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Cover image: A specimen of the mud shrimp *Upogebia pugettensis* from Oregon, USA, with the branchial chamber opened to show the presence of the parasitic isopod *Orthione griffenis*. First reported in 2004, this isopod has been documented parasitizing populations of *Upogebia* spp. from Vancouver to southern California. Because of its sudden appearance in a well studied fauna and rapid spread throughout its hosts' ranges, it has been considered an introduced species with a suspected Asian origin. It can cause dramatic reductions in host fecundity of up to 100% in some host populations and may threaten the long term survival of the host species in at least parts of their ranges. Comparison of eastern Pacific parasites and Chinese specimens from another mud shrimp host show conspecificity on both sides of the Pacific. The Chinese specimens date back to the 1950s and predate any records from the eastern Pacific and support that this species was introduced from Asia, presumably via ballast water release. Photo: J. D. Williams. Submitted by Christopher B. Boyko, Jason D. Williams, and Jianmei An, "The cryptogenic parasitic isopod *Orthione griffenis* Markham, 2004 from the eastern and western Pacific."

The cryptogenic parasitic isopod *Orthione griffenis* Markham, 2004 from the eastern and western Pacific

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Synopsis The parasitic isopod *Orthione griffenis* Markham, 2004 was originally described from thalassinid mud shrimp hosts collected in Oregon. Subsequently, *O. griffenis* has been cited as a non-indigenous species in estuaries of the Pacific Northwest of North America; however, no taxonomic work has provided evidence that specimens from the western coast of the United States and other localities are conspecific. We report the first record of *O. griffenis* from Chinese waters based on collections made in the 1950s, which pre-date any records of the species from the United States by at least 20 years. Females of the Chinese specimens match the original description except in the number of articles on antennae 2 (six and five articles in the Chinese material and holotype, respectively). However, newly examined material from the United States showed females are variable in this character, exhibiting 5–6 articles on antennae 2. Although males of *O. griffenis* from Oregon were originally described as having second antennae with five articles, reexamination of the allotype showed that antennae 2 were damaged and missing terminal articles. Thus, the number of articles in the second antennae of males is six, as found in both the Chinese and new samples from the United States. Scanning electron microscopy (SEM) of males from USA and China revealed curled setae on the distolateral margins of the uropods, which were not reported in the original description. In China the species is found on *Austinoagebia wuhsienweni* (Yu) from Shandong province, whereas along the western coast of North America the species extends from British Columbia to California on *Upogebia pugettensis* (Dana) and *U. macginitieorum* Williams (the latter species replacing *U. pugettensis* south of Pt. Conception, California). *Orthione griffenis* has also been reported from Japan on *Upogebia issaeffi* (Balss) and *Austinoagebia narutensis* (Sakai). In Coos Bay, Oregon, the prevalence of the species was ~65% in the mature *U. pugettensis*. The species was presumably introduced as larvae released in ballast water from ships originating in Asia. The epicaridium larvae of *O. griffenis* were examined with SEM, and aspects of the life history of the species are reviewed.

Introduction

As part of a review paper on the parasites of thalassinidean shrimp from China collected in the 1950s and 1960s (An et al. in press), we discovered specimens representing the genus *Orthione* parasitizing *Austinoagebia wuhsienweni* (Yu). Examination of these specimens showed that they are morphologically indistinguishable from *Orthione griffenis* Markham, 2004, originally described from the blue mud shrimp *Upogebia pugettensis* (Dana) collected in Yaquina Bay, Oregon. The type specimens of *O. griffenis* were collected during a study on the particle removal rates by *U. pugettensis* and its commensal clam *Cryptomya californica* (Conrad, 1837) (DeWitt et al. 2004; Griffen et al. 2004).

Orthione griffenis is now considered an introduced species from Asia, receiving considerable popular press since its discovery on the western coast of North America in Oregon and Washington (Chapman et al. 2005; Wagner 2006; McGinnis 2008). The ecology and impacts of *O. griffenis* on its host *Upogebia pugettensis* have been completed on populations from Yaquina Bay, Oregon (Smith et al. 2008). In spite of its listing as a non-indigenous aquatic species (ICES 2006; USGS 2008) and references to it as such in the primary literature (Ferraro and Cole 2007; Pernet et al. 2008), the present paper is the first taxonomic work to provide evidence that specimens from Asia and North America represent the same species.

From the symposium “The Biology of the Parasitic Crustacea” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2009, at Boston, Massachusetts.

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Markham (2001) reviewed what was known of the host relationships and biogeography of bopyrid parasites of thalassinideans and since that time four additional species have been described (Markham 2004; Boyko and Williams 2009; An et al. in press). In addition, a number of ecological studies investigating the effects of parasitic isopods on thalassinideans have been published (Tucker 1930; Reverberi 1942; Leija-Tristán and Salazar-Vallejo 1991; Munoz and George-Nascimento 1999; Munoz 2001; Astete-Espinoza and Caceres 2000; Saito and Kinoshita 2004; Pernet 2008; Smith et al. 2008). Thalassinidean shrimp are important ecosystem engineers (Berkenbusch and Rowden 2003, 2007; Itani 2004; Berkenbusch et al. 2007) reworking sediment and providing a home for a variety of commensals and parasites. In addition, thalassinidean shrimp can have detrimental effects on shellfish industries (Feldman et al. 2000; Dumbauld et al. 2004) and researchers have investigated the use of these parasites as potential biological controls (Lafferty and Kuris 1996; Chapman et al. 2005; Dumbauld et al. 2005). Some researchers have suggested that declines in populations of *Upogebia pugettensis* in estuaries of the American Pacific Northwest may be due to the effects of *O. griffenis* (Ferraro and Cole 2007; Smith et al. 2008). Thus, knowledge of the taxonomy and natural history of bopyrid parasites of these hosts is critical to an understanding of their potential ecological and economic impacts.

The purpose of this article is to redescribe *O. griffenis* based on Chinese material and provide a comparative analysis of the specimens from China with the types from Oregon and newly examined specimens from additional localities along the western coast of North America. In addition, the morphology of the males and of epicaridium larvae are described with the aid of scanning electron microscopy (SEM). Present knowledge on the distribution of the species on the eastern and western sides of the Pacific are discussed and hypotheses on its spread are evaluated.

