

## EVIDENCE OF OCEANIC DISPERSAL OF A DISJUNCTLY DISTRIBUTED AMPHIDROMOUS SHRIMP IN WESTERN NORTH AMERICA: FIRST RECORD OF *MACROBRACHIUM OCCIDENTALE* FROM THE BAJA CALIFORNIA PENINSULA

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### ABSTRACT

Six morphological species of the genus *Macrobrachium* occur in the Baja California Peninsula (*M. americanum*, *M. digueti*, *M. hobbsi*, *M. michoacanus*, *M. olfersii*, and *M. tenellum*). Their presence is an interesting topic for the systematics of the group, given that their distribution shows a distinct disjunct on the coastal plains of the northern part of the Gulf of California slope. Extensive collection of freshwater shrimp of the peninsula allowed us to discover individuals whose morphology corresponds to *Macrobrachium occidentale* Holthuis, 1950. This species, described in 1950 from the Pacific slope of Central America has received little attention. The type locality is in Guatemala, but it is also found in Mexico, El Salvador, Costa Rica, and Panama. In Mexico it has been reported in the states of Sinaloa, Nayarit, Guerrero, and Oaxaca. The aim of the present work is to contribute to the systematics of *M. occidentale* through two approaches. First, by reviewing the geographical distribution in Mexico, using taxonomic morphological revision of extensive field collections, as well as material deposited in three scientific collections. Second, through molecular genetic analysis of fragments of the mitochondrial genes 16S rRNA and cytochrome oxidase I, determine whether individuals from the peninsula belong to the same entity found on the mainland Pacific slope of Mexico or whether they form a distinct lineage. The results indicate the presence of the same genetic entity in both regions and show a disjunct distribution similar to other species of the genus in this region. We present a systematic account for *M. occidentale*, including a taxonomic treatment of the studied populations and a report of their genetic identity and relationships. Further, we suggest and discuss that the presence of this amphidromous species on the peninsula is explained by the oceanic dispersal hypothesis.

**KEY WORDS:** 16S rRNA, COI, biogeography, haplotype diversity, mitochondrial DNA, Mexico, Palaemonidae, systematics

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### INTRODUCTION

In a previous study, Hernández et al. (2007) published an updated taxonomic account of the freshwater caridean *Macrobrachium* from the Baja California Peninsula (peninsula), recording six of the seven morphological species that occur along the Pacific slope of mainland Mexico: *M. americanum* Bate, 1868, *M. digueti* (Bouvier, 1895), *M. hobbsi* Nates and Villalobos, 1990, *M. michoacanus* Nates and Villalobos, 1990, *M. olfersii* (Wiegmann, 1836), and *M. tenellum* (Smith, 1871). Their presence in the peninsula is an interesting topic for the systematics and biogeography of the group, given that the genus shows a disjunct distribution along the coastal plains of the northern part of the Gulf of California slope (Hernández et al., 2007). The northernmost records of the genus in the Gulf are in the Mulegé basin, Baja California Sur (26°53'N, 111°57'W) for the peninsula and at Guaymas, Sonora (27°86'N, 110°85'W) for the continental side (mainland), which is the general northernmost boundary of

the genus along the Pacific slope (Hernández et al., 2007). Considering that native fish and reptiles of the peninsula are believed to have a vicariant origin (Follett, 1960; Grismer and McGuire, 1993; Grismer, 2000; Murphy and Aguirre-León, 2002), Hernández et al. (2007) advanced the hypothesis that the *Macrobrachium* found in the peninsula may represent relict strains of species distributed in mesophilic continental environments during the formation and separation of the peninsula from the mainland during the Miocene. Also, they proposed that relict populations of the seventh morphological species, *M. occidentale* Holthuis, 1950, which was reported from southern Panama up to the Mexican state of Sinaloa (Holthuis, 1950, 1952; Hendrickx et al., 1983; Wicksten, 1983; Villalobos-Hiriart et al., 2010), may also be present on the peninsula.

The peninsula functions biologically as an island for non-flying tetrapods like semiaquatic gartersnakes, for which overwater colonization has been a molecularly-supported

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proposal to explain their disjunct distribution in this region (de Queiroz and Lawson, 2008). The old concept of oceanic dispersal is resurrected in modern historical biogeography as a probable process to explain disjunct distributions of terrestrial and freshwater taxa (de Queiroz, 2005). *Macrobrachium* occurs in the tropics and several subtropical areas, where the dominant ecological group is composed of amphidromous species having at least part of their life cycle in freshwater (Holthuis, 1980; Short, 2004; Cook et al., 2009). Several species, *Macrobrachium idae* (Heller, 1862), *M. lar* (Fabricius, 1798), *M. latidactylus* (Thallwitz, 1891), *M. mammillodactylus* (Thallwitz, 1892), *M. nipponense* (De Haan, 1849) and *M. rosenbergii* (De Man, 1879), may even show wide distributions across interoceanic areas, especially in the Indo-Pacific region (Short, 2004; Murphy and Austin, 2005). Using mitochondrial DNA sequence data, recent studies suggest that oceanic dispersal better explains these wide distributions than the vicariance models (Murphy and Austin, 2005; Chen et al., 2009; Dennenmoser et al., 2010; Page et al., 2013; Rossi and Mantelatto, 2013). Therefore, oceanic dispersal has remained an alternative scenario to explain the presence of the freshwater *Macrobrachium* along the shores of the peninsula.

New collections of freshwater shrimp on the peninsula have uncovered individuals whose morphology corresponds to *M. occidentale*. This species has received little attention since its description by Holthuis. With the type locality in Guatemala, it is known from El Salvador, Costa Rica and Panama (Holthuis, 1950, 1952; Vega et al., 2006; Rólier-Lara and Wehrtmann, 2011). In Mexico, *M. occidentale* has been reported from the mainland Pacific slope in four states, Sinaloa (Hendrickx et al., 1983; Wicksten, 1983, 1989; Wicksten and Hendrickx, 1992, 2003), Nayarit (Guzmán Arroyo et al., 2009), Guerrero (Román-Contreras, 1991) and Oaxaca (Martínez Guerrero, 2007; Villalobos-Hiriart et al., 2010).

The aim of this study is to contribute to the systematics of *M. occidentale* by two approaches. First, we review its geographical distribution in Mexico. For this phase, we made an extensive field collection along a great part of the Mexican Pacific slope in eight states, from Baja California Sur in the north, to Guerrero in the south, and we prepared a taxonomic morphological revision of both the material obtained in the field and the material deposited in two Mexican scientific collections. Second, we performed molecular genetic analysis with newly generated fragments of the mitochondrial genes 16S rRNA (16S) and cytochrome oxidase I (COI) to determine whether individuals from the peninsula belong to the same entity found along the Pacific slope of mainland Mexico or whether they form a distinct lineage. The results indicated the presence of the same genetic entity morphologically identified as *M. occidentale* in both regions. Thus, we present a systematic account for this species that includes a taxonomic treatment of the studied populations and a report of their genetic identity and relationships. Further, we discuss the probable scenarios that explain the presence of *M. occidentale* on the peninsula.

## MATERIALS AND METHODS

### Field Collections

We collected *Macrobrachium* with hand nets and casting nets. At most of the sites, we recorded water temperature, total dissolved solids (TDS), and pH (EC300, pH100, YSI, Yellow Springs, OH, USA). Geographic position of each site was determined with a GPS unit. The specimens were fixed in 100% ethanol and deposited in the Colección de Crustacea at Centro de Investigaciones Biológicas del Noroeste (CIB).

### Material Examined

Material examined is organized according to the country, political state, drainage basin, name of the site, collection date, senior collector's name, catalog code, number of males and females that were revised, number of individuals used for DNA analysis shown between brackets, and total length for *M. occidentale* and carapace length for other species. Nomenclature of drainage basins is that of the Mexican federal classification published by the Comisión Nacional del Agua (available online at [http://www.conagua.gob.mx/CONAGUA07/Contenido/Documentos/SINA/TM\(Cuencas\\_Hidrologicas\).xls](http://www.conagua.gob.mx/CONAGUA07/Contenido/Documentos/SINA/TM(Cuencas_Hidrologicas).xls)).

*Macrobrachium americanum* Bate, 1868.—MEXICO: BAJA CALIFORNIA SUR: Las Pocitas-San Hilario basin: Rancho Las Cuevas, 29.05.2010, A. Maeda, CIB 1189, 2 females (21.1 and 22.5 mm); La Cuchilla, 29.5.2010, A. Maeda, CIB 1190, 2 males (38.3 and 46.1 mm); Santa Rita basin: San Pedro de la Presa, 13.06.2011, A. Maeda, CIB 1191, 1 male (30.4 mm), 1 female (18.7 mm); Santa Maria de Toris, 23.05.2010, A. Maeda, CIB 1192, 2 males (21.1 and 21.9 mm); Todos Santos basin: Canales Todos Santos, 28.11.2006, J. Salcido, CIB 1038, 1 male (39.5 mm). OAXACA: Río Verde basin: Río Viejo, 10.10.2008, J. Bautista, CIB 1063, 1 male (51.5 mm), 10.05.2008, CIB 1060, 1 female (40.8 mm).

*Macrobrachium digueti* (Bouvier, 1895).—MEXICO: BAJA CALIFORNIA SUR: San José del Cabo basin: Boca de la Sierra, 08.09.2004, L. Hernández, CIB 801, 1 male (32.8 mm); Todos Santos basin: La Poza, Todos Santos, 18.11.2008, J. Salcido, CIB 1104, 1 male (28.8 mm); Santa Rita basin: San Pedro de la Presa, 10.06.2011, G. Talamantes, CIB 1103, 1 male (40.1 mm). NAYARIT: Río Ameca-Ixtapa B basin: El Colomo, 03.08.2003, L. Hernández, CIB 866, 1 male (34.2 mm), 1 female (27.4 mm). JALISCO: Río Purificación basin: La Huerta, 07.05.2011, A. Maeda, CIB 1111, 1 male (36.8 mm). GUERRERO: Río Coyuca 2 basin: Vado Aguas Blancas, Río Coyuca, 11.05.2011, A. Maeda, CIB 1114, 1 male (30.3 mm).

*Macrobrachium hobbsi* Nates and Villalobos, 1990.—MEXICO: BAJA CALIFORNIA SUR: La Purísima basin: San Isidro, 19.07.2004, L. Hernández, CIB 1148, 1 male (31.5 mm), 1 female (54.0 mm); Santa Rita basin: San Pedro de La Presa, 30.05.2004, L. Hernández, CIB 821, 1 male (28.9 mm); Río Ameca-Ixtapa B basin: El Colomo, Bahía Banderas, 05.05.2011, A. Maeda, CIB 1183, 1 male (22.4 mm). OAXACA: Río Verde basin: Río Viejo, J. Bautista, 09.07.2008, CIB-1187, 1 male (22.5 mm), 1 female (24.1 mm).

*Macrobrachium michoacanus* Nates and Villalobos, 1990.—MEXICO: BAJA CALIFORNIA SUR: Todos Santos basin: La Poza, Todos Santos, 18.11.2008, H. García, CIB 1117, 1 female (64.6 mm); Pescaderos basin: San Pedrito, 12.09.2006, A. Maeda, CIB 1121, 1 male (37.1 mm). GUERRERO: Río Coyuca 2 basin: Vado Aguas Blancas, Río Coyuca, 11.05.2011, A. Maeda, CIB 1130, 1 male (63.8 mm).

*Macrobrachium occidentale* Holthuis, 1950.—MEXICO: BAJA CALIFORNIA SUR: Santa Rita basin: Oasis Santa María de Toris, 03.07.2011, A. Maeda, CIB 1007, 3 (2) males (55.9 to 59.3 mm); San Pedro de La Presa, 13.06.2011, A. Maeda, CIB 1020, 5 (2) males (44.6 to 67.9 mm), 2 females (47.0 and 67.3 mm); Las Pocitas-San Hilario basin: Rancho Las Cuevas, 26.06.2009, A. Maeda, CIB 1004, 7 (7) males (68.0 to 91.3 mm); La Cuchilla, 26.06.2011, A. Maeda, CIB 1021, 5 (2) males (46.9 to 53.7 mm), 7 females (33.1 to 55.2 mm); Todos Santos basin: Canales Todos Santos, 19.11.2008, H. García, CIB 1003, 1 male (23.6 mm), 2 juveniles (25.7 mm); Plutarco E. Calles basin: Las Vinoramas, 20.11.2008, H. García, CIB 1008, 2 (2) males (22.9 and 32.1 mm); El Chucarro, 20.11.2008, H. García, CIB 1006, 7 (3) males (27.7 to 44.9 mm), 5 (2) females (26.1 to 46.9 mm); San Venancio, 20.11.2008, H. García, CIB 1005, 4 (4) males (24.1 to 41.7 mm); San José del Cabo basin: Oasis Santa Rosa, 17.05.2007, E. Calvillo, CIB 1022, 1 male (40.76 mm). SONORA: Río Mayo 3 basin: Echoropo, Huatabampo, 22.04.2011, G. Murugan, CIB 1009, 2 (2) males (34.5 and 43.5 mm), 3 (3) females (40.2 to 54.8 mm). SINALOA: Río Sinaloa 2 basin:

