projected dorsally (0); strongly projected dorsally (1).  
51. *Cercus apex*. Straight (0); projected dorsally (1).  
52. *Cercus medial margin*. Nearly flat (0); strongly produced dorsally (1).  
53. *Right cercus basal portion*. Not distended and rounded laterally (0); distended and rounded laterally (1).  
54. *Apex of cerci*. Right cercus not projected beyond left cercus (0); right cercus projected beyond left cercus (1).  
55. *Left cercus apex*. Setulose on dorsal surface (0); glabrous on dorsal surface (1).  
56. *Right cercus apex*. Setulose on dorsal surface (0); glabrous on dorsal surface (1).  
57. *Right cercus apical shape*. Not narrowly pointed (0); narrowly pointed (1).

### Female terminalia

58. *Tergite 8*. Not divided medially (0); completely divided medially (1).  
59. *Sternite 8*. Smooth (0); with apical longitudinal ridges (1); with apical rugosity (2).  
60. *Sternite 8 apex*. Broadly truncate or rounded (0); emarginate (1); distinctly bifurcate (2).  
61. *Sternite 8 base*. Without bulge (0); with bulge (1).  
62. *Tergite 10*. With acanthophorite spines (0); with acanthophorite setae (1).  
63. *Acanthophorite spine or seta number*. Three or more per side (0); two per side (1).

64. *Cercus*. Narrow and pointed (0); broadly rounded (1).  
 65. *Cercus* sclerotization. Heavily sclerotized (0); lightly sclerotized (1).

**TABLE 1.** Character state matrix for *Parathalassius* cladistic analysis (characters 1–65). Outgroup taxa are listed at the beginning of the table. Missing states are indicated by a “?”, inapplicable states are indicated by a “-” and polymorphic states are indicated by a “\*”.

	1	1111111112	2222222223	3333333334	4444444445	5555555556	66666
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12345
<i>Schistostoma armipes</i>	00-0101000	0000111010	0100000000	0---000001	0000000000	0000000100	00000
<i>Plesiothalassius capensis</i>	1100011102	1010000100	0011001000	10-0010010	1100200000	0010000010	01111
<i>Microphorella praecox</i>	1100310102	1111100000	0122212101	2100121021	0030101011	0010000002	01111
<i>Microphorella chiragra</i>	1100111100	0110100000	0112012101	20-0000030	0010110021	1100000100	00000
<i>Parathalassius abela</i>	1111111102	1110011011	0001212111	2111120132	1011200011	1011111110	00100
<i>Parathalassius aldrichi</i>	1111111102	1110101000	0011022111	21*1120120	1030201010	0010010110	10100
<i>Parathalassius blasigii</i>	1111111102	1110101110	0011212111	2101120123	2010200011	1001101110	00100
<i>Parathalassius candidatus</i>	1111111102	1110011011	0001212111	2111120132	1011200011	1011111110	00100
<i>Parathalassius dilatus</i>	111111?112	1110101000	1011002??1	2111121130	1010200011	0010000???	?????
<i>Parathalassius infuscatus</i>	1101111102	1110101000	2012202111	20-1121122	1110200010	0010110110	00000
<i>Parathalassius maritimus</i>	1101011101	1110101110	0011212111	2112111123	2020210000	0001001111	00100
<i>Parathalassius melanderi</i>	1111011112	1110101000	1011002111	2111121130	1010200011	0010000101	00100
<i>Parathalassius midas</i>	1101211102	1110101100	1011212111	2112110013	2020210200	0001000102	00100
<i>Parathalassius sinclairi</i>	1111311102	1110011001	0011212111	2111120132	1011200011	1111111120	00100
<i>Parathalassius socali</i>	1111011102	1110101010	0011102111	2101121120	1010200110	0011000101	10100
<i>Parathalassius susanae</i>	1111311102	1110011010	0011212111	2111120132	1010200011	1011011110	00100
<i>Parathalassius ulrichi</i>	1111111101	1100111011	0011212111	2111120132	1011200011	1111111110	00100
<i>Parathalassius uniformus</i>	1101111102	1110101000	0011102111	2101120122	1010200110	0010000111	10100
<i>Parathalassius wheeleri</i>	1111111102	1110101000	0011022111	21*1120120	1030201010	0011011110	10100