Material and methods

Materials for this study came from the National Comprehensive Oceanographic Survey (1958–1960) and a series of investigations of marine fauna and flora along the China coast by the Institute of Oceanology, Chinese Academy of Sciences (IOCAS). All Chinese material examined was deposited in the IOCAS, Qingdao, China. The Chinese specimens were viewed and drawn under a Zeiss Stemi

SVIIApo. Male specimens of *O. griffenis* from China were prepared for SEM by fixing in 2.5% glutaraldehyde in 0.2 M Millonig's phosphate buffer at pH 7.4 for 1.5 h and postfixed in 1% osmium tetroxide in 0.2 M Millonig's buffer for 1 h. The specimens were then dehydrated through an ascending ethanol series, followed by critical point drying. After sputter coating with colloidal gold, the specimens were examined with a KYKY2800B scanning electron microscope. Males and epicaridium larvae from Oregon were fixed in 70% ethanol and prepared for SEM as indicated above (epicaridium larvae were held in Microporous Specimen Capsules, Ted Pella, Inc.) followed by examination with a Hitachi S-2460N SEM. Type and voucher specimens were borrowed from and deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), Oregon Institute of Marine Biology synoptic collection, Charleston, Oregon, USA (OIMB), and Santa Barbara Museum of Natural History, Santa Barbara, California, USA (SBMNH).

Results

Order Isopoda Latreille, 1817

Suborder Epicaridea Latreille, 1831

Family Bopyridae Rafinesque-Schmaltz, 1815

Subfamily Pseudioninae Codreanu, 1967

Genus *Orthione* Markham, 1988

Orthione griffenis Markham, 2004

(Figs. 1–8)

Orthione griffenis Markham, 2004: 186–191; Figs. 1–3 [Yaquina Bay, Oregon, USA; infesting *Upogebia pugettensis* (Dana)].

Pseudioninae sp. 1 Itani, 2004: Table 3 (Shikoku, Japan; infesting *Upogebia issaeffi* (Balss) and *Austinogebina narutensis* (Sakai); Note: Pseudioninae sp. 1 actually represents two species, one of which is morphologically indistinguishable from *Orthione griffenis* and found on the aforementioned hosts, the other is an unidentified pseudionine species found on *Upogebia yokoyai* Makarov; Itani, pers. comm.)

Ione sp.: Lamb and Hanby, 2005: 280, Fig. AR19.A [Stanley Park, Vancouver Harbour, British Columbia, Canada; infesting *U. pugettensis*].

?*Ione* sp.: Lamb and Hanby, 2005: 280, Fig. AR19.B [Stanley Park, Vancouver Harbour, British Columbia, Canada; infesting *Acantholithodes hispidus* (Stimpson)].

Orthione griffensis[sic]: Brusca et al. 2007: 512; Fig. 252B [list].

Material examined from China

Infesting *Austinoagebia wuhsienweni* (Yu). Baohai, Stn.1068, 120°30'E, 38°20' N, 31 m, October 25, 1959, CIET106801, ♂. Baohai, Stn.1068, 120°30'E, 38°20'N, 31 m, October 25, 1959, CIET106802, ♂. Sifang, Qingdao, Shandong province, 115°42'E, 33°45'N, April 7, 1951, CIET510401, ♀, CIET510402, ♂. Baohai, Stn.1010, 121°45'E, 40°10'N, 20 m, November 1, 1958, Guangyu Lin, coll., CIET101001, ♀, CIET101002, ♂. The Yellow Sea, stn2020, 122°15'E, 37°45' N, 21m, July 14, 1959. Chenmu, coll., CIET202001, 1 ♀ (immature), CIET202002, 1 ♂.

Description of a reference female from China (CIET106801)

Length 9.64 mm, maximal width across pereomere 4, 6.90 mm, head length 1.53 mm, head width 1.81 mm, pereon length 4.84 mm, pleon length 3.06 mm. All body segments distinct, almost symmetrical (Fig. 1A).

Head ovate, frontal lamina as wide as head, posterior edge of head round, without eyes. Antennae (Fig. 1C) extending beyond frontal lamina and observable from dorsal view, antenna 1 with three articles, antenna 2 with six articles, terminal segment setose. Maxilliped (Fig. 1D) subrectangular, lacking palp, with short and blunt plectron. Barbula (Fig. 1E) with one pair of falcate pointed lateral projections, median region flat.

Pereon broadest across third and fourth pereomeres, first pereomere shortest. Dorsolateral bosses and coxal plates on first four pereomeres prominent, tergal projections on first pereomere smaller than those on second to fourth pereomeres. Fifth pereomere lacking dorsolateral boss, with tergal projection distinct. Tergal projection of fifth pereomere and margin of sixth pereomere tuberculate on left side. Oostegites almost enclosing brood pouch, first oostegite (Fig. 1F and G) subsquare, its two articles of about same size, internal ridge is produced into a broad triangular flap reaching far posteriorly, without ornamentation, no posterolateral point. Pereopods (Fig. 1H and I) with all articles distinct, larger posteriorly; basis with rounded carinae; dactyli short. First pereopod with indistinct basis carina, ischium short with tuft setae terminally; propodus deeply set behind basis. Seventh pereopod with distinct carina, ischium longer without setae; propodus separated from basis.

Pleon of five pleomeres plus pleotelson, all pleomeres concave posteriorly. Pleomeres 1–5 bearing lateral plates and biramous pleopods, endopodites

