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New records of invasive tubeworms (*Ficopomatus*, Serpulidae) in Mexico

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Abstract

Ficopomatus Southern, 1921 is a serpulid genus currently composed of six species, two of which (*F. enigmaticus* and *F. miamiensis*) are reef-builders. The former has invaded subtropical and warm-temperate estuaries worldwide, causing environmental and economic harm. In this study, *Ficopomatus miamiensis* and *F. uschakovi* are reported from brackish-water coastal localities in both Atlantic and Pacific sides of Mexico, including a Biosphere Reserve, estuaries, as well as shrimp and oyster farms. *Ficopomatus miamiensis* is reported from Veracruz (southern Gulf of Mexico, Mexico territory) and Sinaloa (southern Gulf of California). *Ficopomatus uschakovi* is reported for the first time in the southern Gulf of Mexico (Mexico territory) and repeatedly recorded in Chiapas (southern Mexican Pacific). There are no phenotypic differences between specimens of *F. miamiensis* from both coasts of Mexico. Comparison of mitochondrial cytochrome b (Cytb) DNA sequences further support the notion that *F. miamiensis* from the type locality (Florida) and Atlantic coasts of Mexico is also found along the Pacific coast of Mexico. Morphological variability within specimens of *F. uschakovi* from a single locality (either Laguna del Ostión or La Encrucijada) in Mexico suggest potential presence of multiple cryptic species. Molecular genetics studies are needed to confirm the taxonomic and invasive status of *F. uschakovi*.

Introduction

The genus *Ficopomatus* Southern, 1921 comprises six species currently considered valid, namely, *F. macrodon* Southern, 1921 from Chilka Lake, India; *F. enigmaticus* (Fauvel, 1923) from Canal de Caen, France; *F. miamiensis* (Treadwell, 1934) from Miami River, Florida, USA; *F. uschakovi* (Pillai, 1960) from Panadura River Estuary, Sri Lanka; *F. talehsapensis* Pillai, 2008 from Taléh Sap, Thailand; and *F. shenzhensis* Li *et al.*, 2012 from Guangdong, China. Little is known about three of them (*F. macrodon*, *F. talehsapensis*, *F. shenzhensis*) beyond the basic taxonomic description.

All *Ficopomatus* are tropical species, except for *F. enigmaticus* that is found in subtropical and warm-temperate regions. They are extremely euryhaline, and are found in freshwater, marine, and hypersaline environments such as estuaries and mangroves (ten Hove & Weerdenburg, 1978; Pillai, 2008; Li *et al.*, 2012), while *F. enigmaticus* was recently reported in living stromatolites (Miranda *et al.*, 2016). All species of the genus may occur as solitary individuals or in dense aggregations. *Ficopomatus enigmaticus* is the best known ecologically and economically important reef-building species of the genus that has invaded warm-temperate estuaries worldwide (reviewed in Dittmann *et al.*, 2009).

Morphologically, the species in the genus are characterized by an operculum with a bulbous fleshy ampulla, uncovered or covered with either a chitinous endplate or bearing numerous chitinous spines, and very distinct coarsely serrated collar chaetae (Kupriyanova *et al.*, 2019). *Ficopomatus uschakovi* has a distinct apomorphy, dorsally fused thoracic membranes. Opercular shapes and ornamentations of *Ficopomatus* have been traditionally used to identify to the species level (ten Hove & Weerdenburg, 1978). While *F. macrodon*, *F. miamiensis*, *F. shenzhensis* and *F. talehsapensis* lack opercular spines, chitinous spines in *F. enigmaticus* and *F. uschakovi* show a remarkable variation in shape, number, size and arrangement within a species. Such a variability might be a result of intraspecific variability or attributed to ontogenetic development, but it can be an indication of cryptic species as well. Moreover, *F. enigmaticus* and *F. uschakovi* in Australia were confused by Straughan (1966) who synonymized both species claiming that there is a cline between isolated populations between Sydney (temperate) and Brisbane (tropical). This was refuted by Hartmann-Schröder (1971), Pillai (1971) and ten Hove & Weerdenburg (1978).