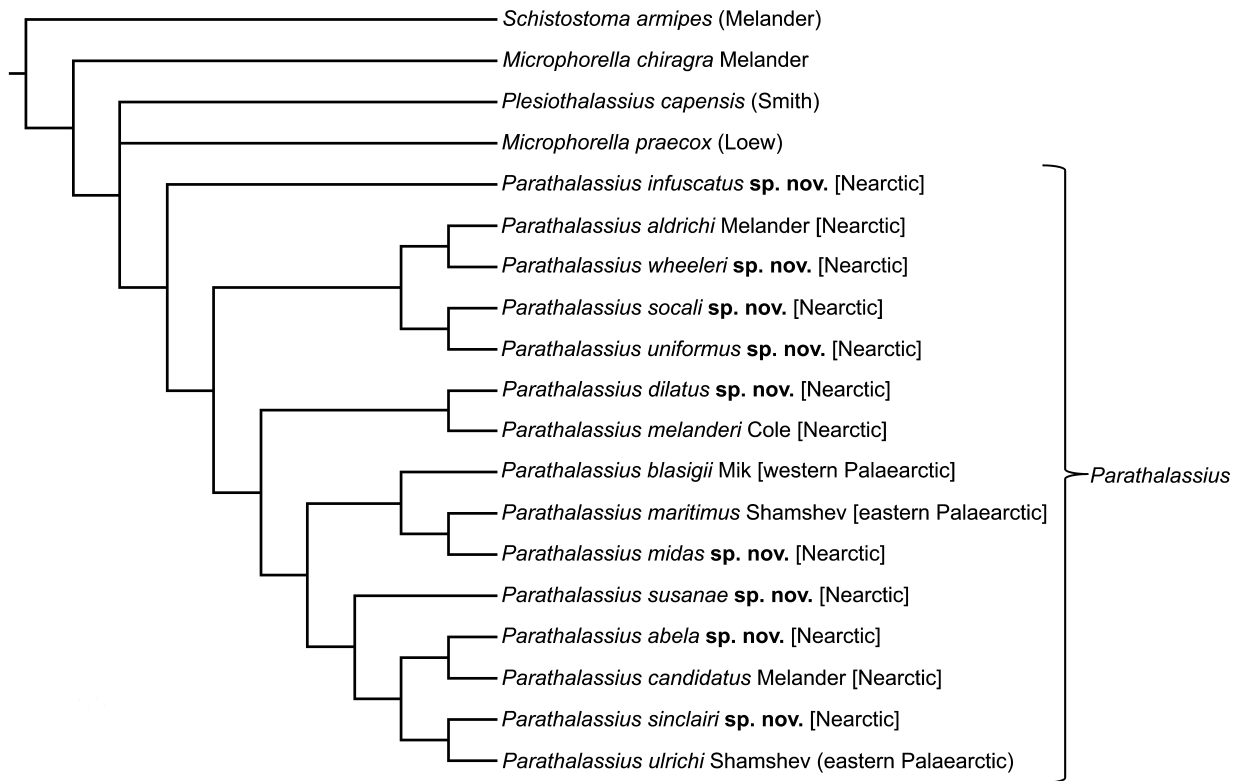
The parsimony analysis resulted in two most parsimonious trees (length = 165, CI = 0.54, RI = 0.61, RC = 0.33). These two trees varied only in the placement of the outgroup taxa *Plesiothalassius capensis* and *Microphorella praecox*, as depicted in the strict consensus tree (Fig. 155). One of the two cladograms was selected to show the character state distributions (Fig. 156).

The analysis confirms the monophyly of our revised concept of *Parathalassius* on the basis of a suite of seven character states. Within *Parathalassius* five major groupings of species are resolved, namely *P. infuscatus*, *P. aldrichi* + *P. wheeleri* + *P. socali* + *P. uniformus*, *P. dilatus* + *P. melanderi*, *P. blasigii* + *P. maritimus* + *P. midas*, and *P. susanae* + *P. abela* + *P. candidatus* + *P. sinclairi* + *P. ulrichi*.

*Parathalassius infuscatus* is a very distinctive species that appears to be the sister group to the rest of the genus. Although somewhat similar morphologically, *P. aldrichi*, *P. wheeleri*, *P. socali* and *P. uniformus* are only supported as a group by the uniquely derived bulging base of female sternite 8 (61.1). *Parathalassius dilatus* and *P. melanderi* are a distinctive sister species pair that share a male palpus with a dense brush of setae (9.1), an infusate male wing apex (21.1), and presence of a right ventral epandrial process (37.1). *Parathalassius blasigii*, *P. maritimus* and *P. midas* are united as a group on the basis of five synapomorphies, including the uniquely derived preapically broadened left postgonite lobe with a deflected distal portion (40.3) and a right postgonite lobe with a trifurcate apex (41.2).