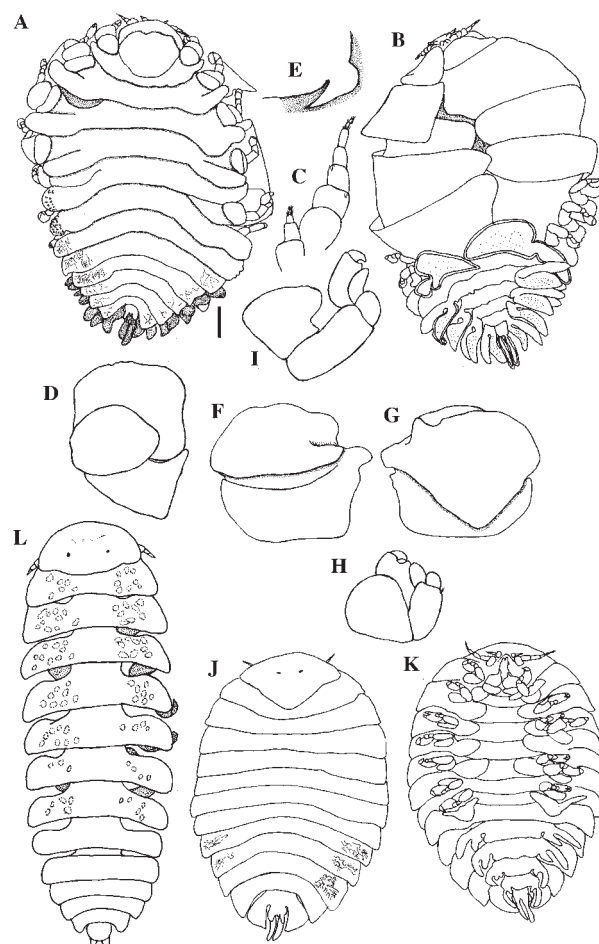


Fig. 1 *Orthione griffenis* from China. (A–I) female (CIET106801); (J and K) immature female (CIET202001); (L) male (CIET106802). (A) dorsal view of a female; (B) ventral view of a female; (C) right antennae; (D) external view of right maxilliped; (E) left projection of barbula; (F) external view of first right oostegite; (G) internal view of first right oostegite; (H) first right pereopod; (I) seventh right pereopod; (J) dorsal view of an immature female; (K) ventral view of an immature female; (L) dorsal view of a male. Scale bars: A and B = 1 mm; C = 0.13 mm; D and E = 0.37 mm; F and G = 0.64 mm; H and I = 0.17 mm; J and K = 0.43 mm; L = 1 mm.

of first pleopod much larger than others and crossing each other in middle of pleon. Pleotelson with short rounded lateral plates and the slender uniramous uropods, short rounded middle anal cone between two rami of lateral plates.

Description of an Immature female from China (CIET202001)

Body much narrower and flatter, segments distinctly separated, with triangular head and small eyes, without frontal lamina, dorsolateral boss, and tergal projections (Fig. 1J and K). Oostegites very rudimentary. Pleon of five pleomeres plus pleotelson,

but last two pleomeres less distinctly separated. Pleomeres 1–5 with five pairs of biramous pleopods and the pleotelson is the same as in mature females.

Description of a reference male from China (CIET106802)

All body regions and segments distinct, length 4.57 mm, head width 1.05 mm, head length 0.59 mm, pereon length 2.73 mm, maximal width across pereomere 5, 1.68 mm, pleon length 1.91 mm, pleomere 1 width 1.45 mm. All body regions and segments distinctly separated (Figs. 1L and 2A).

Head almost semicircular, narrower than first pereomere. Small dark eyes on middle region of head (Fig. 1L). Pigmentation scattered on anterior region of head. Antenna 1 with three articles, setose terminally; antenna 2 with six articles

extending beyond the margin of the head, distal four segments setose terminally (Fig. 2B).

Pereon with dark yellow spots scattered toward sides of pereomeres; pereomeres deeply separated by anterolateral notches except for first pereomere (Fig. 1L). Fourth to seventh pereomeres almost equally wide. All pereomeres distinctly separated, without midventral projections. All pereopods similar in size except carpi longer posteriorly and dactyli of first three pereopods larger than others; dactyli with groove parallel to long axis on surface; propodi bearing a line of scales with concentric ridges on surface; carpi and meri setose (Fig. 2C and D).

Pleon with six pleomeres, the first five pleopods tuberculiform, sessile and rectangular, progressively smaller posteriorly, without midventral projections (Fig. 2E). Last pleomere with pair of cylindrical uniramous uropods, with curly distal setae (Fig. 2F and G).

Material examined from the western coast of North America

Infesting *Upogebia pugettensis* (Dana) (carapace length = 23–38 mm). Idaho Inlet, Yaquina Bay, OR, USA, 44° 35.4'N, 124°01.5'W, intertidal, unspecified date, 2000, Griffen, B. D., coll., USNM1008784, ♀ holotype, USNM1008785, ♂ allotype; Yaquina Bay, Idaho Mudflat, Oregon, USA, intertidal, July 2005, Chapman, J. W., coll., OIMB synoptic collection, 2♀, 2♂; Coos Bay, Charleston, Oregon, USA (most likely collected on Metcalf Marsh below Charleston Bridge), intertidal, May 18, 2000, Emlet, R., coll., USNM1123917, 2♀, 2♂ (one male mounted for SEM); Coos Bay, Metcalf Marsh, Charleston, Oregon, USA, 43° 20' 00.44" N, 124° 19' 33.7" W, intertidal, June 26, 2008, Williams, J. D., coll., USNM1123918, 71♀, 1♂; same collection data as previous, 31 July 2008, USNM1123919–1123924, 5♀, 1♂ and personal collection, 2♀, 1♂; Coos Bay, Pigeon Point Mudflat, Charleston, Oregon, USA, 43° 22' 08.56" N, 124° 17' 47.83" W, intertidal, 22 July 2008, Williams, J. D., coll., personal collection, 1♀, 1♂; Ross Islet, Barkley Sound, Vancouver Island, British Columbia, 48° 52.395' N, 125° 09.709' W, intertidal, July 26, 2006, G. Jensen, USNM1123925, 1♀, 1♂; Morro Bay, California, USA (35° 09' N, 120° 00' W, intertidal, January 21, 2004, Heerhartz, S., SBMNH347784, 347790, 348265, 348267, 348278, 348279, 348285, 9♀, 5♂; Willapa Bay, Goose Point, Washington, USA (46° 38' 10" N, 123° 57' 25" W), intertidal, January 19, 2003, Dumbauld, B., Ashley, E., Brehem, M. and Kuris, A., SBMNH348496, 348501, 348503, 348509, 4♀, 4♂.