- Dique, Sinaloa de Leyva, 25.04.2011, G. Murugan, CIB 1010, 1 (1) female (16.5 mm), 2 (1) chelas; Vado Guasave, Río Sinaloa, 26.04.2011, G. Murugan, CIB 1023, 1 male (22.2 mm); Río Elota basin: Puente El Roble, La Cruz de Elota, 28.04.2011, G. Murugan, CIB 1011, 2 (2) males (80.4 and 87.6 mm), 1 chela; Puente La Cruz de Elota, 28.04.2011, G. Murugan, CIB 1012, 1 (1) male (60.4 mm); Río Quelite 2 basin: Arroyo San Pablo, 25.11.2003, A. V. Derheiden, CNCR 25064, 1 male (59.7 mm); Río Presidio 2 basin: Villa Unión 2, 02.05.2011, G. Murugan, CIB 1014, 2 (2) males (18.2 and 39.3 mm), 1 (1) female (17.9 mm), 2 (2) juveniles (14.8 and 25.2 mm); Estero Colonias Espejos and Urías, Mazatlán, 19.10.1940, D. Peláez, CNCR 247, 2 males (67.5 and 68.6 mm); Río Baluarte 2 basin: El Rosario, Puente Río Baluarte, 30.04.2011, G. Murugan, CIB 1015, 12 (1) males (23.9 to 69.1 mm), 21 (4) females (23.2 to 60.3 mm), 2 juveniles (8.6 and 11.3 mm); El Rosario, 03.05.2011, G. Murugan, CIB 1013, 2 (2) males (30.2 and 31.8 mm). NAYARIT: Río Huaynamota basin: Río Huaynamota, Las Adjuntas, 08.06.1991, A. Cantú, CNCR 11472, 7 males (58.5 to 93.1 mm), 5 females (47.1 to 80.2 mm); 19.03.1992, A. Cantú, CNCR 11853, 3 males (23.3 to 48.1 mm), 6 females (35.4 to 68.7 mm); 27.04.1992, P. Cervantes, CNCR 11838, 1 male (59.5 mm), 2 females (28.0 and 47.2 mm); Río Huaynamota, 500 m Las Adjuntas, 09.06.1991, A. Cantú, CNCR 13360, 1 male (74.4 mm), E. Lira, CNCR 11480, 1 male (90.4 mm); 19.11.1991, J. L. Villalobos, CNCR 11747, 2 males juveniles; 20.03.1992, J. L. Villalobos, CNCR 11855, 2 males (51.8 and 77.0 mm), 1 female (46.2 mm); 28.04.1992, A. Cantú, CNCR 11840, 1 male (55.0 mm), 3 females (43.9 to 71.3 mm); Río Huaynamota, Los Sabinos, 01.04.1991, J. L. Villalobos, CNCR 11212, 2 males (67.6 and 77.9 mm), 2 females (51.9 and 63.8 mm); 10.04.1991, J. L. Villalobos, CNCR 11215, 4 males (40.9 to 83.9 mm); 11.04.1991, J. L. Villalobos, CNCR 11211, 3 females (38.5 to 42.4 mm); 11.06.1991, A. Cantú, CNCR 11476, 1 male (55.5 mm), 4 females (58.6 to 65.7 mm), CNCR 13358, 1 male (56.4 mm), CNCR 13359, 4 females (44.6 to 54.4 mm); 19.01.1992, A. Cantú, CNCR 11756, 1 male (76.7 mm), CNCR 11923, 1 female (14.4 mm); 17.03.1992, J. L. Villalobos, CNCR 11832, 5 males (35.3 to 81.4 mm), 5 females (47.7 to 69.6 mm); 22.04.1992, A. Cantú, CNCR 11837, 1 male (90.6 mm); Río Huaynamota, Los Sabinos, 300 m Carrito Aforador, 18.03.1992, J. L. Villalobos, CNCR 11852, 1 male (85.6 mm), 1 female (58.7 mm); Playa de Golondrinas, 12.04.1991, H. Espinoza and C. Rosales, CNCR 11207, 1 male (110.1 mm); Río Santiago 4 basin: Colorado de La Mora, 12.04.1991, A. Cantú, CNCR 11206, 2 males (61.8 and 72.6 mm), 3 females (36.1 to 46.0 mm); 21.05.1991, C. Rosales, CNCR 11500, 2 males (68.0 and 82.9 mm); 25.09.1991, A. Cantú, CNCR 11549, 1 male (82.1 mm); 21.11.1991, J. L. Villalobos, CNCR 11932, 1 male (31.2 mm), 3 females (26.2 to 31.5 mm). 15.06.2009, C. Galicia, CNCR 11483, 1 female (74.6 mm); Río Ameca Ixtapa B basin: Canal El Colomo, Bahía Banderas, 05.05.2011, G. Murugan, CIB 1016, 3 (3) males (40.1 to 47.4 mm), 2 (2) females (33.9 and 58.2 mm). JALISCO: Río Cuale basin: Río Horcones, 20 km S Puerto Vallarta, Tuito, 03.1992, A. Novelo, CNCR 13374, 2 males (34.8 and 38.9 mm), 1 female (37.2 mm); Río Cuitzmala basin: Río Cuitzmala, Chamela, 02.04.1984, J. L. Villalobos, CNCR 3544, 1 male (73.7 mm); Río Ayotitlán, Sierra de Manantlán, 03.04.1987, P. Schmidtsdorf, CNCR 7659, 2 males (40.7 and 70.7 mm); Río Ayotitlán, Las Juntas, Río Agua Mala, Sierra de Manantlán, 03.04.1987, P. Schmidtsdorf, CNCR 7819, 4 males (67.4 to 92.0 mm), 2 females (46.3 and 51.9 mm); Río Cuitzmala, km 43 Melaque-Puerto Vallarta, 30.01.1984, J. L. Villalobos, CNCR 20712, 6 females (38.0 to 59.8 mm); 31.01.1984, J. L. Villalobos, CNCR 3126, 5 males (37.1 to 54.9 mm), 20 females (34.1 to 59.5 mm); J. C. Nates, CNCR 3128, 6 males (33.0 to 43.5 mm), 16 females (38.5 to 58.1 mm); 02.04.1984, J. L. Villalobos, CNCR 3487, 8 males (31.1 to 43.0 mm), 12 females (30.6 to 60.6 mm); 29.01.1986, J. C. Nates, CNCR 13054, 1 female (48.5 mm); San Nicolás, Melaque-Puerto Vallarta, La Huerta, 07.04.1987, J. C. Nates, CNCR 13308, 1 male (25.8 mm), 1 female (36.2 mm); Río Cuitzmala, 04.02.1983, J. L. Villalobos, CNCR 22270, 5 males (33.5 to 52.0 mm), 2 females (43.2 and 51.0 mm); 06.04.1987, E. Lira, CNCR 7678, 1 male (91.6 mm), 2 females (54.9 and 64.1 mm); Río Cuitzmala, 3 km Venustiano Carranza, La Huerta, 06.04.1987, P. Schmidtsdorf, CNCR 7641, 1 male (37.3 mm), 1 female (34.9 mm); Río Purificación basin: Zenzontla, Sierra de Manantlán, 02.04.1987, P. Schmidtsdorf, CNCR 7651, 1 male (46.4 mm). Río Purificación, La Huerta, 07.05.2011, G. Murugan, CIB 1017, 9 (5) males (58.9 to 72.6 mm); CIB 1018, 2 (1) males (45.3 and 65.9 mm), 4 (4) females (30.2 to 37.4 mm). COLIMA: Río Armería basin: Potrero Las Juntas, 3 km SE Pueblo Juárez, 23.06.1986, R. Navarro, CNCR 5898, 1 male (89.8 mm), 1 female (91.4 mm); Presa El Seis, 9 km W Colima, 15.12.1973, S. Contreras, UANL, 14 males juveniles. MICHOACÁN: Río Bajo Balsas basin: Río Popoyuta, 30.07.1984, J. C. Nates, CNCR 3553, 1 male (39.9 mm); 30.12.1989, J. C. Nates, CNCR 3551, 6 males (33.2 to 44.3 mm); La Villita, Michoacán-Guerrero, 30.07.1984, J. L. Villalobos, CNCR 3546, 1 male (81.4 mm); Río Chucutitlán, 25.07.1984, J. L. Villalobos, CNCR 3577, 1 male (45.3 mm); Río Mexcaltitlán, junto Barra, 31.07.1984, J. L. Villalobos, CNCR 3576, 3 males (30.2 to 41.9 mm), 1 female (38.7 mm). GUERRERO: Río Petatlán 2 basin: Río Murga, Murga, 17 km NE Petatlán, 19.08.1980, J. L. Villalobos, CNCR 2653, 1 female (53.7 mm), J. L. Villalobos, CNCR 2683, 2 males (74.2 and 75.5 mm); 11.09.1981, J. L. Villalobos, CNCR 13032, 1 female (54.5 mm); 28.07.1984, J. L. Villalobos, CNCR 3539, 15 males (40.2 to 75.7 mm), 4 females (43.0 to 49.1 mm), J. L. Villalobos, CNCR 13396, 1 male (54.8 mm); Río Atoyac 2 basin: Río Verde, Vallecito de Zaragoza, Puebla, 03.08.1984, Pepe y Paramillo, CNCR 3542, 2 males (42.0 and 42.6 mm), 6 females (32.8 to 66.9 mm); Río Atoyac, Atoyac de Álvarez, 07.04.2007, C. Ortiz, UANL, 2 males (70.3 mm); Río Coyuca 2 basin: Río Coyuca, Vado Aguas Blancas, Coyuca de Benítez, 11.05.2011, G. Murugan, CIB 1019, 2 (1) pereionipods; Aguas Blancas, 15 km NW Aguas Blancas, 20.08.1980, J. L. Villalobos, CNCR 2621, 2 females (48.2 and 60.4 mm), J. L. Villalobos, CNCR 2630, 1 male (72.2 mm), 3 females (50.9 to 56.4 mm); Río Papagayo 3 basin: Río Papagayo, CFE La Venta, 24.06.1988, L. Márquez, CNCR 10112, 2 males (82.6 and 84.4 mm), 1 female (59.6 mm), L. Márquez, CNCR 10117, 3 males (45.3 to 48.4 mm), 2 females (49.7 and 73.1 mm), M. Gómez, CNCR 10126, 3 males (35.1 to 44.1 mm), 9 females (33.2 to 61.4 mm); Río Pinola and Río Tonalá, 18.12.1987, J. P. Gallo, CNCR 8778, 1 male (42.0 mm); Río Papagayo 4 basin: Tres Palos, Acapulco, 28.07.1984, CNCR 13646, 3 males (48.6 to 57.3 mm), 1 female (62.9 mm). OAXACA: Río Verde basin: El Carnero, Chatañu, 24.11.2007, J. Bautista, CIB 1001, 1 (1) male (48.8 mm), 5 (2) juveniles (8.7 to 11.5 mm); Río Viejo, 05.2008, J. Bautista, CIB 1002, 1 (1) female (82.3 mm); Río Zimatán 1 basin: Río Grande before junction to Río Jícara, Merced del Potrero, San Miguel del Puerto, 15.01.2007, J. L. Villalobos, CNCR 24734, 1 male (67.9 mm), 12.04.2007, J. L. Villalobos, CNCR 24798, 2 females (50.9 and 61.5 mm); Río Zimatán 2 basin: Río Zimatán, Santa María Petatengo, Huatulco, 07.09.2000, M. A. Casariego, CNCR 18891, 1 male (69.8 mm), 1 female (84.6 mm); Río Zimatán, bridge Huatulco-Salina Cruz, San Miguel del Puerto, 13.04.2007, J. L. Villalobos, CNCR 24810, 1 male (32.8 mm), 26.10.2007, J. L. Villalobos, CNCR 25098, 1 male (26.9 mm); Río Copalita 2 basin: Río Ayuta, Huatulco, 07.09.2000, M. A. Casariego, CNCR 18892, 2 females (34.8 and 48.3 mm); Río Copalita, Las Hamacas, bridge Huatulco-San Miguel del Puerto, 10.04.2007, J. L. Villalobos, CNCR 24777, 1 male (40.7 mm); 24.10.2007, J. L. Villalobos, CNCR 25031, 2 males (45.2 and 48.3 mm), 2 females (26.2 and 34.7 mm); 12.06.2007, J. L. Villalobos, CNCR 24964, 14 males (67.1 to 95.2 mm), 5 females (79.2 to 89.5 mm); Río Copalita, bridge Huatulco-Salina Cruz, Santa María Huatulco 17.01.2007, J. L. Villalobos, CNCR 24758, 1 male (39.5 mm), 1 female (44.5 mm), 13.04.2007, J. L. Villalobos, CNCR 24820, 3 males (32.9 to 34.7 mm), 6 females (31.6 to 51.8 mm); Río Copalita 1 basin: Junction Río Copalita-Río Yuviaga, San Miguel del Puerto, 16.01.2007, J. L. Villalobos, CNCR 24744, 1 male (83.3 mm); Río Yuviaga, San Miguel del Puerto, 13.06.2007, J. L. Villalobos, CNCR 24978, 4 males (67.4 to 88.1 mm), 3 females (69.5 to 76.5 mm); Las Brisas de Copalitilla, Río Copalita, San Miguel del Puerto, 10.04.2007, J. L. Villalobos, CNCR 24783, 1 female (54.2 mm); Río Tequisistlán basin: Río Tequisistlán, 74.5 km Tehuantepec, 28.12.1955, A. Villalobos Figueroa, CNCR (IB/CC) 246, 1 male (32.5 mm), 4 females (17.2 to 22.4 mm); Río Tehuantepec 2 basin: Presa de Mistequilla, Tehuantepec, 19.12.1955, A. Villalobos Figueroa, CNCR (IB/CC) 253, 7 males (23.1 to 29.9 mm), 27 females (23.0 to 29.9 mm); Río Coyula basin: Río Coyula, Arroyo Magdalena, Rancho Hagia-Sophia, Santa María Huatulco, 13.04.2007, J. L. Villalobos, CNCR 24838, 2 females (38.5 and 47.6 mm); 15.06.2007, J. L. Villalobos, CNCR 25022, 2 males (51.1 and 57.1 mm), 1 female (48.9 mm); Río Coyula, bridge Huatulco-Salina Cruz, Santa María Huatulco, 17.01.2007, J. L. Villalobos, CNCR 24765, 3 females (40.9 to 59.1 mm), 13.04.2007, J. L. Villalobos, CNCR 24829, 1 male (39.2 mm), 15.06.2007, J. L. Villalobos, CNCR 25013, 3 males (25.1 to 39.9 mm), 1 female (31.0 mm). CHIAPAS: Laguna Mar Muerto C basin: Río Lagartero, Arriaga, 30.07.1983, J. L. Villalobos, CNCR 13050, 1 female (54.6 mm); Río Huixtla basin: Río Vado Ancho, Villa de Colmaltitlán, 20.12.1971, C. Martínez Palacios, CNCR (IB/CC) 248, 4 males (15.2 to 31.7 mm), 2 females (20.6 and 21.2 mm), 24.07.1971, C. Martínez Palacios, CNCR (IB/CC) 249, 1 male (27.2 mm); Poza Silva, Río Vado Ancho, Villa de Colmaltitlán, 29.07.1971, C. Martínez Palacios, CNCR 255, 2 males (34.9 and 73.9 mm). COSTA RICA: Río

Térraba basin, MZUCR 29651, 1 male (CL = 21 mm), and 1 female (CL = 25 mm).

*Macrobrachium olfersii* (Wiegmann, 1836).—MEXICO: BAJA CALIFORNIA SUR: Todos Santos basin: Todos Santos, 26.11.2004, L. Hernández, CIB 836, 2 males (32.1 and 27.9 mm), 1 female (23.3 mm); La Poza, Todos Santos, 18.11.2008, H. García, CIB 1133, 1 male (27.5 mm). SINALOA: Río Presidio basin 2: Río Presidio, Villa Unión, 02.05.2011, G. Murugan, CIB 1029, 7 males (16.6 to 25.0 mm). OAXACA: Río Verde basin: Río Viejo, 09.07.2008, J. Bautista, CIB 1147, 4 males (16.6 to 19.0 mm).

*Macrobrachium tenellum* (Smith, 1871).—MEXICO: BAJA CALIFORNIA SUR: Las Pocitas-San Hilario basin: Santa Fe, 29.05.2010, A. Maeda, CIB 1193, 2 males (23.5 and 42.2 mm), 3 females (22.8 to 44.2 mm); Santa Rita basin: Agua de León, 03.07.2011, A. Maeda, CIB 1194, 2 males (27.1 and 51.8 mm), 3 females (24.5 to 46.3 mm); Santa Agueda basin: Santa Rosalía, 17.09.2010, A. Maeda, CIB 1068, 1 male (26.7 mm). SONORA: Río Mayo 3 basin: Primavera, Huatabampo and Jarupa, 22.04.2011, G. Murugan, CIB 1074, 4 male (28.5 to 54.2 mm), 1 female (38.6 mm). GUERRERO: Laguna de Coyuca: 11.05.2011, A. Maeda, CIB 1096, 5 males (21.9 to 41.0 mm). OAXACA: Río Verde basin: Río Verde (Río Viejo), 23.07.2008, J. Bautista, CIB 1099, 5 males (49.0 to 60.2 mm).