*Parathalassius susanae*, *P. abela*, *P. candidatus*, *P. sinclairi* and *P. ulrichi* form another group of species that share four derived states, including 3–4 notopleural setae (16.1), a left postgonite lobe with a broadly lamelliform distal portion (40.2), and a glabrous right cercus apex (56.1). This group is the sister group to *P. blasigii* + *P.*

*maritimus* + *P. midas*, and both groups together are the sister group to *P. dilatatus* + *P. melanderi*. This large clade of 10 species appears to be the sister group to the *P. aldrichi* + *P. wheeleri* + *P. sociali* + *P. uniformus* group of species.



**FIGURE 155.** Strict consensus tree of the two most parsimonious cladograms for the world species of *Parathalassius* and outgroups, produced by analysis of data in Table 1 (see text for explanation).

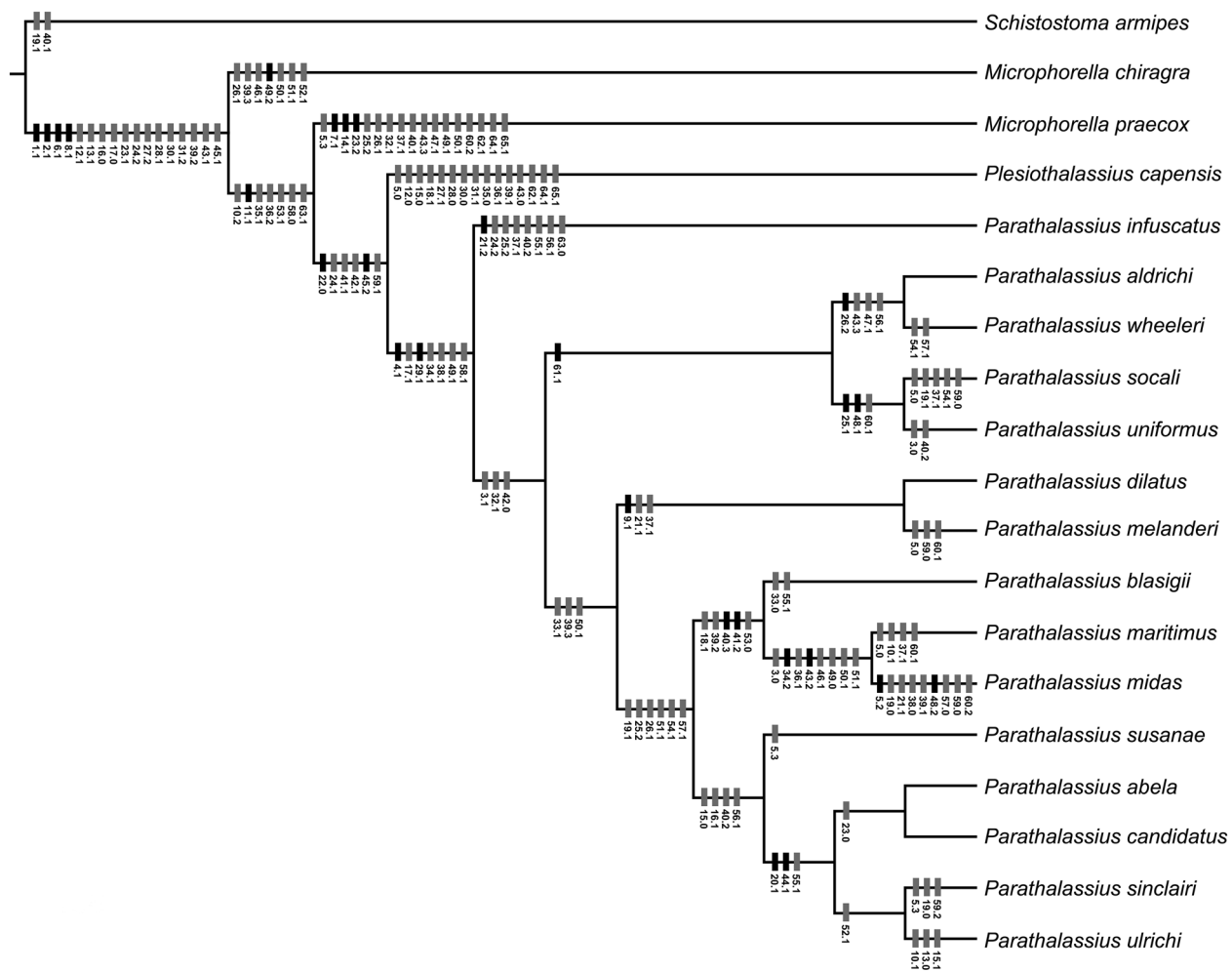
In addition, within all these major groups, *P. aldrichi* + *P. wheeleri*, *P. sociali* + *P. uniformus*, *P. maritimus* + *P. midas*, *P. abela* + *P. candidatus*, and *P. sinclairi* + *P. ulrichi* are all obvious sister species pairs that are relatively similar morphologically.