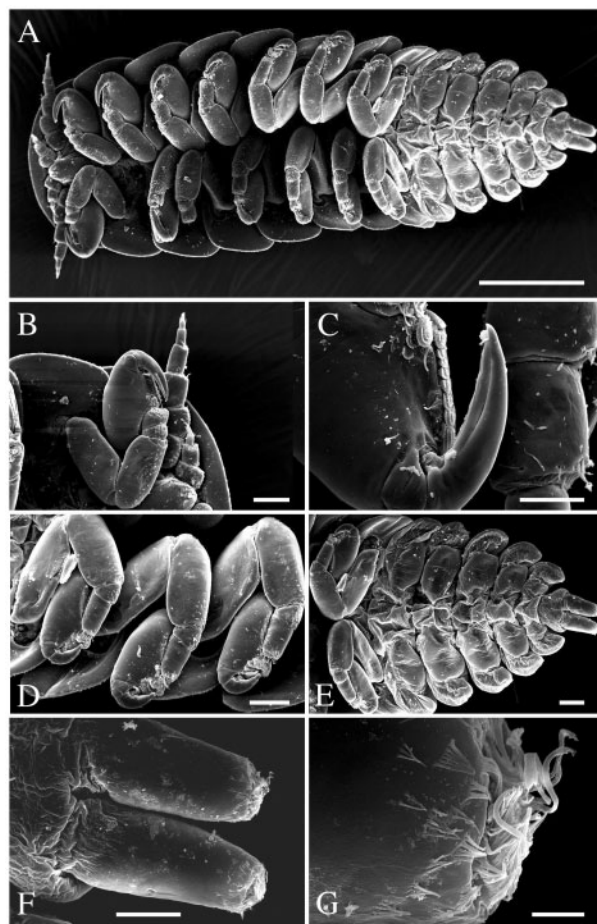


Fig. 2 *Orthione griffenis* from China. (A–G) male (CIET106802), SEM micrographs. (A) ventral view of a male; (B) left antennae and first pereopod; (C) first left pereopod, showing propodi bearing a line of scales; (D) left pereopods (fifth–seventh); (E) ventral view of pleon, showing first five pleopods; (F) last pleomere, showing a pair of uniramous uropods; (G) extremity of uropods, showing curly distal setae. Scale bars: A = 1 mm; B, D and E = 100 µm; C and F = 50 µm; G = 10 µm.

Upogebia macginitieorum Williams. Santa Barbara County, Carpinteria Salt Marsh, California, USA (34° 23' 50" N, 119° 32' 15" W), intertidal, August 15, 2003, Kuris, A. and Hechinger, R., SBMNH350743, 1♀, 1♂.

Notes on adult and immature specimens from the western coast of North America

Largest female (OIMB synoptic collection), total length 24.0 mm, maximal width across pereomere 4–5, 16.5 mm, head length 2.9 mm, head width 3.7 mm, pereon length 15.0 mm, pleon length 9.0 mm [means for females ($n=24$): total length = 16.5 ± 3.2 mm, maximal width 11.5 ± 3.0 mm, head length 2.2 ± 0.4 mm, head width 2.8 ± 0.6 mm, pereon length 10.3 ± 1.9 mm, pleon length 6.2 ± 1.5 mm] (Figs. 3–5). Females are positioned on hosts such that the cephalic end is in the posterior-dorsal portion of the branchial chamber with the dorsal surface facing the gills of the hosts; the mouthparts and brood chamber of the females face the branchiostegite (Fig. 3A and B). The pereopods of the females are used to hold onto the edge of the branchiostegite and some hosts were found to bear minute scars from these appendages and from the mouthparts of the females. Externally the parasite is evidenced by the rounded distension it causes in the branchiostegite.

The new female specimens from Vancouver, British Columbia, Canada, and Oregon and California, USA (Figs. 3 and 4) match the original

description by Markham (2004) and the newly described material from China. Although Markham (2004) indicated females of *O. griffenis* have first antennae with five articles and second antennae with 1–3 articles (presumably he meant 1–3 articles on antennae 1 and five articles on antennae 2), reexamination of the holotype showed that antenna 1 has three articles and antennae 2 has five articles on the left side (second antennae damaged on right side). All newly examined eastern Pacific specimens had three articles on antennae 1 and five or six articles on antennae 2 (Fig. 4E). Of the west-coast specimens examined, 13 were slightly (~10–15%) sinistrally deflexed and the left coxal plates of pereomeres 5 and 6 had small tubercles (Fig. 4A) whereas eight specimens were dextrally deflexed with small tubercles on the coxal plates of the right side of pereomeres 5 and 6; these differences in handedness reflect whether the left or right branchial chamber was infested. As in the Chinese specimens,

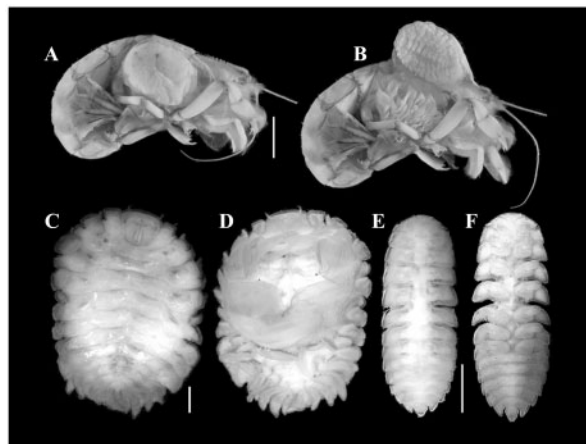


Fig. 3 *Orthione griffenis* from Oregon, USA. (A, B) male and female pair in situ (USNM1123923); (C–F) male and female pair (USNM1123917). (A) lateral view of *Upogebia pugettensis* with *O. griffenis* in situ; (B) lateral view of *Upogebia pugettensis* with carapace of branchial chamber lifted up to show position of *O. griffenis*; (C) female, dorsal view; (D) female, ventral view; (E) male, dorsal view; (F) male, ventral view. Scale bars: A and B = 10 mm; C–F = 2 mm.

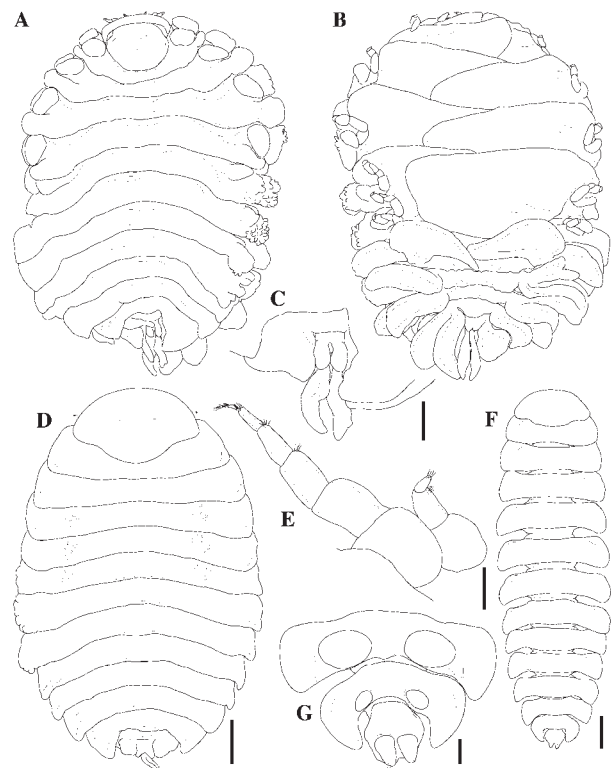


Fig. 4 *Orthione griffenis* from Barkley Sound, British Columbia, Canada, and Oregon, USA. (A–C) female (USNM1123925); (D) immature female (SBMNH347784); (E) female (SBMNH347790); (F and G) male (USNM1123925). (A) dorsal view of a female. (B) ventral view of a female; (C) dorsal view of last pleomere and uropods; (D) dorsal view of an immature female; (E) left antennae of a female; (F) dorsal view of a male; (G) ventral view of male posterior pleomeres and uropods. Scale bars: A and B = 2 mm; C, D and F = 1 mm; E and G = 0.25 mm.

pleomeres 1–5 bear lateral plates and biramous pleopods; the large, sickle-shaped endopodites of pleopod 1 cross each other in the middle of the pleon (this was observed in live specimens and is not an artifact of preservation). The lateral plates of pleomere 5 are reduced, short digitiform extensions, approximately one-third the length of the slender uniramous uropods, small protuberances found on some uropods (Fig. 4C). One of the female specimens (SBMNH348501) exhibited asymmetrical uropods, most likely representing a developmental abnormality.