#### Taxonomic Morphological Revision

We made a morphological revision of specimens collected in the field and previously deposited in the Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México (CNCR), the Colección Carcinológica, Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León Mexico (UANL), and the Museo de Zoología, Universidad de Costa Rica, San José, Costa Rica (MZUCR). In the laboratory, the specimens that we collected were sorted according to gender. Males were distinguished by the presence of the appendix masculina on the second pleopods and confirmed by the morphology of the thoracic sternite 8 (T8) (see Results: additional taxonomic morphological characters). A digital caliper (700-113, Mitutoyo, Kawasaki, Japan), was used for measuring total length (tip of rostrum to posterior end of telson), carapace length (CL) (tip of rostrum to posterior dorsal margin of carapace), length and height of merus, carpus, and propodus (palm), and length of dactylus of the larger chela of the second pair of pereopods. The number of teeth on both margins of the rostrum was also recorded. Specimens were revised and determined as *M. occidentale*, following the descriptions and keys for the species of *Macrobrachium* by Holthuis (1950, 1952), Wicksten (1989), Hendrickx (1995), and Hernández et al. (2007). Anatomical nomenclature used in this work is according to Holthuis (1952), McLaughlin (1980) and Hernández et al. (2007). We included revision of additional characters, such as the inferior orbit shape, bec ocellaire, epistome, thoracic sternite 4 (T4), thoracic sternite 8 (T8), and pre-anal carina on inter-uropodal sclerite, as proposed by Short (2004). For comparative purposes, the shape of T4 in adults of other species (*M. americanum*, *M. digueti*, *M. hobbsi*, *M. michoacanus*, *M. olfersii* and *M. tenellum*) found in Mexico and Costa Rica was analysed. A database containing all morphometric and meristic data was deposited at CIB.

#### Molecular Analysis

Molecular analysis was used to characterize the genetic identity of *Macrobrachium occidentale* and define whether the individuals from the peninsula that were morphologically identified belonged to the same entity found along the mainland coast of Mexico or whether they form a distinct molecular lineage by using fragments of the 16S and COI mitochondrial genes. In the GenBank, sequences of 16S and COI genes of *M. occidentale* were not available. We obtained sequences from 30 individuals from the peninsula and 41 from the mainland (see Material examined). The genetic identity of these individuals was determined through the definition of the haplotypes. The two geographical groups (peninsula and the mainland) were compared through analyses of their haplotypic diversity, population structure, and demography. Additionally, phylogenetic analyses with some selected freshwater shrimp from the American continent were performed to test the monophyly and species status of the studied populations.

#### DNA Extraction, Amplification and Sequencing

DNA was extracted from muscle tissue using Genra Puregene kit (Qiagen). A fragment of 16S was amplified with primers 1471B and 1472B (Liu et al., 2007) under the cycling conditions: initial denaturation at 94°C for 4 minutes, 35 cycles of denaturation at 94°C for 30 seconds, annealing at 53°C for 30 seconds, extension at 72°C for 40 seconds, and a final extension

at 72°C for 5 minutes. Using the same cycling conditions, the COI fragment was also amplified with primers COI-a and COI-f (Palumbi and Benzie, 1991). Amplified products were sequenced with forward primers, and a few samples were sequenced in both directions to verify the accuracy of the sequences. Sequences were edited using DNA Baser 3.5 and aligned with Clustal X (Thompson et al., 1997) under default settings. Sequences were deposited in GenBank under accession numbers KF636829-KF636970.

#### Haplotypic Diversity, Population Structure and Demography

Number of polymorphic sites ( $s$ ), nucleotide diversity ( $\pi$ ), number of haplotypes ( $h$ ) and haplotype diversity ( $H$ ) were calculated with DnaSP 5.10 (Librado and Rozas, 2009). Genetic distances (uncorrected  $p$ -distance) among the haplotypes were calculated using Molecular Evolutionary Genetics Analysis 5 (Tamura et al., 2011). To examine the distribution of haplotypes among populations, a median-joining haplotype network for each gene was constructed with the program Network 4.6 (available online at <http://www.fluxus-engineering.com>) (Bandelt et al., 1999). We performed a hierarchical analysis of molecular variance (AMOVA) of the combined 16S and COI sequence data of specimens from four drainage basins of the peninsula as one group and specimens from nine of the mainland basins as another group, using Arlequin 3.5 (Excoffier and Lischer, 2010) to assess distribution of genetic variation. The demographic history of populations was examined with mismatch distributions based on the observed and simulated differences among haplotypes (Slatkin and Hudson, 1991; Roger and Harpending, 1992) in the Arlequin and DnaSP.

#### Phylogenetic Analysis

Using combined data of fragment sequences of 16S and COI genes, the phylogenetic relationship of *M. occidentale* (using haplotypes that showed the wider range of genetic distances) with other selected freshwater shrimp species from the American continent (Pileggi and Mantelatto, 2010; Rossi and Mantelatto, 2013) (see below) was analysed using maximum parsimony (MP) and maximum likelihood (ML) methods executed in PAUP\* 4 beta 10 (Swofford, 2002) and Bayesian inference (BI) in MrBayes 3.2 (Ronquist et al., 2012). From the GenBank database, we included fragment sequences of 16S and COI of *M. acanthurus* (Wiegmann, 1836) (HM352444 and HM352485), *M. amazonicum* (Heller, 1862) (HM352443 and HM352488), *M. americanum* (HM352447 and HM352489), *M. brasiliense* (Heller, 1862) (HM352429 and HM352481), *M. carcinus* (Linnaeus, 1758) (HM352451 and HM352493), *M. crenulatum* Holthuis, 1950 (HM352463 and HM352498), *M. digueti* (Bouvier, 1895) (JQ805806 and JQ805903), *M. faustinum* (de Saussure, 1857) (JQ805809 and JQ805907), *M. heterochirus* (Wiegmann, 1836) (HM352454 and HM352494), *M. jelskii* (Miers, 1877) (HM352437 and HM352484) and *M. olfersii* (HM352458 and HM352497) as the ingroup and *Exopalaemon carinicauda* (Holthuis, 1950) (EF560650), *E. modestus* (Heller, 1862) (DQ194971 and AB235307) and *E. orientis* (Holthuis, 1950) (DQ194972 and AB235306) as the outgroup. Nucleotide substitution model for the combined data (16S-COI) was determined with jModelTest 2.1.3 (Darriba et al., 2012) and the best-fit model, based on the Bayesian Information Criterion (BIC), was selected to implement in the ML and BI. Branch support in the ML was evaluated by bootstrapping with 200 pseudo-replicates, while the BI was run for five million generations. In the BI, trees were sampled at every 1000 generations. A 50% majority rule consensus tree with posterior probabilities was generated after the elimination of burn-in trees. In the MP analysis, the heuristic search option with tree bisection and reconnection branch-swapping with 5000 bootstrapping and 100 random taxon additions per bootstrap were used to generate trees. For the MP and ML, we also generated a majority rule consensus tree.

#### Presentation of the Results

Geographical distribution data of *M. occidentale* in Mexico and its morphological and haplotypic identity are presented in a taxonomic account that includes: Name, author, and year of description of the family, genus, and species, species synonymy (restricted to Mexican material), type locality, diagnosis, additional taxonomic characters, haplotypic identity, distribution in Mexico, and general distribution. The morphological diagnosis is based on the species description by Holthuis (1952) and updated according to the morphological variations found in the Mexican material. In Table S1 of the supplementary material, that is part of the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>, we provide geographical information about the studied sites (from our field prospecting and from scientific collections), including available data of the water characteristics. Data on genetic identity and



geographical distribution of 16S and COI haplotypes from the peninsula and the mainland are presented in the section “Haplotypic diversity, population structure, and demographic history,” and data on the phylogenetic relationship of selected species are presented in the section “Phylogenetic analyses.”

## RESULTS

Palaemonidae Rafinesque, 1815

*Macrobrachium* Bate, 1868

*Macrobrachium occidentale* Holthuis, 1950

(Figs. 1-4)

*Macrobrachium occidentale* Holthuis, 1950; Hendrickx et al., 1983; Wicksten, 1983, 1989; Wicksten and Hendrickx, 1992, 2003; Román-Contreras, 1991; Villalobos-Hiriart et al., 1993, 2010; Hendrickx, 1994, 1995; Martínez-Guerrero, 2007; Guzmán Arroyo et al., 2009.

Type Locality.—Río de los Esclavos, S of Cuilapa, Guatemala (Holthuis, 1950); holotype and types deposited at the U.S. National Museum (U.S.N.M. Cat. No. 84151) (Holthuis, 1952).

Diagnosis.—Rostrum narrow, straight or slightly curved downward (Fig. 1), it reaches the second joint and sometimes the basal part of the third joint of the antennular peduncle (Fig. 2D); upper margin bears 10 to 14 teeth, 4 to 7 of which are postorbital, lower margin bears 2 to 4 teeth; antennules and eyes are normal in shape. Second pereopods similar in shape but unequal in size in adult males (Fig. 2). Propodus elongate, twice as long as high, little compressed laterally; dorsal and right lateral sides of propodus and fixed finger with distinct spines (Figs. 1 and 2); ventral and inner sides of propodus and dactylus with small spines and tubercles (Fig. 2C); fingers of largest chela with narrow gap between cutting edges filled with plumose setae, and are about 2/3 of the length of the propodus, sometimes shorter; cutting edges with a row of 5 to 9 denticles similar in size; about 1/5 of the cutting edge near the tip of the fingers no denticles are present, but instead a blade-like crest is placed along the edge (Fig. 1). Carpus is about twice as long as high, and about 3/4 of the length of the propodus and as long or shorter than merus, while the merus is about twice as long as high, and about 3/4 of the length of the propodus. Ischium is about 2/3 of the length of the merus. Pleopods and uropods were normal in shape. Carapace length of largest male was 48.9 mm and largest female was 38.2 mm.

Additional Morphological Characters.—Shape of inferior orbit distinctly convex, moderately produced; bec ocellaire strongly developed with apex truncated (Fig. 3A-B); ocular cornea large and well pigmented with accessory pigment spot (Fig. 2D); epistome with lobes rounded; thoracic sternite 4 (T4) with well-developed median process showing two posterior separated protuberances and a small anterior central protuberance (Fig. 4A-D); thoracic sternite 8 (T8) in male with joined lobes and in female with widely-separated lobes (Fig. 3C-D); inter-uropodal sclerites with well developed preanal carina, normally with dorsal setae (Fig. 3E-F).

Haplotypic Identity.—Sequences of the mitochondrial genes 16S and COI were obtained from 71 individuals. Align-

ment of sequences was unambiguous with no indels in either gene. The 16S sequences of 479 bp length had 17 polymorphic sites (*s*), of which only four were parsimoniously informative. Haplotype analysis performed in the DnaSP 5.10 software yielded 17 haplotypes (*h*) for this gene. Their specific sequence is shown in Table S2 of the supplementary material, that is part of the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>. For COI, the 564 bp sequences had 22 parsimoniously informative sites from 65 polymorphic sites. The number of haplotypes found for this gene was 49, and their specific sequence is shown in Table S3 of the supplementary material, that is part of the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>. All polymorphic sites in the 16S are of the transition type, whereas 53 sites of COI are transition type and only seven of the remaining 12 sites are of the transversion type. One of the two transitions found in the first position of codons produced amino-acid substitutions.

Distribution in Mexico.—We studied 139 sites on the Pacific slope distributed among 62 drainage basins in 11 Mexican states (Table S1). Here, we report the first records of *M. occidentale* on the Baja California Peninsula. The species exhibits a broad distribution along the Mexican Pacific slope, from the southern part of the peninsula in the State of Baja California Sur to the State of Chiapas in southern Mexico, bordering Guatemala. Extensive field prospecting for *Macrobrachium* in the area indicate that the distribution of this species is not continuous, given a gap of records of about 2000 kilometers along the coastal plains of the northern part of the Gulf of California (Fig. 5). *M. occidentale* occurs in 10 Mexican states in 34 drainage basins (five on the peninsula and 29 on the mainland): BAJA CALIFORNIA SUR: First records for the state; specimens were collected from five drainage basins: Santa Rita, Las Pocitas-San Hilario, Todos Santos, and Plutarco E. Calles on the peninsular Pacific slope (western side of the peninsula), and San José del Cabo on the Gulf of California slope (eastern side of the peninsula). SONORA: Río Mayo 3 basin, first record for the state. SINALOA: Río Baluarte basin (Hendrickx et al., 1983; Wicksten, 1983, 1989; Wicksten and Hendrickx, 1992, 2003), and the first records for the basins of Río Sinaloa 2, Río Elota, Río Quelite 2, and Río Presidio 2. NAYARIT: Río Santiago (Guzmán Arroyo et al., 2009), and the first records for the basins of Río Huaynamota and Río Ameca Ixtapa B. JALISCO: First records for the state from the basins of Río Cuale, Río Cuitzmala, and Río Purificación. COLIMA: Río Armería basin, first record for the state. MICHOACÁN: Río Bajo Balsas basin, first record for the state. GUERRERO: Río Coyuca basin (Román-Contreras, 1991), and the first records for the basins of Río Petatlán 2, Río Atoyac 2, and Río Papagayo. OAXACA: La Ventosa (Martínez Guerrero, 2007), Río Coyula, Río Copalita, and Río Zimatán basins (Villalobos-Hiriart et al., 2010), and the first records for the basins of Río Verde, Río Tequisistlán, and Río Tehuantepec 2. CHIAPAS: First records for the state from the basins of Laguna Mar Muerto C, and Río Huixtla. Specimens were found in waters with TDS 0.12 to 1.28 g l<sup>-1</sup>, at pH 8.0-8.3, and 22.5-34.2°C.



Fig. 1. Anterior part of body with larger chela of the second pair of pereiopods in left lateral view of adult males of *Macrobrachium occidentale*. A, Specimen from mainland Mexico, El Colomo, Río Ameca Ixtapa basin, Nayarit (CIB 1016), scale bar = 9 mm; B, Specimen from the Baja California Peninsula, San Pedro de la Presa, Santa Rita basin, Baja California Sur, Mexico (CIB 1020), scale bar = 14.5 mm. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/1937240x>.

**General Distribution.**—*Macrobrachium occidentale* is distributed along the Pacific slope of North America and Central America from the Baja California Peninsula to Panama (Fig. 5). Besides Mexico, the species has been recorded in Guatemala in Río de los Esclavos (Holthuis, 1950), and Río Naranjo and Río Guacalate (Holthuis, 1952); El Salvador in Río del Desague and Río Lempa (Holthuis, 1952); Costa Rica in Río Grande de Térraba (Rólier-Lara and Wehrtmann, 2011); and Panama in Boca de Pavarando (Holthuis, 1952) and Río Santa María, Río Cobre, Río La Villa, and Río Parita (Vega et al., 2006).