## Discussion

As indicated by the current phylogenetic analysis, *Parathalassius* appears to be a monophyletic Holarctic genus within the subfamily Parathalassiinae that occupies a distinct habitat (i.e., sandy coastal beaches). The subfamily presently comprises eight genera and preliminary investigations (Brooks & Cumming 2010, 2011, 2016) suggest that *Parathalassius* is the possible sister group to a large lineage that includes *Chimerothalassius* Shamshev & Grootaert, *Eothalassius* Shamshev & Grootaert, *Microphorella*, *Neothalassius* Brooks & Cumming and *Thalassophorus* Saigusa. Precise relationships between these genera are confounded by the probable paraphyly of at least *Microphorella* and must await a forthcoming detailed phylogenetic analysis of the entire subfamily at the species group level.

Prior to this study, *Parathalassius* contained three Nearctic species and three Palaearctic species. The genus now includes 12 Nearctic species, in addition to the three previously known Palaearctic species. Detailed study of sandy coastal habitats in the Palaearctic Region will likely reveal additional hidden diversity in that region. For example, our examination of the morphological diversity exhibited by the current concept of the western Palaearctic species *P. blasigii*, suggests that it probably includes more than one species. Further surveys of coastal areas throughout the eastern Palaearctic might also substantially increase species diversity within the genus.

The few sister lineage connections in *Parathalassius* between the Palaearctic and Nearctic Regions (Fig. 155) are primarily Asio-Nearctic disjunct distributions (i.e., *P. maritimus* + *P. midas* and *P. ulrichi* + *P. sinclairi*) that are



**FIGURE 156.** One of the two most parsimonious cladograms for the world species of *Parathalassius* and outgroups, produced by analysis of data in Table 1 (see text for explanation). Character distribution for uniquely derived states shown by black hash marks and by grey hash marks for homoplasious states (including subsequent transformations).

already well documented in the Empidoidea (Sinclair *et al.* 2011; Saigusa 2012). An Asio-Nearctic disjunct distribution is also known within the parathalassiine genus *Thalassophorus* (Brooks & Cumming 2011). These distributions are generally considered to be the result of early to mid-tertiary vicariant events (Sinclair & Saigusa 2002; Cumming *et al.* 2014). Younger vicariant events appear evident within *Parathalassius* in at least the two allopatric sister species pairs found along the Nearctic Pacific coast (i.e., *P. aldrichi* + *P. wheeleri* and *P. abela* + *P. candidatus*). These two sister species pairs (Fig. 155) apparently do not overlap geographically and show only a moderate amount of genetic divergence (i.e., minimally 8.2% and 3.6%, respectively) (Fig. 154) suggesting more recent separations.

DNA barcode sequence data (Fig. 154) have allowed evaluation of species status between similar allopatric populations, in addition to assisting in confirmation of male and female associations for most species. Certain widespread species (e.g., *P. sinclairi*, *P. susanae*) show very little genetic divergence over the geographic range sequenced, suggesting considerable gene exchange between populations, presumably as a result of good dispersal ability and/or human-assisted movement. Other species (e.g., *P. aldrichi*, *P. wheeleri*, *P. sociali*) however, exhibit substantially more intra-specific genetic divergence of populations on different beaches, suggesting considerable isolation of these populations and possible constraints on their dispersal abilities.

Future studies of this interesting genus should focus on habitat partitioning, as several different species often occupy a single beach at the same time of year (e.g., on Benson Beach, Washington and on Surf Beach, California). Some species appear to inhabit different parts of the beach (e.g., fore dune versus back dune), whereas some are

frequently seen on open sand with others mostly collected on or near beach vegetation. Seasonality may also be involved in maintaining more than one species on a single beach. Some species, such as *P. aldrichi*, *P. candidatus* and *P. melanderi*, are undoubtedly multivoltine, but at least two species, *P. infuscatus* and *P. dilatus*, appear to be vernal species that are only active in late winter and spring. However, late winter and early spring collecting of *Parathalassius* flies has rarely been undertaken. Finally a few species (i.e., *P. dilatus*, *P. infuscatus*, *P. uniformus*) appear restricted to one or two neighbouring beaches, suggesting that these beaches are ecologically distinctive in some way. These latter *Parathalassius* species may turn out to be biological indicators of optimal beach health that are worthy of additional ecological study.

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