Immature females (SBMNH347784 and USNM1123924), total length 4.0–7.9 mm, head width 1.4–3.0 mm, head length 0.7–1.5 mm, pereon length 2.4–5.3 mm, maximal width across pereomere 6, 2.1–5.4 mm, pleon length 1.6–2.6 mm. The new immature females specimens from Oregon and California, USA (Fig. 4D), match the original description by Markham (2004) and the newly described material from China (Fig. 1J and K).

Largest male (USNM1123925), total length 10.3 mm, head width 2.2 mm, head length 1.0 mm, pereon length 6.8 mm, maximal width across pereomere 4–5, 2.7 mm, pleon length 3.5 mm [means for males ($n=17$): total length = 8.1 ± 1.5 mm, maximal width 2.8 ± 0.5 mm, head length 0.9 ± 0.2 mm, head width 1.9 ± 0.3 mm, pereon length 5.3 ± 1.6 mm, pleon length 2.8 ± 0.6 mm]. Males are positioned on the ventral surface of the female, typically at the posterior end among the pleopods (Fig. 7). Reexamination of the allotype showed that antennae 2 of this specimen are damaged (four articles on the right side, five articles on the left side) and appear to be missing terminal articles (as shown by the blunt end of antenna 2 in Fig. 2D of Markham, 2004). Thus, the number of antennal articles of males of *O. griffenis* is three and six for antennae 1 and 2, respectively (as found in the Chinese specimens) (Fig. 5B). Otherwise, the new male specimens from Vancouver, British Columbia, Canada, and Oregon and California, USA (Figs. 4F, G and 5A–F) follow the original description by Markham (2004) and the newly described material from China.

Description of epicaridium larvae from the western coast of North America

Epicaridium larvae (Fig. 6) with a length of $371.2 \pm 34.8 \mu\text{m}$ ($n=10$) and a maximum width of $169.8 \pm 14.2 \mu\text{m}$ ($n=10$); body ovate in shape (Fig. 6A). Anterior margin of head slightly rounded, with posterolateral projections extending beyond antenna 1 (Fig. 6A–C). Antenna 1 of two articles,

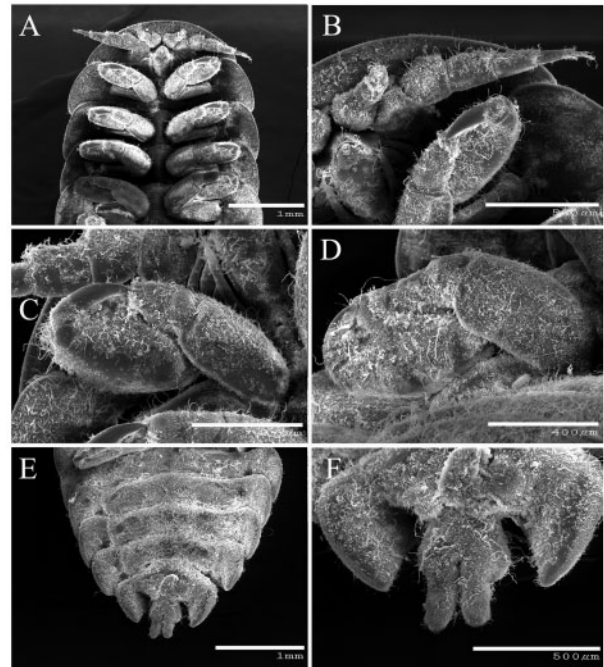


Fig. 5 *Orthione griffenis* from Oregon, USA. (A–F) male (USNM1123917) covered with unidentified mesomycetozoean, SEM micrographs. (A) anterior end, ventral view; (B) right antennae and first pereopod; (C) first left pereopod; (D) left pereopod 7, (E) ventral view of pleon; (F) last pleomere and uropods. Scale bars: A and E = 1 mm; B and F = 500 μm ; C and D = 400 μm .

first article broad, round with 2–3 setae anterior to a group of 4–6 stout, terminal setae (Fig. 6C); antenna 2 of seven articles, articles 1–4 lacking setae, with cuticular plates, article 5 longest, with two distal setae, article 7 with two short setae below two long terminal setae, nearly as long as articles 1–7 (Fig. 6A and B).

Pereomere 4 broadest, tapering slightly anteriorly and posteriorly. Body pigmentation is lacking. Six gnathopodal pereopods with slightly curved dactyli, approximately half as long as the propodus (Fig. 6D, E, and G); surface of merus, carpus and propodus with scales ending in rows of minute setae, propodus sometimes with a stout seta observable along the edge apposed to the dactylus; pereopods 1–2 largest (Fig. 6D), pereopods 3–6 diminishing in size posteriorly (Fig. 6E).