#### Haplotypic Diversity, Population Structure, and Demographic History

Neither of the two genes showed a distinct population structure. Single individuals represented the majority of the haplotypes: 82.4% in 16S and 87.8% in COI. Haplotype-sharing among the drainage basins and between the peninsula and the mainland were observed for both genes. In the 16S gene, the predominant 16S haplotype (Hap 13) was found in 53 individuals and occurred in all 13 drainage basins (Table 1). This haplotype formed the central node for star-like clusters



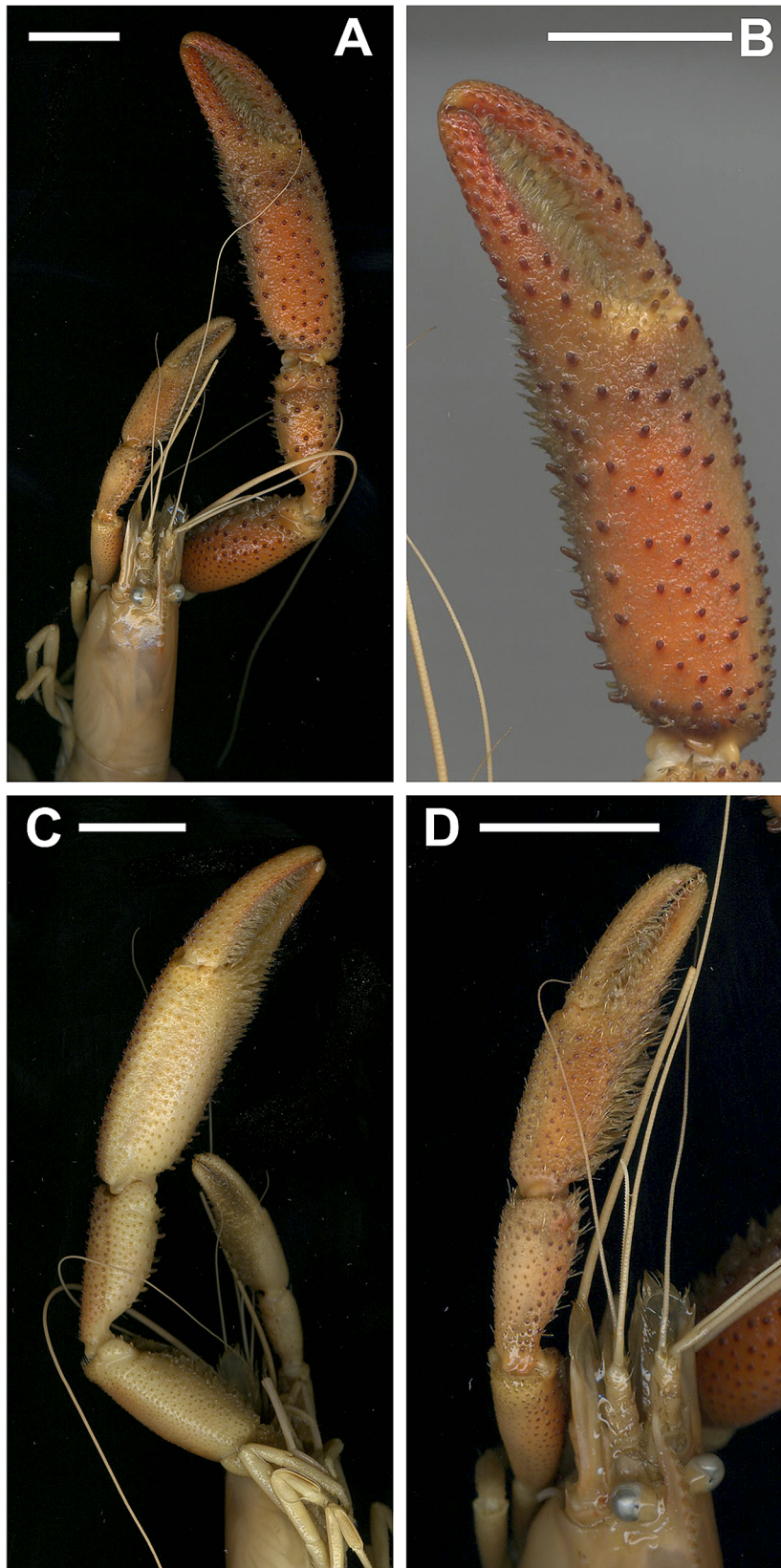


Fig. 2. Adult male of *Macrobrachium occidentale* from the Baja California Peninsula, Rancho Las Cuevas, Las Pocitas-San Hilario basin, Baja California Sur, Mexico (CIB 1004). A, Anterior part of body in dorsal view; B, Larger chela of the second pair of pereopods in right lateral view; C, Larger chela of the second pair of pereopods in ventral view; D, Smaller chela of the second pair of pereopods in left lateral view. Scale bars = 14 mm. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/1937240x>.



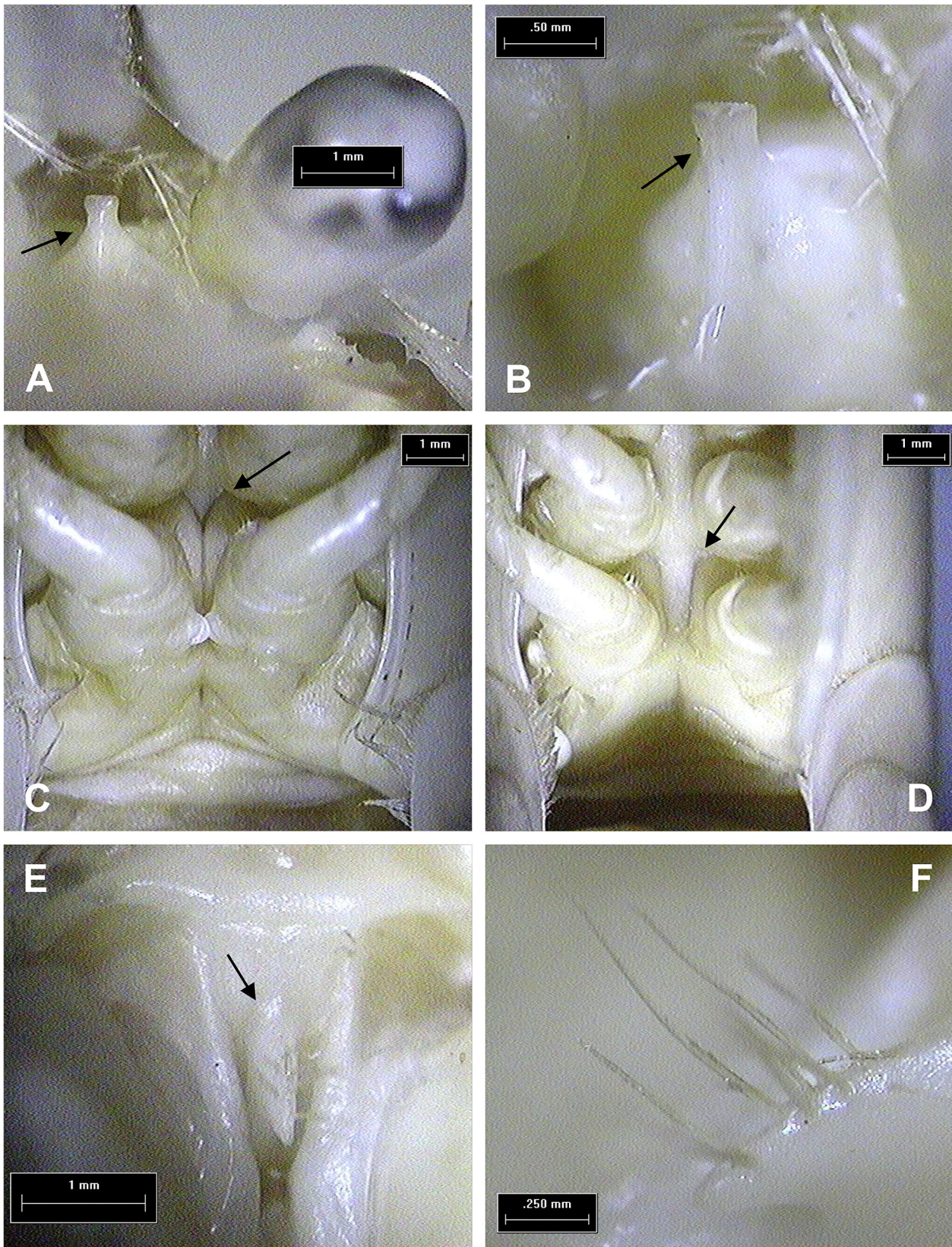


Fig. 3. Male and female of *Macrobrachium occidentale* from the Baja California Peninsula, San Pedro de la Presa, Santa Rita basin, Baja California Sur, Mexico (CIB 1020). A, Bec ocellaire with apex truncated from a male in anterior view; B, Magnified view from A; C, Thoracic sternite 8 (T8) of a male showing joined lobes in ventral view; D, Thoracic sternite 8 (T8) of a female showing widely separated lobes in ventral view; E, Inter-uropodal sclerite with well developed preanal carina of a male in ventral view; F, Preanal carina in left lateral view (from E) showing dorsal setae. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/1937240x>.



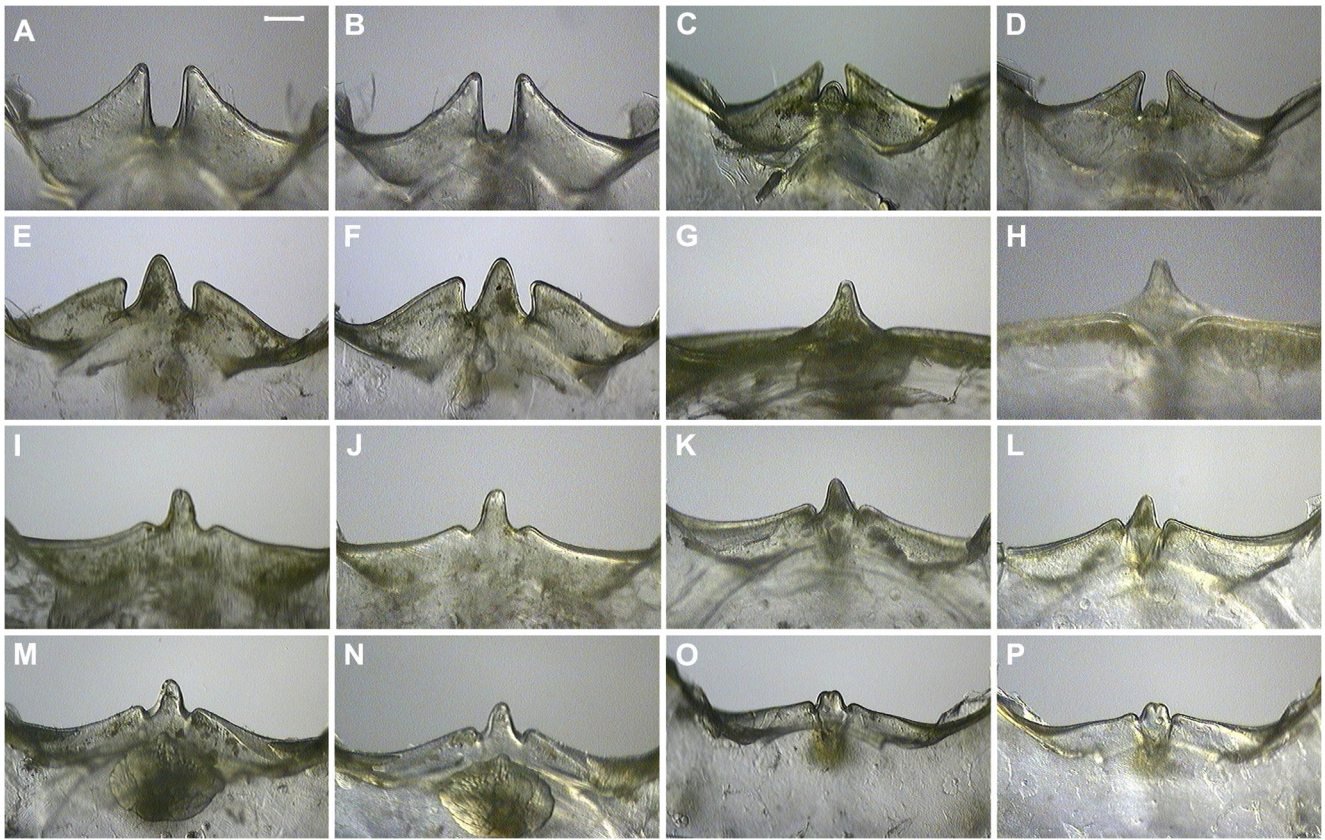


Fig. 4. Stereomicroscope photographs of thoracic sternite 4 (T4) of males of seven species of *Macrobrachium* from Mexico. A, C, E, G, I, K, M and O, in anterior view; B, D, F, H, J, L, N and P, in posterior view. A-D, *M. occidentale*: A-B, from Santa María Toris, Santa Rita basin, Baja California Sur (CIB 1007, CL = 24.9 mm); C-D, from La Huerta, Río Purificación basin, Jalisco (CIB 1018, CL = 20.8 mm). E-F, *M. americanum* from Rancho Huatamote, Las Pocitas-San Hilario basin, Baja California Sur (CIB 1024, CL = 27.5 mm). G-H, *M. tenellum* from La Poza, Todos Santos basin, Baja California Sur (CIB 1028, CL = 50.3 mm). I-J, *M. digueti* from La Poza, Todos Santos basin, Baja California Sur (CIB 1027, CL = 19.3 mm). K-L, *M. michoacanus* from Rancho Huatamote, Las Pocitas-San Hilario basin, Baja California Sur (CIB 1026, CL = 24.4 mm). M-N, *M. olfersii* from Villa Unión 2, Río Presidio 2 basin, Sinaloa (CIB 1029, CL = 25.2 mm). O-P, *M. hobbsi* from Rancho Huatamote, Las Pocitas-San Hilario basin, Baja California Sur (CIB 1025, CL = 19.2 mm). Scale bar = 0.25 mm. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/1937240x>.

in the median-joining haplotype network (Fig. 6). Another haplotype (H 17) was shared by two populations, at Todo Santos on the peninsula and Río Purificación on the mainland. From this haplotype, the haplotype 16 at Las Pocitas-San Hilario was derived. In the COI gene, the predominant COI haplotype 8 was found in individuals from eight of the 13 drainage basins (Table 2) and formed a central node for star-like clusters in the median-joining haplotype network (Fig. 7). COI haplotype 8 was shared by 14 individuals collected from the peninsula and the mainland (two basins of the peninsula and two basins from Sinaloa and one basin each from Sonora, Nayarit, Jalisco and Oaxaca on the mainland). COI haplotypes 1, 6 and 49 occurred in both geographic regions (Fig. 7). Haplotypes derived from the shared haplotypes were found in the peninsula and the mainland. For 16S, all haplotypes, except for one, differed by a single mutations step, whereas 1 to 5 mutations steps separated the COI haplotypes. Uncorrected pairwise distance between the 16S haplotype 13, the most common, and the others ranged from 0.21-0.63%. A maximum distance of 1.0% was observed between the 16S-haplotype 16 found at Plutarco E. Calles basin on the peninsula and 16S haplotypes 2 and 14 found in the Río Presidio 2 and Río Purificación basins on

the mainland. Uncorrected pairwise distance between COI haplotype 8, the most common, and the others ranged from 0.18-1.77%. A maximum distance of 2.5% was observed between COI haplotype 40 found in the Río Baluarte 2 basin on the mainland and COI haplotypes 13 and 18 found in the same Río Baluarte 2 and Río Ameca Ixtapa B basins on the mainland.