The last decades have seen significant progress in the development of genetic tools for annelids that allow to address questions about evolution, development, gene regulation, chronobiology and behaviour on a functional level (Zantke *et al.*, 2014) and documentation of cryptic species as well (Bickford *et al.*, 2007). In *Ficopomatus* only a handful of molecular studies have assessed phylogenetic relationships among species and population structure within species. The first phylogenetic analysis based on 18S rDNA and 28S rDNA sequences



of *F. enigmaticus* from Australia, *F. macrodon* from Thailand and *F. miamiensis* from Florida, USA (Kupriyanova *et al.*, 2009) confirmed monophyly of the brackish-water genus *Ficopomatus* and its sister group relationship with the freshwater species *Marifugia cavatica* Absolon & Hrabě, 1930. *Ficopomatus shenzansis* Li *et al.* (2012) from China was the first species of the genus in which the morphological description was accompanied by an analysis of 18S sequence data obtained from the type material. No further molecular data on *Ficopomatus* species, other than *F. enigmaticus*, are available to date. Within *F. enigmaticus*, an analysis of Cytb sequences revealed three genetic lineages (tentative species) with overlapping distributions in Australia (Styan *et al.*, 2017). Two of these lineages showed opercular morphology typical for *F. enigmaticus*, but the third clade was morphologically distinct, having opercula similar to those in *F. uschakovi*, but with thoracic membrane not fused dorsally (Fig. 4 in Styan *et al.*, 2017). Recent studies revealed additional Cytb haplotype variability within the *F. enigmaticus* populations from New Zealand, California, Portugal and northern Spain (Yee *et al.*, 2019; Grosse *et al.*, 2021).

In this study we examined two species of *Ficopomatus*: *F. miamiensis* and *F. uschakovi*. *Ficopomatus miamiensis* was originally described (as *Sphaeropomatus*) from Miami River in Florida and reported from Louisiana and Texas, as well from Caribbean localities, such as Jamaica, Barbados, Curaçao and Belize (ten Hove & Weerdenburg, 1978; Bastida-Zavala *et al.*, 2017), and the Colombian Caribbean (Fernández-Rodríguez *et al.*, 2016). In Mexico, *F. miamiensis* has been recorded (as *Mercierellopsis prietoi*) from Tecolutla in the southern Gulf of Mexico by Rioja (1945) and recently from La Mancha, Veracruz (Ruiz Guerrero & López-Portillo, 2014, 2017) and Isla del Carmen, Campeche (Miranda-Salinas *et al.*, 2016). Currently this species has also established on the Pacific coasts of Mexico, being associated with mangrove roots and shrimp farms in the southern Gulf of California (Salgado-Barragán *et al.*, 2004; Tovar-Hernández *et al.*, 2009, 2012, 2014; Tovar-Hernández & Yáñez-Rivera, 2012).

Ficopomatus uschakovi was originally described (as *Neopomatus*) from Sri Lanka and subsequently reported from tropical localities in Asia, for example India (Fauvel, 1931, 1932, 1953), Java, Indonesia (Pillai, 1965), Malaysia (Rosli *et al.*, 2019), Philippines (Pillai, 1965), Thailand (Wangkulangkul *et al.*, 2022), Oceania, for example the Solomon Islands (Gibbs, 1971); tropical Australia: northern New South Wales and Queensland (Dew, 1959 (in part); Straughan, 1967, 1968 (in part), 1971, 1972; Hartmann-Schröder, 1971); and Western Africa: Ivory coast (Rullier, 1955) and Nigeria (Sandison & Hill, 1966). In the Americas, *F. uschakovi* was first reported from Atlantic coast of Brazil (de Assis *et al.*, 2008), Venezuela (Liñero-Arana & Díaz-Díaz, 2012), and during the last decade from Caribbean Colombia (Arteaga-Flórez *et al.*, 2014; Fernández Rodríguez *et al.*, 2016), Southern Mexican Pacific (Bastida-Zavala & García-Madrigal, 2012; Bastida-Zavala *et al.*, 2016) and the east coast of the USA, i.e. Florida and Texas (Bastida-Zavala *et al.*, 2017).

Here we provide new records of *F. miamiensis* and *F. uschakovi* from coastal localities along both Atlantic and Pacific coasts of Mexico, and a comparison of mitochondrial cytochrome b (Cytb) DNA sequences of *F. miamiensis* from the type locality (Florida) and Atlantic and Pacific coasts of Mexico.