Pleon with five pleopods (Fig. 6F); pleopods 1–4 composed of basis (sympod) and exopod (Fig. 6F), pleopod 5 composed only of basis (Fig. 6G); all pleopods with scales ending in rows of minute setae similar to those found on pereopods. Basis of pleopods 1–4 with triangular distal end bearing one long plumose seta, edge of basis apposed to exopod with a serrated convex edge (Fig. 6F inset), exopods

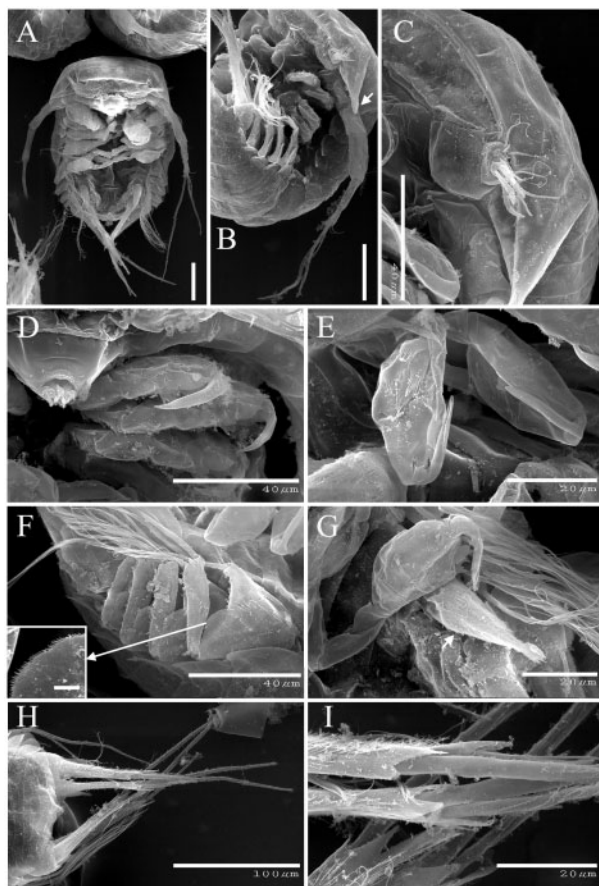


Fig. 6 *Orthione griffenis* from Oregon, USA. (A–I), epicaridium larvae, SEM micrographs. (A) ventral view of whole larvae; (B) oblique view of left side of larvae, showing long second antennae (lateral projection of head shown by arrowhead); (C) first left antennae; (D) buccal cone and left pereopods 1 and 2; (E) left pereopods 5 and 6; (F) left pleopods 1–4; serrated edge of basis shown in inset; (G) pereopod and left pleopod 5 (indicated by arrowhead); (H) dorsal view of pleon, anal cone and uropods; (I) close-up of a uropod showing insertion of plumose setae. Scale bars: A and B = 50 µm; C, D and F = 40 µm (F inset scale = 2 µm); E, G and I = 20 µm; H = 100 µm.

of pleopods 1–4 digitiform and bearing three long plumose setae; pleopod 5 tapering to an acute point with minute setae, lacking serrated convex edge and exopod, pleopod 5 positioned below uropods, more medially than pleopods 1–4. Uropods biramous, endopods and exopods subequal, both bearing approximately four acute projections at the distal end from which two long plumose setae arise (Fig. 6H and I). Anal tube ventral and small (Fig. 6H).

Natural history

The prevalence of *O. griffenis* in *U. pugettensis* in the 2008 collections from Coos Bay, Oregon was 45.8%

(11 of 24 hosts parasitized); however, of those hosts > 20 mm, the prevalence was 64.7% (11 of 17 hosts parasitized). This prevalence is similar to populations of *U. pugettensis* from Yaquina Bay, Oregon where almost 100% of the large individuals sampled were infested by *O. griffenis* (Smith et al. 2008). No specimens of *Neotrypaea californiensis* (Dana) were parasitized by *O. griffenis* in the collections from Coos Bay (where *N. californiensis* and *U. pugettensis* overlap on mudflats). One specimen of *U. pugettensis* appeared to be doubly infested as evidenced by the swelled chambers but only one branchial chamber contained a parasite (the other parasite had apparently died or had been lost during collection). Ovigerous *O. griffenis* were found in collections made from May to July in Oregon and in January from collections made in California; developing eggs were $169.6 \pm 6.7 \mu\text{m}$ ($n = 50$) in diameter (based on British Columbian specimen). Multiple females (4 of 24 specimens, 16.7%) from Oregon had stalked ciliates (*Vorticella*-like sp.) attached to the sides of pereomeres 1–7; three of these specimens (12.5%) also had thalli of an unidentified mesomycetozoean (Class Mesomycetozoea, Order Eccrinales; see Cafaro 2005) attached. In addition, 4 of 24 male specimens (16.7%) from Oregon were covered with a mesomycetozoean (Fig. 5).

Distribution and hosts (Fig. 8): Ross Islet and Vancouver Harbour, British Columbia, on *Upogebia pugettensis* (Dana) and possibly *Acantholithodes hispidus* (Stimpson) (see comments in Discussion section); California, Oregon, and Washington, USA, on *Upogebia pugettensis* (Dana) and *Upogebia macginitieorum* Williams; Shikoku, Japan, on *Upogebia issaeffi* (Balss) and *Austinogebia narutensis* (Sakai); Shandong province, China, on *Austinogebia wuhsienweni* (Yu).

Discussion

We consider the minor morphological differences between the specimens from China and the eastern Pacific to represent intraspecific variation. However, until molecular or reproductive cross studies are completed to confirm these findings, *O. griffenis* should be labeled as cryptogenic (Carlton 1996). Future studies should be completed to explore alternative hypotheses: specifically, that the species may be composed of a complex of morphologically indistinguishable but reproductively isolated species. This appears unlikely given the fact that *O. griffenis* was not found prior to the 1980s in a well-sampled region and parasitizing a well-studied host, although not typically with parasites as the focus of study

(Macginitie 1930; Hornig et al. 1989; Posey et al. 1991; Dumbauld et al. 1996). For *O. griffenis* to have remained overlooked, the species would have needed to have been extremely rare considering other isopod parasites with moderately low prevalences (e.g., *Ione cornuta* Bate on *Neotrypaea californiensis* and *Phyllodurus abdominalis* Stimpson on *Upogebia pugettensis*) have been known from the west coast for over a century. However, there are examples of other species (e.g., *Progebiophilus bruscai* Salazar-Vallejo and Leija-Tristan, 1989 from *Upogebia dawsoni* Williams) that remained unknown on the western coast of North America until the late 1980s (Salazar-Vallejo and Leija-Tristan 1989, 1991; see Markham, 1992 for review of the diversity of bopyrids along the eastern Pacific).

Alternatively, it could be argued that *O. griffenis* was introduced to Asia from the western coast of North America. Considering that the specimens from China are based on collections from the 1950s (~30 years prior to any record of the species from the eastern Pacific), and given the fact that it appears to not have been overlooked along the western coast of North America, it is most parsimonious to conclude that the species had an origin in Asia. The point of origin for *O. griffenis* in Asia remains unknown until future molecular work but considering that the bopyrid fauna from Japan is relatively well studied due largely to the efforts of Shiino (see Schotte et al. 2008), it may be that the species was introduced to Japan and China from another locality in the Indo-West Pacific. Thus, it appears that this species was not previously overlooked in North America but rather represents a human mediated introduction perhaps as early as the 1980s (Wagner 2006), most likely via release of larvae from ballast waters in ships arriving from China or elsewhere in Asia. The earliest confirmed record that we know of the species along the west coast of north America is from California in 1992 (A. Kuris, personal communications). The expansion of the species along the West Coast would represent a rapid spread, similar to that found in free-living marine crustaceans introduced to the eastern and western coasts of North America, e.g., *Hemigrapsus sanguineus* (de Haan), McDermott (2000); *Carcinus maenas* (Linnaeus), Carlton and Cohen (2003).