Haplotype diversity was high in COI ( $H = 0.957$ ), compared to 16S ( $H = 0.445$ ) because there were a large number of haplotypes detected in the COI. The nucleotide diversity was similar to the haplotype diversity by showing high values ( $\pi = 0.00866 \pm 0.00062$ ) in comparison to 16S ( $\pi = 0.00134 \pm 0.00029$ ). Within each region, COI haplotype diversity was high at all locations except Río Elota, which showed no haplotype diversity in both genes. In 16S, haplotype diversity was low in Río Ameca Ixtapa B, Río Baluarte 2, Río Mayo 3, and Río Purificación populations and, in addition to Río Elota, Río Verde also showed no haplotype diversity. The AMOVA of combined *M. occidentale* 16S and COI sequences from the peninsula and the mainland indicated the absence of genetic structure between the two geographical regions, among drainage basins within geographical regions and within

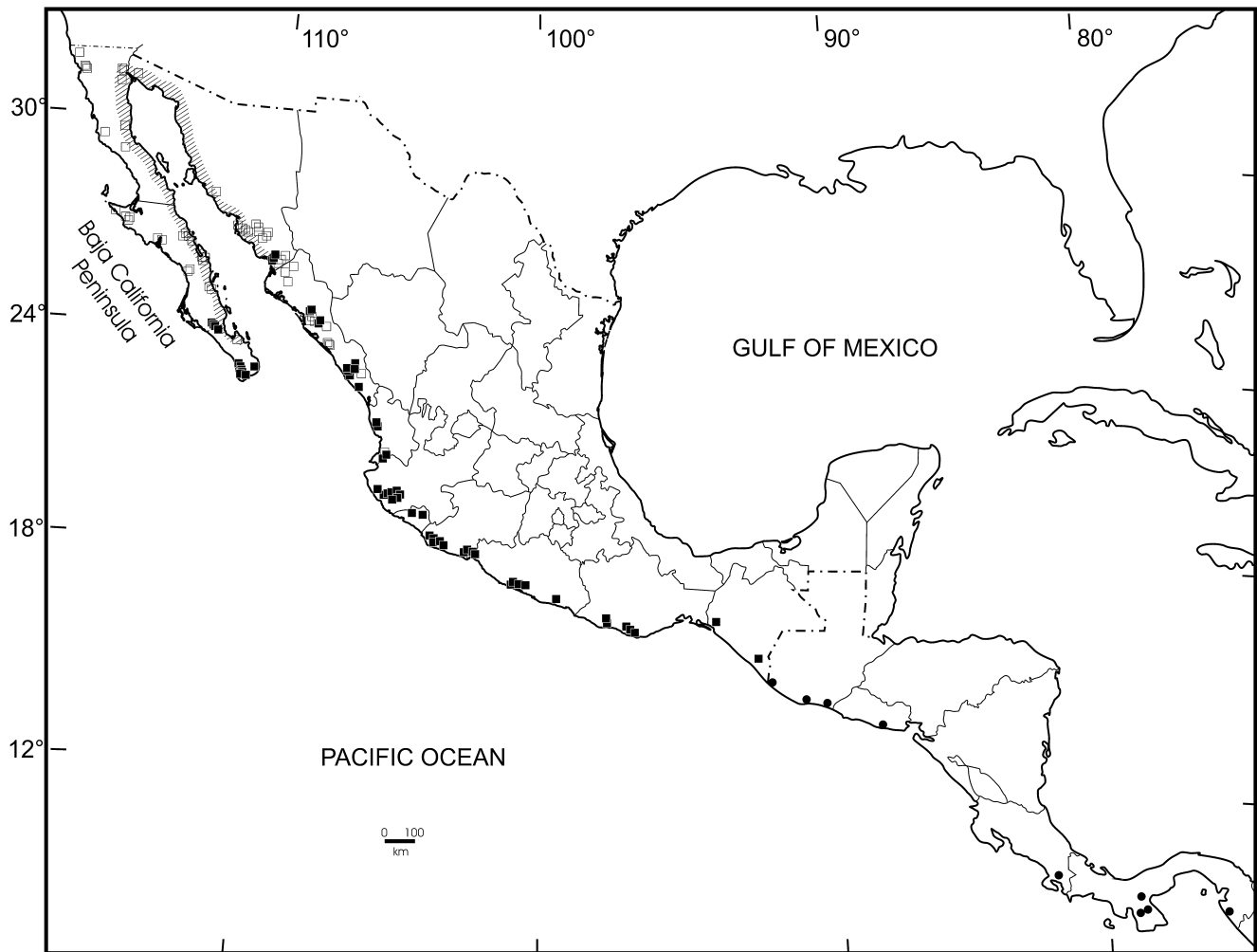


Fig. 5. Geographical distribution of *Macrobrachium occidentale*. Solid spheres represent records of the species in Central America. Solid squares represent records of the species in Mexico. Empty squares represent sampled areas without records of the species. Area with dashed lines show the disjunct distribution of the genus *Macrobrachium* along the coastal plains of the northern part of the Gulf of California (= Sea of Cortés).

drainage basins ( $P > 0.05$ ) (Table 3). Highest percentage of variation (97.73%) was observed in *M. occidentale* within drainage basins compared to very low percentage of variation (0.41%) between the two regions (Table 3). Mismatch analyses (raggedness index) also supported a model of sudden populations expansion (Harpending's = 0.0066,  $P > 0.05$ ) in a monomodal distribution curve (Fig. 8).

#### Phylogenetic Analyses

The three methods of phylogenetic analyses, MP, ML, and BI, performed with the combined data set showed no significant conflict ( $P = 0.80$ ) in the partition homogeneity test (Farris et al., 1995) and indicated that sequences for *M. occidentale* formed a monophyletic group (Fig. 9). It was placed as a sister clade to *M. heterochirus*. Monophyly of this group was strongly supported (99-100%) by the three methods of the phylogenetic analyses. The *M. heterochirus*- and *M. occidentale*-groups formed a sister clade with six freshwater species, *M. americanum*, *M. carcinus*, *M. crenulatum*, *M. digueti*, *M. faustinum* and *M. olfersii*. This rela-

tionship was strongly supported by BI (100%), MP (71%) and ML (86%) (Fig. 9). In the ML and BI, we implemented the transversal model HKY + I + G, with base frequencies A = 0.3130, C = 0.2075, G = 0.1632, T = 0.3163, transition/transversion ratio 3.5252, and the gamma shape parameter 0.7500, which was selected, based on BIC in the jModeltest.

#### DISCUSSION

##### Morphology of *Macrobrachium occidentale*

The morphological diagnosis of the species is updated according to the variation of morphological characters of the Mexican material. The range of the number of teeth of the rostrum established by Holthius (1952) is extended from 10 to 14 in the dorsal carina, of which 4 to 7 are postorbital, and the ventral carina from 2 to 4. As described by Holthius (1952), the fingers of largest chela contain a row of 5 to 9 denticles that are similar in size and about 1/5 of the cutting edge; however, near the tip of the fingers, no denticles are present, but instead, there is a blade-like crest along the edge. Not previously mentioned, we report that

Table 1. Geographical distribution of 16S rDNA haplotypes (479-bp length) of *Macrobrachium occidentale* Holthuis, 1950 obtained from 71 individuals, 30 from four drainage basins of the Baja California Peninsula and 41 from nine drainage basins of the mainland Pacific slope of Mexico distributed in the states of Sonora, Sinaloa, Nayarit, Jalisco, Guerrero and Oaxaca. The drainage basins from the peninsula are: SR = Santa Rita; LP-SH = Las Pocitas-San Hilario; TS = Todos Santos; PEC = Plutarco E. Calles. The drainage basins from the mainland are: RM = Río Mayo 3; RS = Río Sinaloa 2; RE = Río Elota; RP = Río Presidio 2; RB = Río Baluarte 2; RA-I = Río Ameca Ixtapa; RPU = Río Purificación; RCO = Río Coyuca 2; RV = Río Verde. The number of individuals for each haplotype found in the basins is indicated.

Haplotype	Baja California Peninsula				Sonora	Sinaloa				Nayarit	Jalisco	Guerrero	Oaxaca	Total number of individuals (basins)
	SR	LP-SH	TS	PEC	RM	RS	RE	RP	RB	RA-I	RPU	RCO	RV	
Hap 1					1									1 (1)
Hap 2								1						1 (1)
Hap 3		1												1 (1)
Hap 4		1												1 (1)
Hap 5										1				1 (1)
Hap 6									1					1 (1)
Hap 7								1						1 (1)
Hap 8	1													1 (1)
Hap 9				2										2 (1)
Hap 10				1										1 (1)
Hap 11				1										1 (1)
Hap 12			1											1 (1)
Hap 13	3	6	1	9	4	1	3	3	6	4	8	1	4	53 (13)
Hap 14											1			1 (1)
Hap 15		1												1 (1)
Hap 16				1										1 (1)
Hap 17			1								1			2 (2)

the shape of the inferior orbit is distinctly convex and shows consistency between sexes. The morphological characters, such as the bec ocellaire, epistome, thoracic sternites T4 and T8, and the pre-anal carina are for the first time described for *M. occidentale*. The consistency of these characters was also observed in a male and a female from Río Térraba, Costa Rica. To our knowledge, these structures have not been studied in any other Mexican species or in other species from the American continent. The bec ocellaire, a structure that has not been described in most species of *Macrobrachium* (Short, 2004) is strongly developed with a truncated apex in *M. occidentale* (Fig. 3A-B). The epistome in *M. occidentale* is divided into two anteriorly-rounded lobes, as present in many Australian *Macrobrachium* (Short, 2004). The T4 in Australian *Macrobrachium* is armed with a well-developed median process, but in some species can be greatly reduced or absent (Short, 2004). The characteristic shape of the T4 of *M. occidentale* is consistent between sexes and unique among the seven morphological species reported for the whole Pacific slope of Mexico; therefore, it is useful to have additional diagnostic characters for this species. In all revised material (adult males and females), the T4 is well-developed with a median process showing two posteriorly-separated protuberances and a small, anterior central protuberance (Fig. 4A-D). In *M. americanum*, it is well developed with a median process showing two posteriorly-separated protuberances and a larger anterior central protuberance (Fig. 4E-F); in *M. tenellum*, it is well developed with a median process showing a large anterior central protuberance (Fig. 4G-H). In the other species (*M. digueti*, *M. michoacanus*, *M. olfersii* and *M. hobbsi*), it is well developed and similar among them with a median process showing two, posteriorly separated, small

protuberances and a larger anterior protuberance (Fig. 4I-P). Regarding the morphology of the T8, Short (2004) reported that male Australian *Macrobrachium* has anterolateral lobes that can be well separated, narrowly separated, or contiguous postero-medially, but did not mention the morphology of this structure in females. The T8 in *M. occidentale* is a useful sexual dimorphic character, where the lobes are joined postero-medially in males, and widely separated in females (Fig. 3C-D). Short (2004) reports that the presence and morphology of the pre-anal carina in the inter-uropodal sclerite of 13 Australian *Macrobrachium*, only six bear such a developed structure; *M. occidentale* shows a well-developed preanal carina with dorsal setae in both sexes (Fig. 3E-F).

#### Molecular Identity and Geographical Distribution of *Macrobrachium occidentale*

The MP, ML and BI analyses with 16S and COI data sets confirmed the species status of *M. occidentale* (monophyletic group), and that together with *M. heterochirus*, formed a sister clade with the other six species analyzed (Fig. 9). No molecular evidences were found to support a hypothesis that the peninsular populations form a distinct lineage. The molecular genetic analyses demonstrated haplotype-sharing drainage basins between the two major geographic regions (peninsula and mainland; Tables 1 and 2). This indicates that the populations from both regions belong to the same genetic entity at the species level, morphologically identified as *M. occidentale*. These results support the notion that the geographical distribution of *M. occidentale* in its northern range extends to the southern parts of the peninsula and Sonora. This is the first report for the presence of the species in five states, completing the records from all



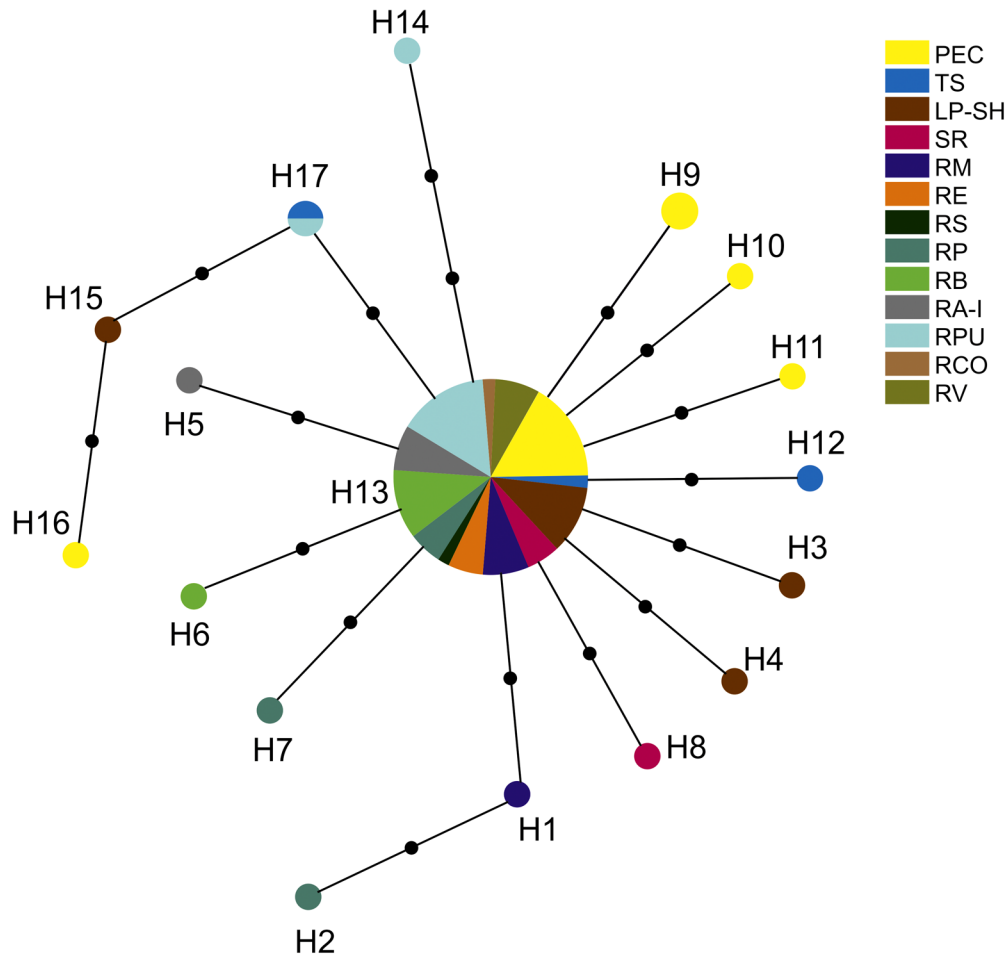


Fig. 6. Median-joining network based on 16S rDNA haplotypes of *Macrobrachium occidentale*. Haplotypes derived from 13 basins are represented by colors with node size proportional to number of individuals with that haplotype. Mutational steps are indicated as black dots along network branches and Network software inferred median vectors as white dots. Drainage basins from the peninsula: SR = Santa Rita; LP-SH = Las Pocitas-San Hilario; TS = Todos Santos; PEC = Plutarco E. Calles. Drainage basins from the mainland: RM = Río Mayo 3; RE = Río Elota; RS = Río Sinaloa 2; RP = Río Presidio 2; RB = Río Baluarte 2; RA-I = Río Ameca Ixtapa B; RPU = Río Purificación; RCO = Río Coyuca 2; RV = Río Verde.

states on the mainland, from Chiapas in the south to Sonora in the north. Therefore, the number of freshwater *Macrobrachium* from the peninsula increases from six (Hernández et al., 2007) to seven morphological species.

In the Indo-Pacific region *M. idae*, *M. lar*, *M. latidactylus*, *M. mammillodactylus* and *M. rosenbergii* show wide interoceanic distributions (Short, 2004), and mtDNA analyses supports the mechanism of oceanic dispersal rather than vicariance events (de Bruyn et al., 2005; Murphy and Austin, 2005; Chen et al., 2009). As reported for the other species of the genus from the Gulf of California (Hernández et al., 2007), *M. occidentale* also shows a disjunct distribution (Fig. 5). Similar disjunct distributions along the shores of this gulf occur for the caridean shrimp *Palaemonetes hiltoni* Schmitt, 1921 and the Mexican longbeak shrimp *Plesionika mexicana* Chace, 1937 (Hendrickx, 1995), and other animals, such as semi-aquatic gartersnakes. Their geographical records support the concept that the peninsula functions biologically as an island. Recently, using mitochondrial markers, de Queiroz and Lawson (2008) proposed that the Cape gartersnake *Thamnophis validus*, found in the southern part of the peninsula is likely a result of oceanic dispersal from

the mainland. The case of the distribution of the rosy boa *Lichanura trivirgata* has been explained by oceanic dispersal, but from the peninsula to the mainland Mexico (Wood et al., 2008).

*Macrobrachium occidentale* has been collected from coastal areas in upstream freshwater environments (Martínez Guerrero, 2007; Villalobos-Hiriart et al., 2010; Rólier-Lara and Wehrtmann, 2011), which suggests that it is an amphidromous species (Holthuis, 1980; Short, 2004; Cook et al., 2009). When there is high connectivity and free gene flow that are recent and constant, the same haplotypes are expected to be found in different geographical regions (Tero et al., 2003; Hughes et al., 2009). The presence of the same haplotypes of the amphidromous *M. occidentale* along the slopes of the Baja California Peninsula and the mainland of Mexico (Tables 1 and 2) indicates a constant genetic flow, likely to occur in both directions, which is most likely determined by seasonal reversals in long-shore currents within the Gulf of California. The median-joining haplotype network of COI indicated the probable derivation of haplotypes H 17 and H 32 from the peninsula to haplotypes H 18 in Nayarit and H 31 in Sinaloa, and the probable derivation of

Table 2. Geographical distribution of COI haplotypes (564-bp length) of *Macrobrachium occidentale* Holthuis, 1950 obtained from 71 individuals, 30 from four drainage basins of the Baja California Peninsula and 41 from nine basins of the mainland Pacific slope of Mexico distributed in the states of Sonora, Sinaloa, Nayarit, Jalisco, Guerrero and Oaxaca. The drainage basins from the peninsula are: SR = Santa Rita; LP-SH = Las Pocitas-San Hilario; TS = Todos Santos; PEC = Plutarco E. Calles. The drainage basins from the mainland are: RM = Río Mayo 3; RS = Río Sinaloa 2; RE = Río Elota; RP = Río Presidio 2; RB = Río Baluarte 2; RA-I = Río Ameca Ixtapa; RPU = Río Purificación; RCO = Río Coyuca 2; RV = Río Verde. The number of individuals for each haplotype found in the basins is indicated.

Haplotype	Baja California Peninsula				Sonora	Sinaloa				Nayarit	Jalisco	Guerrero	Oaxaca	Total number of individuals (basins)
	SR	LP-SH	TS	PEC	RM	RS	RE	RP	RB	RA-I	RPU	RCO	RV	
Hap 1				1	1				2	1				5 (4)
Hap 2		1												1 (1)
Hap 3											1			1 (1)
Hap 4			1											1 (1)
Hap 5												1		1 (1)
Hap 6				1							2			3 (2)
Hap 7				1										1 (1)
Hap 8	2			2	1		3	2		1	2		1	14 (8)
Hap 9	1													1 (1)
Hap 10					1									1 (1)
Hap 11		1												1 (1)
Hap 12								1		1				2 (2)
Hap 13								1						1 (1)
Hap 14											1			1 (1)
Hap 15								1						1 (1)
Hap 16		1												1 (1)
Hap 17		1												1 (1)
Hap 18										1				1 (1)
Hap 19					1									1 (1)
Hap 20				1										1 (1)
Hap 21		1												1 (1)
Hap 22								1						1 (1)
Hap 23				1										1 (1)
Hap 24											1			1 (1)
Hap 25													1	1 (1)
Hap 26					1									1 (1)
Hap 27											1			1 (1)
Hap 28		1		1										2 (1)
Hap 29	1													1 (1)
Hap 30				1										1 (1)
Hap 31								1						1 (1)
Hap 32			1											1 (1)
Hap 33		1												1 (1)
Hap 34													1	1 (1)
Hap 35													1	1 (1)
Hap 36				1										1 (1)
Hap 37			1											1 (1)
Hap 38		1												1 (1)
Hap 39				1										1 (1)
Hap 40									1					1 (1)
Hap 41				1										1 (1)
Hap 42								1						1 (1)
Hap 43				1										1 (1)
Hap 44									1					1 (1)
Hap 45		1												1 (1)
Hap 46											1			1 (1)
Hap 47											1			1 (1)
Hap 48										1				1 (1)
Hap 49				1		1								2 (1)

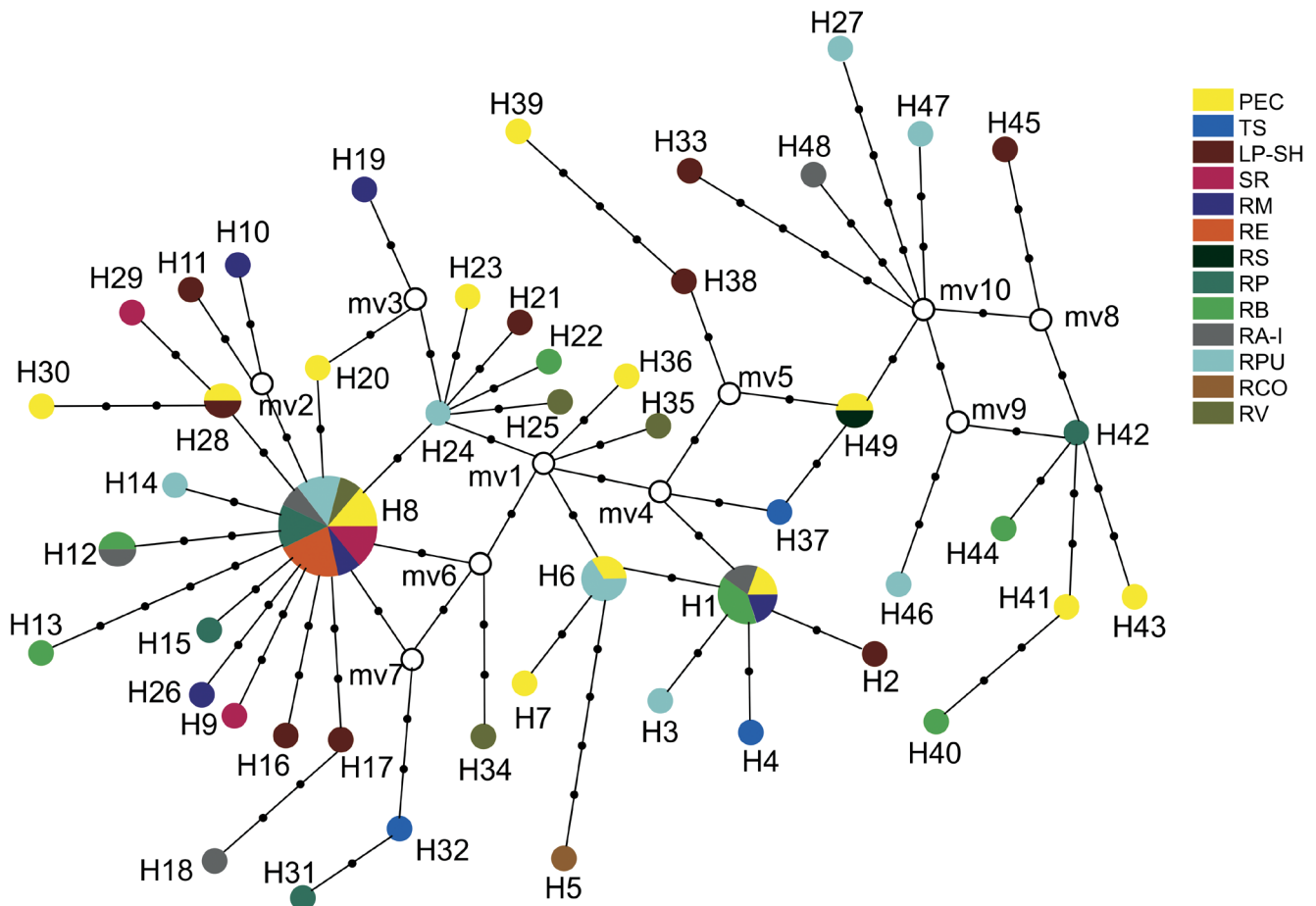


Fig. 7. Median-joining network based on COI haplotypes of *Macrobrachium occidentale*. Haplotypes derived from 13 basins are represented by colors with node size proportional to number of individuals with that haplotype. Mutational steps are indicated as black dots along network branches and Network software inferred median vectors as white dots. Drainage basins from the peninsula: SR = Santa Rita, LP-SH = Las Pocitas-San Hilario, TS = Todos Santos, and PEC = Plutarco E. Calles. Drainage basins from the mainland: RM = Río Mayo 3; RE = Río Elota; RS = Río Sinaloa 2; RP = Río Presidio 2; RB = Río Baluarte 2; RA-I = Río Ameca Ixtapa B; RPU = Río Purificación; RCO = Río Coyuca 2; RV = Río Verde.

Table 3. Analysis of molecular variance (AMOVA) of the combined 16S and COI genes sequence data of specimens of *Macrobrachium occidentale* Holthuis, 1950 from four drainage basins of the Baja California Peninsula as one group, and from nine drainage basins of the mainland Pacific slope of Mexico as another group in Arlequin 3.5 (Excoffier et al., 2010).

Source of variation	Df	Sum of squares	Percentage of variation	Fixation indices	p value
Among regions	1	0.616	0.41	0.00408	0.20298
Among basins, within regions	11	5.688	1.87	0.01875	0.10571
Within basins	58	27.386	97.73	0.02275	0.07904

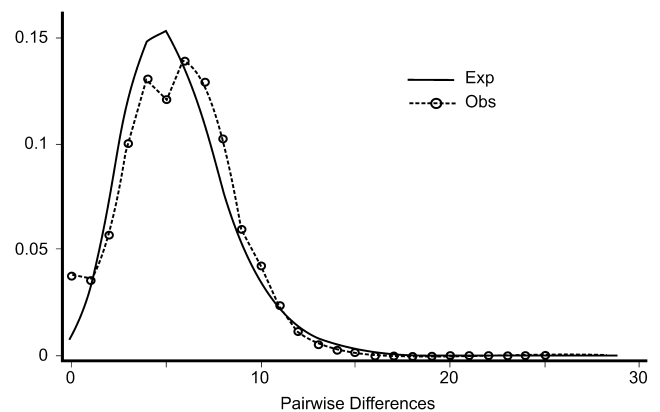


Fig. 8. Distribution curve from the mismatch analyses (raggedness index) showing observed (Obs) frequencies of pairwise differences among haplotypes and the expected (Exp) under the hypothesis of population expansion.

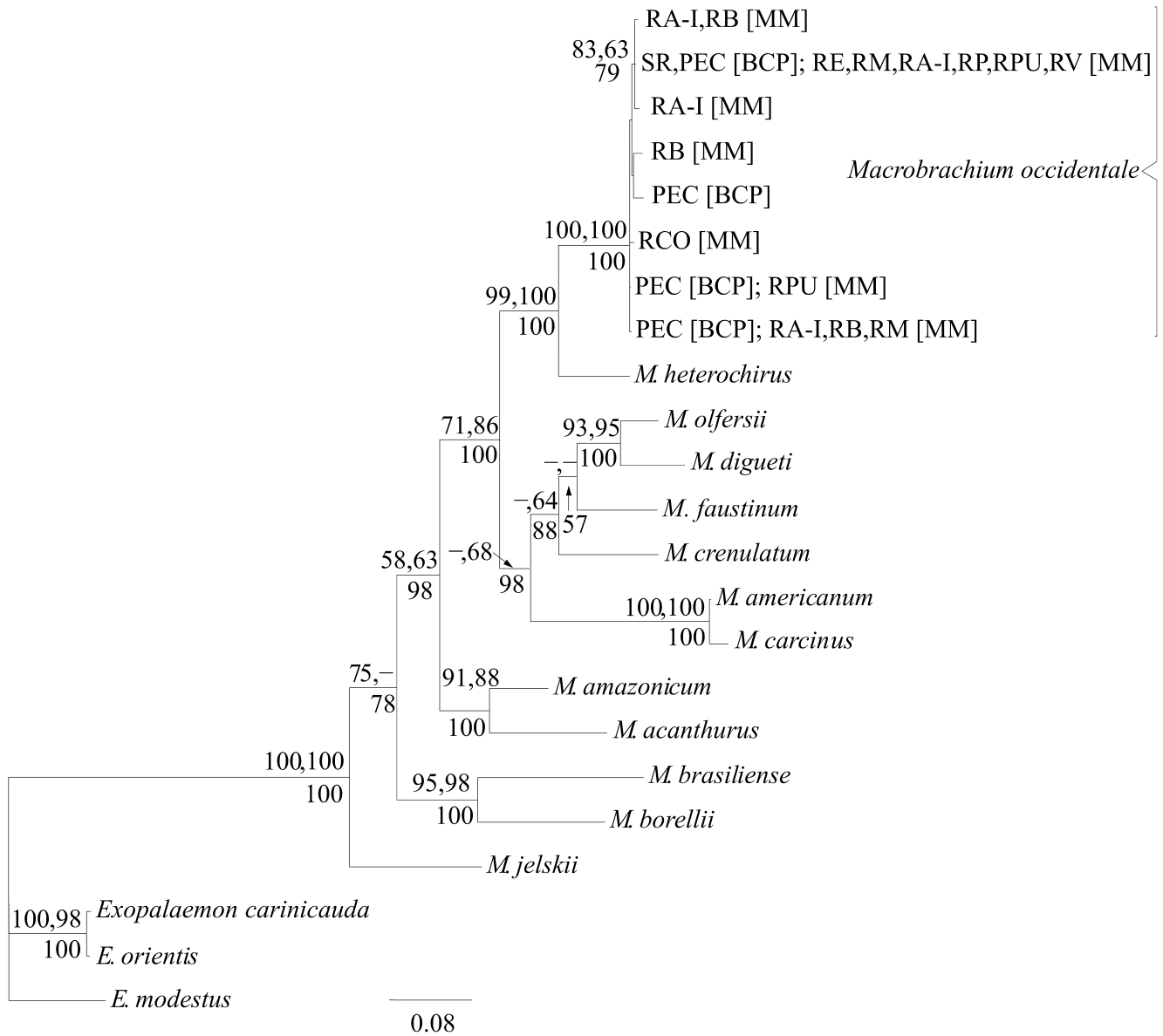


Fig. 9. Phylogenetic relationships of *Macrobrachium occidentale* with other *Macrobrachium* spp. represented by MrBayes tree-based analysis of 16S and COI sequences. Numbers above the nodes represent bootstrap values of maximum parsimony and maximum likelihood; below the nodes numbers represent the posterior probability of MrBayes. Bootstrap values < 50 are indicated as “-.” RCO = Río Coyoaca 2; RM = Río Mayo 3; RE = Río Elota; RA-I = Río Ameca Ixtapa B; RB = Río Baluarte 2; RP = Río Presidio 2; RPU = Río Purificación; SR = Santa Rita; PEC = Plutarco E. Calles; BCP = Baja California Peninsula; MM = Mainland of Mexico.

haplotype H 24 from Jalisco to haplotypes H 1, 6, 21, 23, 36 and 37 in the peninsula (Fig. 7). Single haplotypes in the 16S and COI genes found in this study may represent recent origins (Cook et al., 2002). The Gulf of California is a long and narrow marginal sea that started to form about 3 million years ago, but the present peninsula and its environmental conditions developed during the late Pliocene and Pleistocene (Murphy and Aguirre-León, 2002). Oceanic dispersal inside the Gulf of California, connecting populations of *Macrobrachium* between the peninsula and the mainland likely occurs through marine surface circulation patterns, which are influenced by seasonal winds and tidal mixing. These flow patterns are cyclonic in summer and anticyclonic the rest of the year (Bray, 1988; Paden et al., 1991). Floating

mangrove leaves and clumps of drifting algae from estuarine waters may function as a transport medium of macrocrustaceans, such as *Macrobrachium* (Wehrmann and Dittel, 1990). Thus, contrary to the vicarian hypothesis advanced by Hernández et al. (2007), the presence of *M. occidentale* in the Baja California Peninsula is better explained by the hypothesis of oceanic dispersal events.