Orthione griffenis was likely introduced as a larval form (free-living epicaridium larvae, microniscus larvae attached to copepod intermediate hosts, or free living cryptoniscus larvae). The complete life cycle follows that of other bopyrid parasites

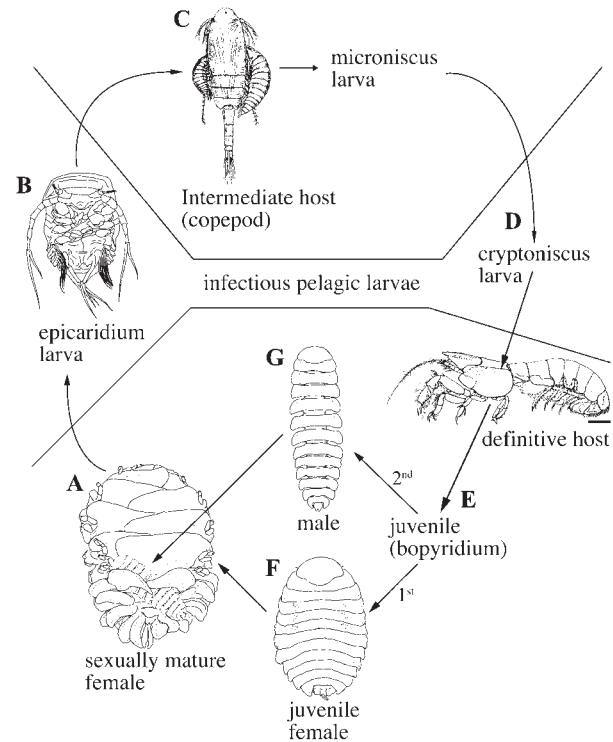


Fig. 7 Life cycle of *O. griffenis*. (A) sexually mature female and dwarf male are found in the gill chamber of the definitive host (*Upogebia pugettensis* and other thalassinid mud shrimp); (B) epicaridium larvae released from the female seek out a copepod intermediate host in the water column, upon which it is an ectoparasite; (C) microniscus larva feed on the copepod host and eventually transforms into a cryptoniscus larva; (D) cryptoniscus larva detaches and after a free-swimming period settles onto a suitable definitive host; (E) bopyridium (recently settled juvenile) infests host, if the host is novel the isopod becomes female; subsequent isopods become males; (F) juvenile female; (G) male. Scale bar: 1 cm for definitive host (rest not to scale). Modified from Boyko and Williams (2009), Wägele (1989), Janssen and Brandt (1994); drawing of infested copepod from Sars (1899); drawing of *Upogebia pugettensis* from Hornig et al. (1989).

(Fig. 7), with female bopyrids producing large broods [up to 60,000 eggs; Smith et al. (2008)] that are contained in a marsupium covered by the oostegites and fertilized by dwarf males. Development proceeds in the marsupium until the first larval stage, the epicaridium, hatches. This stage is released into the water column, and eventually parasitizes an intermediate host, a calanoid copepod. The epicaridium larva becomes a microniscus larva that continues to feed on the copepod host, going through several molts and eventually metamorphosing into a cryptoniscus larva. The cryptoniscus larva is free swimming and will settle on the definitive host, invading the branchial chamber. The sex of these parasites is under epigenetic control wherein the first undifferentiated juvenile (bopyridium) to

settle becomes a female and subsequent individuals become males (Reinhard 1949). If the female dies, males of some species have the ability to change sex and become females, and are thus considered protandric hermaphrodites (Reverberi 1947; Reinhard 1949). The present description of the epicaridium represents one of the few studies to examine the morphology of this larval stage with SEM (see Anderson and Dale 1981; Dale and Anderson 1982) and could aid in future taxonomic studies of the genus *Orthione*. The morphology of the microniscus and cryptoniscus larvae has not been studied and unfortunately the identity of the copepod intermediate host remains unknown. The introduction of a copepod intermediate host may explain the spread of this species in the eastern Pacific, a more suitable copepod species could have facilitated the spread of the parasitic isopod in a process of invasional 'meltdown' (Simberloff and Von Holle 1999). In fact, multiple species of copepods have been introduced to the eastern Pacific from Asia (e.g., Bollens et al. 2002; Cordell et al. 2007, 2008). The intermediate host use patterns and specificity should be examined as was studied in *Epipenaeon ingens* Nobili, which has been found to parasitize up to 14 different species of copepod hosts (Owens and Rothlisberg 1991, 1995).

Documented cases of introduced marine parasites are limited (Torchin et al. 2002, 2003; Torchin and Kuris 2005) especially those with life cycles involving multiple hosts (Miura et al. 2006). Whereas two species of rhizocephalan parasites on crabs (Innocenti and Galil 2007; Kruse and Hare 2007) and three species of cymothoid isopods parasitic on fish have been documented as non-natives (Bariche and Trilles 2006, 2008; Trilles and Bariche 2006), there are no reported cases of introduced bopyrid isopods. However, *O. griffenis* is not the only bopyrid with distributions on both sides of the Pacific. Other examples include the thalassinidean parasite *Ione cornuta* Bate (see An et al. in press), *Aporobopyrus oviformis* Shiino (a parasite of *Pachycheles* sp.; Markham, 1992), and *Argeia pugettensis* Dana (a parasite of crangonid and hippolytid shrimps; Markham 1992). Whereas the geographic distribution of the latter species, with its low host specificity, appears to represent a natural pattern, research should explore the possibility that other parasitic isopods have been introduced (or their ranges have been extended) through human activity. Free-living isopods that have been introduced to the western coast of the United States have been studied in detail (Bowman et al. 1981;

Carlton and Iverson 1981; Chapman and Carlton 1991, 1994; see Poore 1996 for dissenting view; Davidson 2008; Davidson et al. 2008a, 2008b).

Presently the distribution of *O. griffenis* in the western Pacific is from China to Japan (a distance of ~800 miles, 454 latitudinal miles) where it infests three host species (Fig. 8). Other than records of *O. griffenis* in China and Japan, the geographic range of the species in Asia remains unknown and identification of the source population(s) from the eastern Pacific needs to be addressed with future molecular investigations (as has been completed for introduced rhizocephalans; Kruse and Hare 2007). Along the eastern Pacific, the species have been documented from Vancouver, British Columbia, Canada to San Pedro, California (a distance of >1100 miles, ~1050 latitudinal miles). The species has been found on *Upogebia pugettensis*, which extends from Alaska to California (Jensen 1995; Kuris et al. 2007). In addition, it parasitizes *U. macginitieorum*, which replaces *U. pugettensis* south of Pt. Conception, California (Jensen 1995; Kuris et al. 2007). Although there are no documented cases of the parasite in Alaska, researchers should look for *O. griffenis* in southeastern Alaska where *U. pugettensis* is prevalent. The finding of *O. griffenis* (originally identified as *Ione* sp.) in the lithodid crab *Acantholithodes hispidus* by Lamb and Hanby (2005) is unexpected but unfortunately the specimens were not saved (G.C. Jensen, personal communication) and the identification cannot be confirmed. However, only two other bopyrids are known to parasitize lithodid crabs in this region: *Pseudione giardi* Calman and *Pseudione galacanthae* Hansen (Markham 2003). The morphology of the female specimen shown in the branchial chamber of *Acantholithodes hispidus* by Lamb and Hanby (2005) does not match either of the *Pseudione* species or *Ione cornuta* (known only from thalassinoids) and appears to be a mature specimen of *O. griffenis* (based on the orange coloration of the body indicating egg development; no male is shown). The finding of *O. griffenis* parasitizing a lithodid crab most likely represents an accidental association but its ability to parasitize and successfully reproduce on other hosts awaits further investigation. It is important to note that while the initial introduction of *O. griffenis* was likely made in the larval stage, transportation of infested hosts (after harvesting for bait; Hornig et al. 1989) may spread adults of the parasite along the coast of North America, as examined in *Ione cornuta* parasitizing the host *Neotrypaea californiensis* (Pernet et al. 2008).

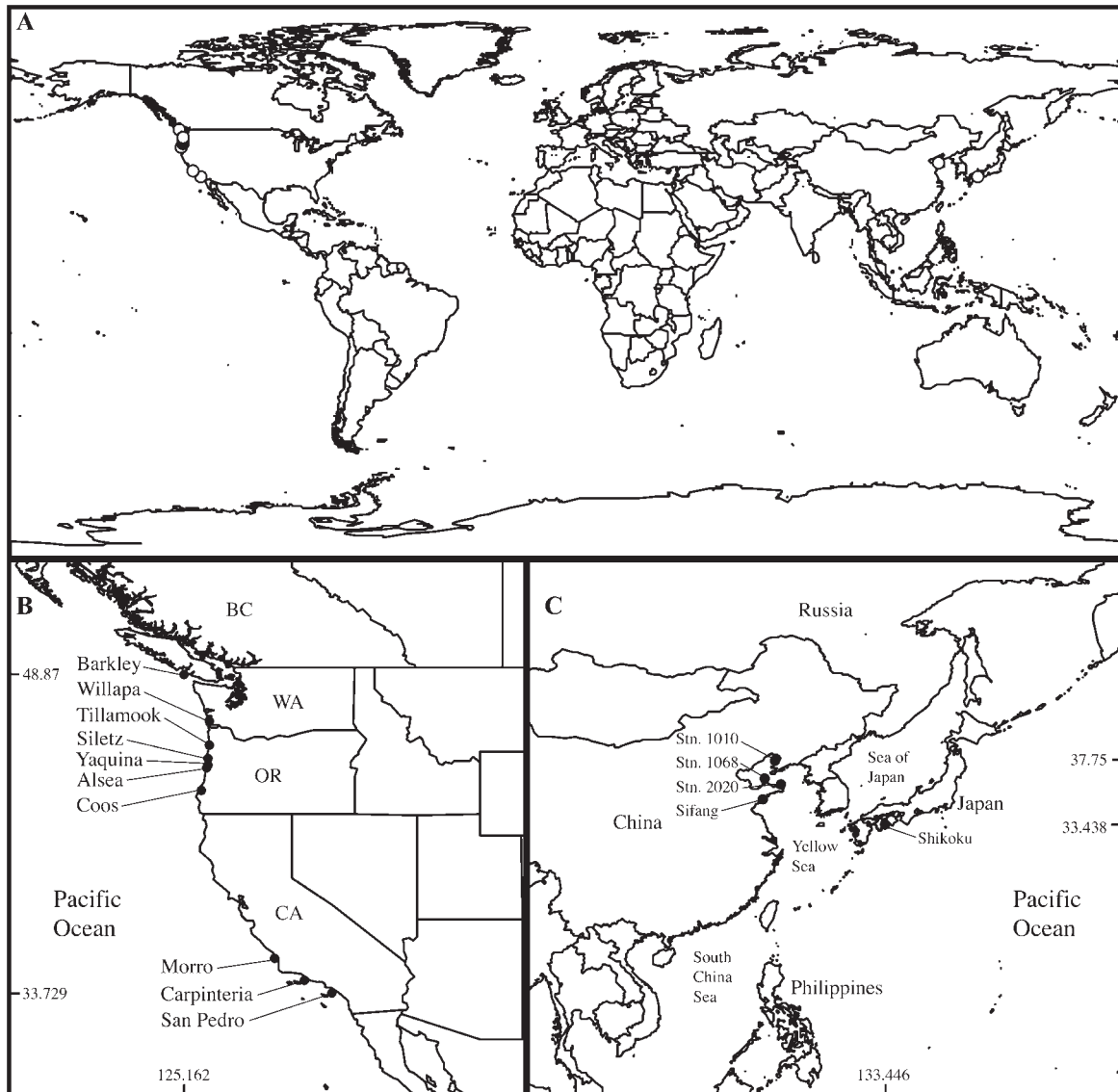


Fig. 8 Geographic distribution of *O. griffenis*. (A) overview of global distribution; (B) distribution of *O. griffenis* along the western coast of North America where it parasitizes *Upogebia pugettensis* from Barkley Sound, British Columbia, Canada, to San Pedro, California; the species is also known from *U. macginitieorum* in California (names of bays where the *O. griffenis* has been documented in Oregon and Washington are listed); (C) distribution of *O. griffenis* within China and Japan where it parasitizes *Austinogebina wuhsienweni* in Shandong province, China and *U. issaeffi* and *Austinogebina narutensis* in Shikoku, Japan. In parts B and C latitudinal points indicate extremes of the northern and southern range of the species.

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