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## SUPPLEMENTARY MATERIAL

Table S1. Studied sites. Information collected and recorded from the sites and from scientific collections is organized according to the political state, drainage basin (basin number), site name, geographic coordinates, elevation (meters above sea level), and date of visit. For sites where *Macrobrachium occidentale* was found, water characteristics, temperature, total dissolved solids (TDS), and pH are listed. Scientific collections are: CIB = Colección de Crustacea, Centro de Investigaciones Biológicas del Noroeste, La Paz, Baja California Sur, Mexico; CNCR = Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City; and UANL = Colección Carcinológica, Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León, San Nicolás de los Garza, Nuevo León.

## State of Baja California

## Pacific slope

## 1. Descanso-Los Médanos Basin (102)

1.1. La Misión, 32°05'51.56"N, 116°51'41.09"W by GEM, 22.06.2009.

## 2. San Carlos Basin (105)

2.1. Arroyo San Carlos, 31°47'52.40"N, 116°29'54.30"W by GEM, 06.2009, 01.06.2012.

## 3. Maneadero-Las Animas Basin (106)

3.1. Rancho Magaña, Arroyo San Francisquito, 31°42'09.28"N, 116°28'31.58"W by GEM, 15.05.2012.

3.2. Ejido Uruapan, Agua Caliente, 31°37'56.14"N, 116°26'14.41"W by GEM, 06.2009, 09.06.2012.

## 4. Santo Tomás Basin (107)

4.1. Ejido Ajusco, 31°35'07.58"N, 116°25'17.47"W by GEM, 06.2009.

4.2. La Séquia, Santo Tomás, 31°33'20.10"N, 116°24'28.49"W by GEM, 16.04.2012.

## 5. San Rafael Basin (110)

5.1. Punta Colonet, 31°02'05.36"N, 116°12'06.55"W by GEM.

## 6. El Rosario Basin (116)

6.1. El Rosario, La Bocana, 30°02'08.1"N, 115°46'16.2"W, 08 masl, 17.06.2008.

6.2. El Rosario, 30°02'16.49"N, 115°45'22.04"W, 09 masl, 06.2009.

## 7. Santa Catarina Basin (201)

7.1. Cataviña, 29°43'33.56"N, 114°42'48.25"W, 540 masl, 17.09.2010.

## Gulf of California slope

## 8. Río Colorado Basin (701)

8.1. Ejido Sinaloa, Mexicali-San Luis Río Colorado, 32°35'10.55"N, 115°22'22.00"W, 07 masl, 22.09.2011.

8.2. Laguna Mosqueda, 32°09'23.6"N, 115°16'42.9"W, 03 masl, 14.06.2008.

8.3. Campo Río Mayor, Río Hardy, 32°07'53.5"N, 115°16'47.5"W, 09 masl, 13.06.2008.

8.4. Río Colorado, 32°02'20.5"N, 115°07'10.0"W, 07 masl, 15.06.2008.

## 9. Cerrada Laguna Salada Basin (401)

9.1. Laguna Salada, 31°59'17.5"N, 115°13'23.4"W, 06 masl, 15.06.2008.

9.2. Laguna Salada 2, 31°58'17.1"N, 115°12'59.9"W, 06 masl, 15.06.2008.

## 10. San Fermín Basin (406)

10.1. Puertecitos, 30°20'44.9"N, 114°38'27.87"W, 15.06.2008.

## State of Baja California Sur

## Pacific slope

## 1. Punta Eugenia Basin (215)

1.1. Punta Eugenia, 27°50'35.23"N, 115°04'33.17"W, 50 masl, 12.01.2009.

1.2. Vizcaíno-Bahía Tortugas, 27°41'29.22"N, 114°53'44.44"W, 07 masl, 14.01.2009.

1.3. San José de Castro, 27°32'19.15"N, 114°28'21.1"W, 269 masl, 15.01.2009.

1.4. Puerto Nuevo, El Rancho Tanaleote, 27°28'26.8"N, 114°33'44.5"W, 240 masl, 15.01.2009.

1.5. Arroyo Los Ajos, 27°28'24.8"N, 114°33'21.2"W, 324 masl, 15.01.2009.

1.6. Punta Abrejos, 26°43'55.52"N, 113°32'54.59"W, 02 masl, 13.01.2009.

## 2. San Ignacio Basin (216)

2.1. Canales San Ignacio, 27°17'55.56"N, 112°53'44.18"W, 122 masl, 29.03.2010.

## 3. La Purísima Basin (301)

3.1. San Isidro, 26°14'19.7"N, 112°08'04.0"W, 55 masl, 27.10.2002, 15.07.2004, 19.07.2004.

3.2. Presa Carambuche, 26°14'19.8"N, 112°00'05.3"W, 142 masl, 25.01.2009.

3.3. Canales de Carambuche, 26°13'31.9"N, 112°00'45.7"W, 128 masl, 25.01.2009.

3.4. Arroyo La Purísima, junction to San Juanico, 26°09'29.6"N, 112°07'39.3"W, 54 masl, 24.01.2009.

## 4. Santa Rita Basin (305)

4.1. Oasis Santa María de Toris, 24°53'00.0"N, 111°02'17.0"W, 227 masl, 03.07.2011. Water characteristics: 29.6-29.9°C, TDS 0.30-0.58 g l<sup>-1</sup>, CIB.

4.2. San Pedro de La Presa, 24°50'57.9"N, 110°59'28.1"W, 224 masl, 13.06.2011. Water characteristics: 29.9-30.8°C, TDS 0.28-0.30 g l<sup>-1</sup>, CIB.

4.3. Las Ánimas, 24°50'24.0"N, 110°57'13.0"W, 297 masl, 27.07.2009.

## 5. Las Pocitas-San Hilario Basin (306)

5.1. Rancho Las Cuevas, 24°49'02.2"N, 110°52'45.1"W, 350 masl, 26.06.2009. Water characteristics: 28.8°C, TDS 0.56 g l<sup>-1</sup>, CIB.

5.2. La Cuchilla, 24°48'37.1"N, 110°51'01.3"W, 331 masl, 26.06.2011. Water characteristics: 34.2°C, TDS 0.68 g l<sup>-1</sup>, CIB.

## 6. Todos Santos Basin (311)

6.1. Canales Todos Santos, 23°27'16.6"N, 110°13'28.8"W, 17 masl, 19.11.2008. Water characteristics: 24.9-25.2°C, TDS 0.34-0.87 g l<sup>-1</sup>, pH 8.1-8.3, CIB.



Table S1. (Continued.)

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7. Pescaderos Basin (312)  
7.1. Oasis San Pedrito, 23°23'23.5"N, 110°12'40.6"W, 10 masl, 19.11.2008.
8. Plutarco E. Calles Basin (313)  
8.1. Las Vinoramas, 23°17'33.2"N, 110°01'16.4"W, 236 masl, 28.12.2010. Water characteristics: 24.6–24.8°C, TDS 0.42 g l<sup>-1</sup>, CIB.  
8.2. El Chucarro, 23°17'18.8"N, 110°01'47.3"W, 220 masl, 20.11.2008. Water characteristics: 23.9–24.8°C, TDS 0.26–0.41 g l<sup>-1</sup>, pH 8.1–8.3, CIB.  
8.3. San Venancio, 23°16'31.8"N, 110°02'12.9"W, 191 masl, 20.11.2008. Water characteristics: 31.7°C, TDS 0.27 g l<sup>-1</sup>, CIB.
- Gulf of California slope
9. Santa Rosalía Basin (513)  
9.1. Santa Rosalía, 27°22'16.8"N, 112°17'25.9"W, 01 masl, 18.06.2008.
10. Santa Agueda Basin (512)  
10.1. Arroyo Santa Águeda, 27°18'58.1"N, 112°14'36.7"W, 01 masl, 29.03.2010 and 18.09.2010.
11. San Marcos-Palo Verde Basin (509)  
11.1. San Marcos Tierra, 27°06'57.4"N, 112°04'09.0"W, 02 masl, 16.01.2009.
12. Mulegé Basin (508)  
12.1. La Presa de Mulegé, 26°53'12.60"N, 111°59'10.18"W, 10 masl, 28.02.2004, 17.01.2009.  
12.2. El Puente de Mulegé, 26°53'19.09"N, 111°58'56.10"W, 05 masl, 24.09.2004, 11.11.2004, 07.04.2005, and 17.01.2009.
13. Loreto Basin (611)  
13.1. Oasis Km 51, Loreto-Mulegé, 26°23'13.5"N, 111°36'01.0"W, 119 masl, 17.01.2009.  
13.2. Oasis costero Notri 1, Bahía de Loreto, 25°52'19.2"N, 111°20'25.1"W, 05 masl, 17.06.2008, and 17.01.2009.  
13.3. Oasis costero Notri 2, Bahía de Loreto, 25°52'17.3"N, 111°20'23.1"W, 05 masl, 17.06.2008, and 17.01.2009.  
13.4. Liguí, Loreto, 25°44'41.10"N, 111°17'00.6"W, 04 masl, 17.01.2009.
14. La Paz Basin (607)  
14.1. Las Vinoramas, 24°11'53.09"N, 110°12'12.11"W, 114 masl, 29.01.2009.
15. Cabo Pulmo Basin (603)  
15.1. La Bocana (La Rivera), 23°36'15.50"N, 109°34'44.20"W by GEM, 29.10.2010.
16. Santiago Basin (604)  
16.1. Agua Caliente, 23°26'N, 109°47'W, 13.12.2003.
17. San José del Cabo Basin (602)  
17.1. Oasis Santa Rosa, San José del Cabo, 23°05'18.8"N, 109°41'58.0"W, 122 masl, 17.05.2007. Water characteristics: 22.5°C, TDS 0.25 g l<sup>-1</sup>, CIB.

## State of Sonora

1. Río Mátape 2 Basin (906)  
1.1. Río del Tular, 27°56'00.06"N, 110°56'34.45"W, 08 masl, 18.04.2011.
2. Río Yaqui 3 Basin (910)  
2.1. Vaso Regulador (Dique 10), 27°44'38.6"N, 109°53'18.0"W, 77 masl, 19.04.2011.  
2.2. Rancho del Toro, Guaymas, 27°36'33.0"N, 110°30'14.9"W, 15 masl, 19.04.2011.  
2.3. Rancho San Carlos, 27°36'18.9"N, 109°55'38.3"W, 55 masl, 20.04.2011.  
2.4. Río Yaqui, Bicam, 27°35'26.1"N, 110°19'12.6"W, 16 masl, 21.04.2011.  
2.5. Bacum, 27°33'41.2"N, 110°05'11.2"W, 25 masl, 19.04.2011.  
2.6. Providencia, 27°30'17.4"N, 109°58'53.3"W, 43 masl, 19.04.2011.
3. Río Mayo 3 Basin (916)  
3.1. La Presa Mocuzarit, 27°13'05.8"N, 109°06'44.5"W, 89 masl, 21.04.2011.  
3.2. Río Mayo, Tesia, 27°10'14.9"N, 109°21'51.5"W, 53 masl, 22.04.2011.  
3.3. Puente Navojoa, Navojoa, 27°07'06.8"N, 109°27'39"W, 42 masl, 21.04.2011.  
3.4. Primavera, Huatabampo-Jarupa, Huatabampo, 26°48'0.1"N, 109°40'22.0"W, 16 masl, 22.04.2011.  
3.5. Echoropo, Huatabampo, 26°46'42.5"N, 109°40'51.8"W, 08 masl, 22.04.2011. Water characteristics: 30.5°C, TDS 0.35 g l<sup>-1</sup>, CIB.

## State of Sinaloa

1. Río Fuerte 2 Basin (1004)  
1.1. El Fuerte, 26°24'56"N, 108°37'33.4"W, 74 masl, 24.04.2011.  
1.2. Pueblo Armenta, 26°24'09.1"N, 108°42'35.9"W, 73 masl, 23.04.2011.  
1.3. La Bocatoma, San Blas, 26°04'38.8"N, 108°46'00.7"W, 38 masl, 24.04.2011.
2. Río Sinaloa 2 Basin (1011)  
2.1. Río Petatlán, Opochi 2, 25°49'09.8"N, 108°12'28.6"W, 64 masl, 25.04.2011.  
2.2. Dique, Sinaloa de Leyva, 25°48'52.58"N, 108°13'46.17"W, 35 masl, 25.04.2011. Water characteristics: 23.6°C, TDS 0.15 g l<sup>-1</sup>, CIB.  
2.3. Paraíso Escondido, 25°48'32.6"N, 108°13'50.3"W, 59 masl, 25.04.2011.  
2.4. Ranchito de Castro, 25°35'00.7"N, 108°24'53.2"W, 22 masl, 26.04.2011.  
2.5. Vado Guasave, Río Sinaloa, 25°33'41.5"N, 108°27'17.2"W, 15 masl, 26.04.2011. Water characteristics: 26.5°C, TDS 1.18 g l<sup>-1</sup>, CIB.  
2.6. Río Sinaloa, 25°29'54.5"N, 108°27'10.7"W, 25 masl, 26.04.2011.  
2.7. Río Sinaloa, Tamazula, Guasave, 25°26'41.6"N, 108°26'43.5"W, 10 masl, 26.04.2011.  
2.8. Río Sinaloa, Rosales, Guasave, 25°20'03.2"N, 108°26'52.3"W, 11 masl, 26.04.2011.
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Table S1. (Continued.)

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2.9. Canal de Riego, Rosales, 25°19'39.0"N, 108°27'35.7"W, 05 masl, 26.04.2011.

3. Río Mocorito 2 Basin (1017)

3.1. La Presa Eustaquio Buelna, Guamuchil, 25°28'45.5"N, 108°04'41.5"W, 48 masl, 27.04.2011.

3.2. Dique Manguito, Guamuchil, 25°26'37.6"N, 108°05'10.5"W, 72 masl, 27.04.2011.

3.3. Río Pericos, Puente Alemán, Mocorito, 25°05'36.9"N, 107°41'36.1"W, 64 masl, 27.04.2011.

4. Río Elota Basin (1013)

4.1. Puente El Roble, La Cruz de Elota, 23°55'11.3"N, 106°48'57.2"W, 20 masl, 28.04.2011. Water characteristics: 25.6°C, TDS 0.18 g l<sup>-1</sup>, CIB.

4.2. Puente Planta de Bombeo, La Cruz de Elota, 23°54'26.5"N, 106°51'20.3"W, 20 masl, 28.04.2011.

4.3. Planta de Bombeo, La Cruz de Elota, 23°54'21.4"N, 106°51'13.2"W, 26 masl, 27.04.2011.

4.4. Puente La Cruz de Elota, 23°54'19.7"N, 106°53'45.8"W, 20 masl, 28.04.2011. Water characteristics: 27.1°C, TDS 0.36 g l<sup>-1</sup>, CIB.

5. Río Piaxtla 2 Basin (1015)

5.1. Río Piaxtla, Estación Dimas, 23°43'39.8"N, 106°47'09.6"W, 20 masl, 29.04.2011.

6. Río Quelite 2 Basin (1021)

6.1. Arroyo San Pablo, 23°26'40.0"N, 106°32'37.4"W by GEM, 25.11.2003, CNCR.

7. Río Presidio 2 Basin (1106)

7.1. Villa Unión 1, 23°11'16.5"N, 106°13'31.0"W, 29 masl, 29.04.2011.

7.2. Villa Unión 2, 23°10'57.7"N, 106°13'50.1"W, 25 masl, 02.05.2011. Water characteristics: 29.6°C, TDS 0.14 g l<sup>-1</sup>, CIB.

7.3. Estero Colonias Espejos and Urías, Mazatlán, 23°09'08.53"N, 16°19'32.59"W by GEM, 19.10.1940, CNCR.

8. Río Baluarte 2 Basin (1108)

8.1. El Rosario, Puente Río Baluarte, 22°59'59.3"N, 105°50'51.1"W, 25 masl, 30.04.2011. Water characteristics: 27.5°C, TDS 0.12 g l<sup>-1</sup>, CIB.

8.2. El Rosario, 22°58'49.3"N, 105°51'01.9"W, 26 masl, 03.05.2011. Water characteristics: 27.6°C, TDS 0.13 g l<sup>-1</sup>, CIB.

9. Río Cañas 2 Basin (1102)

9.1. Río Cañas, Gabriel Leyva, Cuinapa, 22°30'31.5"N, 105°27'49.3"W, 42 masl, 30.04.2011.

State of Nayarit

1. Río Huaynamota Basin (1250)

1.1. Río Huaynamota, Las Adjuntas, 21°57'41.40"N, 104°31'21.02"W by GEM, 08.06.1991, 19.03.1992, and 27.04.1992, CNCR.

1.2. Río Huaynamota, 500 m Las Adjuntas, 21°57'23.19"N, 104°31'49.04"W by GEM, 09.06.1991, 19.11.1991, 20.03.1992, and 28.04.1992, CNCR.

1.3. Río Huaynamota, Los Sabinos, 21°35'16.18"N, 104°51'28.51"W by GEM, 01.04.1991, 10.04.1991, 11.04.1991, 11.06.1991, 19.01.1992, 17.03.1992, and 22.04.1992, CNCR.

1.4. Río Huaynamota, Los Sabinos, 300 m Carrito Aforador, 21°35'10.0"N, 104°31'36.54"W by GEM, 18.03.1992, CNCR.

1.5. Playa de Golondrinas, 21°38'00.06"N, 104°35'13.04"W by GEM, 12.04.1991, CNCR.

2. Río Santiago 4 Basin (1251)

2.1. Colorado de La Mora (Río San Pobleño, Arroyo Los Negros), Tepic, 21°42'37.41"N, 104°39'03.55"W by GEM, 12.04.1991, 21.05.1991, 25.09.1991, 21.11.1991, and 15.06.2009, CNCR.

3. Río Ameca Ixtapa B Basin (1409)

3.1. Canal El Colomo, Bahía Banderas, 20°53'16.5"N, 105°08'25.9"W, 60 masl, 05.05.2011. Water characteristics: 28.2°C, TDS 0.37 g l<sup>-1</sup>, CIB.

State of Jalisco

1. Río Cuale Basin (1303)

1.1. Río Horcones, 20 km S Puerto Vallarta, Tuito, 20°31'34.51"N, 105°17'55.35"W by GEM, 03.1992, CNCR.

2. Río Cuitzmala Basin (1508)

2.1. Río Cuitzmala, Chamela, 19°31'43.55"N, 105°04'39.07"W by GEM, 02.04.1984, CNCR.

2.2. Río Ayotitlán, Sierra de Manantlán, 19°29'46.13"N, 104°10'51.39"W by GEM, 03.04.1987, CNCR.

2.3. Río Ayotitlán, Las Juntas, Río Agua Mala, Sierra de Manantlán, 19°28'57.25"N, 104°10'44.34"W by GEM, 03.04.1987, CNCR.

2.4. Río Cuitzmala, km 43 Melaque-Puerto Vallarta, 19°25'50.8"N, 104°56'26.03"W by GEM, 30.01.1984, 31.01.1984, 02.04.1984, and 29.01.1986, CNCR.

2.5. San Nicolás, Melaque-Puerto Vallarta, La Huerta, 19°24'25.52"N, 104°57'43.57"W by GEM, 07.04.1987, CNCR.

2.6. Río Cuitzmala, 19°23'07.38"N, 104°58'27.48"W by GEM, 04.02.1983, and 06.04.1987, CNCR.

2.7. Río Cuitzmala, 3 km Venustiano Carranza, La Huerta, 19°28'17.26"N, 104°38'33.07"W by GEM, 06.04.1987, CNCR.

3. Río Purificación Basin (1509)

3.1. Zenzontla, Sierra de Manantlán, 19°42'05.59"N, 103°59'19.26"W by GEM, 02.04.1987, CNCR.

3.2. Río Purificación, La Huerta, 19°29'43.0"N, 104°40'20.2"W, 250 masl, 07.05.2011. Water characteristics: 28.8°C, TDS 0.39 g l<sup>-1</sup>, pH 7.5, CIB.

State of Colima

1. Río Armería Basin (1606)

1.1. Potrero Las Juntas, 3 km SE Pueblo Juárez, 19°19'14.03"N, 104°04'57.58"W by GEM, 23.06.1986, CNCR.

1.2. Presa El Seis, 9 km W Colima, 19°16'18.08"N, 103°40'27.19"W by GEM, 15.12.1973, UANL.

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Table S1. (Continued.)

## State of Michoacán

## 1. Río Bajo Balsas Basin (1812)

- 1.1. Río Popoyuta, 18°02'54.08"N, 102°33'26.06"W by GEM, 30.07.1984, and 30.12.1989, CNCR.
- 1.2. La Villita, Michoacán-Guerrero, 18°02'44.39"N, 102°10'57.49"W by GEM, 30.07.1984, CNCR.
- 1.3. Río Chucutitán, 18°00'47.74"N, 102°27'32.06"W by GEM, 25.07.1984, CNCR.
- 1.4. Río Mexcaltitlán, junto Barra, 17°58'36.02"N, 102°19'29.22"W by GEM, 31.07.1984, CNCR.

## State of Guerrero

## 1. Río Petatlán 2 Basin (1910)

- 1.1. Río Murga, Murga, 17 km NE Petatlán, 17°32'12.08"N, 101°16'00.60"W by GEM, 19.08.1980, 11.09.1981, and 28.07.1984, CNCR.
2. Río Atoyac 2 Basin (1922)
  - 2.1. Vallecito de Zaragoza, Pueblito, 17°20'49.04"N, 100°13'22.50"W by GEM, 03.08.1984, CNCR.
  - 2.2. Río Atoyac, Atoyac de Álvarez, 17°12'08.40"N, 100°25'49.28"W by GEM, 07.04.2007, UANL.
3. Río Coyuca 2 Basin (1925)
  - 3.1. Río Coyuca, Vado Aguas Blancas, Coyuca de Benítez, 17°03'20.7"N, 100°01'48.5"W, 80 masl, 11.05.2011. Water characteristics: 30.6–32.1°C, TDS 1.28 g l<sup>-1</sup>, pH 8.2, CIB.
  - 3.2. Aguas Blancas, 15 km NW Aguas Blancas, 17°02'07.44"N, 100°03'45.32"W by GEM, 20.08.1980, CNCR.
4. Río Papagayo 3 Basin (2005)
  - 4.1. Río Papagayo, CFE La Venta, 17°07'33.08"N, 99°33'53.40"W by GEM, 24.06.1988, CNCR.
  - 4.2. Río Pinola and Río Tonalá, 16°52'41.40"N, 99°08'01.44"W by GEM, 18.12.1987, CNCR.
5. Río Papagayo 4 Basin (2006)
  - 5.1. Tres Palos, Acapulco, 16°46'20.50"N, 99°46'42.24"W by GEM, 28.07.1984, CNCR.

## State of Oaxaca

## 1. Río Verde Basin (2032)

- 1.1. El Carnero, Chatañu, 16°21'43.16"N, 97°44'17.15"W by GEM, 24.11.2007, CIB.
- 1.2. Río Viejo, 16°05'56.41"N, 97°43'41.60"W by GEM, 05.2008, CIB.
2. Río Zimatán 1 Basin (2113)
  - 2.1. Río Grande before junction to Río Jícara, Merced del Potrero, San Miguel del Puerto, 16°02'16.98"N, 96°03'02.34"W, 15.01.2007, 12.04.2007, CNCR.
3. Río Zimatán 2 Basin (2114)
  - 3.1. Río Zimatán, Santa María Petatengo, Huatulco, 15°56'12.1"N, 96°01'35.8"W, 07.09.2000, CNCR.
  - 3.2. Río Zimatán, bridge Huatulco-Salina Cruz, San Miguel del Puerto, 15°50'44.60"N, 95°59'51.18"W, 13.04.2007, and 26.10.2007, CNCR.
4. Río Copalita 2 Basin (2111)
  - 4.1. Río Ayuta, Huatulco, 15°49'48.15"N, 96°19'43.48"W, 07.09.2000, CNCR.
  - 4.2. Río Copalita, Las Hamacas, bridge Huatulco-San Miguel del Puerto, 15°53'35.22"N, 96°11'16.2"W, 155 masl, 10.04.2007, 12.06.2007, and 24.10.2007, CNCR.
  - 4.3. Río Copalita, bridge Huatulco-Salina Cruz, Santa María Huatulco, 15°49'19.02"N, 96°03'55.44"W, 14 masl, 17.01.2007, and 13.04.2007, CNCR.
5. Río Copalita 1 Basin (2110)
  - 5.1. Junction Río Copalita-Río Yuviaga, San Miguel del Puerto, 15°57'58.02"N, 96°13'02.34"W, 140 masl, 16.01.2007, CNCR.
  - 5.2. Río Yuviaga, San Miguel del Puerto, 15°57'00.0"N, 96°13'02.34"W, 140 masl, 13.06.2007, CNCR.
  - 5.3. Las Brisas de Copalitilla, Río Copalita, San Miguel del Puerto, 15°54'17.46"N, 96°08'38.34"W, 120 masl, 10.04.2007, CNCR.
6. Río Tequisistlán Basin (2202)
  - 6.1. Río Tequisistlán, 74.5 km Tehuantepec, 16°24'53.44"N, 95°35'29.41"W by GEM, 28.12.1955, CNCR.
7. Río Tehuantepec 2 Basin (2204)
  - 7.1. Presa de Mistequilla, Tehuantepec, 16°22'31.58"N, 95°17'29.17"W by GEM, 19.12.1955, CNCR.
8. Río Coyula 2 Basin (2112)
  - 8.1. Río Coyula, Arroyo Magdalena, Rancho Hagia-Sophia, Santa María Huatulco, 15°52'3.18"N, 96°22'8.56"W, 324 masl, 13.04.2007, and 15.06.2007, CNCR.
  - 8.2. Río Coyula, bridge Huatulco-Salina Cruz, Santa María Huatulco, 15°44'57.43"N, 96°17'52.8"W, 24 masl, 17.01.2007, 13.04.2007, and 15.06.2007, CNCR.

## State of Chiapas

## 1. Laguna Mar Muerto C Basin (2306)

- 1.1. Río Lagartero, Arriaga, 16°13'53.57"N, 93°53'24.07"W by GEM, 30.07.1983, CNCR.
2. Río Huixtla Basin (2319)
  - 2.1. Río Vado Ancho, Villa de Colmaltitlán, 15°13'07.55"N, 92°35'12.18"W by GEM, 20.12.1971, and 24.07.1971, CNCR.
  - 2.2. Poza Silva, Río Vado Ancho, Villa de Colmaltitlán, 15°13'07.55"N, 92°35'12.18"W by GEM, 29.07.1971, CNCR.

Table S2. Variable nucleotide sites among unique sequences of seventeen 16S haplotypes from a 479-bp fragment obtained from 71 individuals of *Macrobrachium occidentale* Holthuis, 1950 from Mexico.

Haplotype	Base position																
	83	86	106	134	141	180	187	214	215	255	291	293	320	373	408	418	450
Hap 1	A	A	C	C	C	T	T	C	T	T	T	T	A	A	C	T	T
Hap 2	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.
Hap 3	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	C
Hap 4	.	.	T	.	.	.	C	.	.	.	.	.	.	.	.	.	.
Hap 5	.	.	T	.	.	.	.	T	.	.	.	.	.	.	.	.	.
Hap 6	.	.	T	.	.	.	.	.	.	.	.	.	G	.	.	.	.
Hap 7	.	.	T	.	.	.	.	.	.	.	.	.	.	.	T	.	.
Hap 8	G	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap 9	.	.	T	.	.	.	.	.	.	.	.	.	.	G	.	.	.
Hap 10	.	.	T	T	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap 11	.	.	T	.	.	.	.	.	.	C	.	.	.	.	.	.	.
Hap 12	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	C
Hap 13	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap 14	.	.	T	.	.	C	.	.	C	.	.	.	.	.	.	.	.
Hap 15	.	.	T	.	T	.	.	.	.	.	.	C	.	.	.	.	.
Hap 16	.	G	T	.	T	.	.	.	.	.	.	C	.	.	.	.	.
Hap 17	.	.	T	.	T	.	.	.	.	.	.	.	.	.	.	.	.