Materials and methods

Sampling was carried out for *Ficopomatus miamiensis* and *F. uschakovi* on red mangrove roots (*Rhizophora mangle* Linnaeus), oysters (*Crassostrea virginica* (Gmelin)) and wood dock pilings in the Laguna de Mandinga, Laguna del Ostión and Alvarado during December 2012 (Atlantic Ocean, Gulf of

Mexico, Mexico, Veracruz State) under the sampling permission granted by the Comisión Nacional de Acuacultura y Pesca (DGOPA.14011.151012.3291). Samples from red mangrove were collected from the Reserva de la Biosfera La Encrucijada (Pacific Ocean, Mexico, Chiapas state) in July 2014. Samples from a shrimp farm near Urías Estuary and del Yugo Estuary (Pacific Ocean, Mexico, Gulf of California, Sinaloa State) were collected in August 2014 and October 2014, respectively (Figure 1).

Mangrove roots and oysters were collected by hand and transported to the laboratory in seawater-filled containers. Tubeworms from shrimp farm pilings were scraped from substrate. Worms were removed from tubes, some were fixed in 95% ethanol and others in formaldehyde as indicated in the material examined sections. A Leica MZ75 stereomicroscope and Olympus CH30 compound microscope were used for identification and digital photographs were taken with an attached Canon S5 digital camera. Several specimens were processed and examined after final dehydration in two changes of 100% ethanol at the Laboratorio de Microscopía Electrónica de Barrido (Facultad de Ciencias, Universidad Autónoma de México). Specimens were critical point dried using CO₂, mounted on stubs with platinum tape and coated with gold (200 Å thickness). They were then viewed using a Cambridge 250 scanning electron microscope (SEM).

Specimens were measured to record total body length, peduncle plus operculum length, operculum diameter, thoracic length and thoracic width. The numbers of left and right radioles and thoracic chaetigers were counted, and the position of peduncle insertion (left or right) was recorded. In Tables 1 and 2, measurements are expressed as mean values + SD, number of specimens analysed (N) and the range of such values. For example, total body length 7.35 mm (6.17 + 2.92, N = 8, r: 3.1–11.4 mm).

The species distribution map (Figure 1) was produced using SimpleMappr (Shorthouse, 2010). It includes new reports of *F. miamiensis* and *F. uschakovi* from this study, as well as previous literature records of *F. miamiensis* and *F. uschakovi* in Tropical America (Rioja, 1945; ten Hove & Weerdenburg, 1978; Bastida-Zavala, 2008; Bastida-Zavala & García-Madrigal, 2012; Liñero-Arana & Díaz-Díaz, 2012; Arteaga-Flórez *et al.*, 2014; Ruiz Guerrero & López-Portillo, 2014, 2017; Tovar-Hernández *et al.*, 2014; Miranda-Salinas *et al.*, 2016; Bastida-Zavala *et al.*, 2017).

Specimens were deposited in the Collection of Reference of El Colegio de la Frontera Sur, Chetumal (ECOSUR-OH-P), the Colección Poliquetológica de la Universidad Autónoma de Nuevo León (UANL), the Colección Regional de Invertebrados Marinos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (ICML-EMU) and the Australian Museum (AM).

DNA extraction, amplification and sequencing

Genomic DNA was extracted from posterior parts of abdomens using the Bioline Isolate II genomic DNA kit according to the manufacturer's protocol. Stock DNA was diluted 1:10 with deionized water to produce template strength DNA for Polymerase Chain Reactions (PCR). The Cytb gene fragments (~350 bp) were amplified with the primer pair Cytb424F (GGWTAYGT WYTWCCWTGRGGWCARAT) and cobr825 (AARTAYCAYT CYGGYTTRATRTG) (Halt *et al.*, 2009). PCR conditions were as follows: an initial denaturation step at 94°C for 3 min, 45 cycles at 94°C for 1 min, 50°C for 30 s, 72°C for 1 min, with a final extension at 72°C for 8 min. PCR success was detected using gel electrophoresis (1% agarose gel stained with gel red (Biotium TM, San Francisco)) and visualized using a Bio-Rad XR + Gel Documentation System. Successful PCR products were sent to

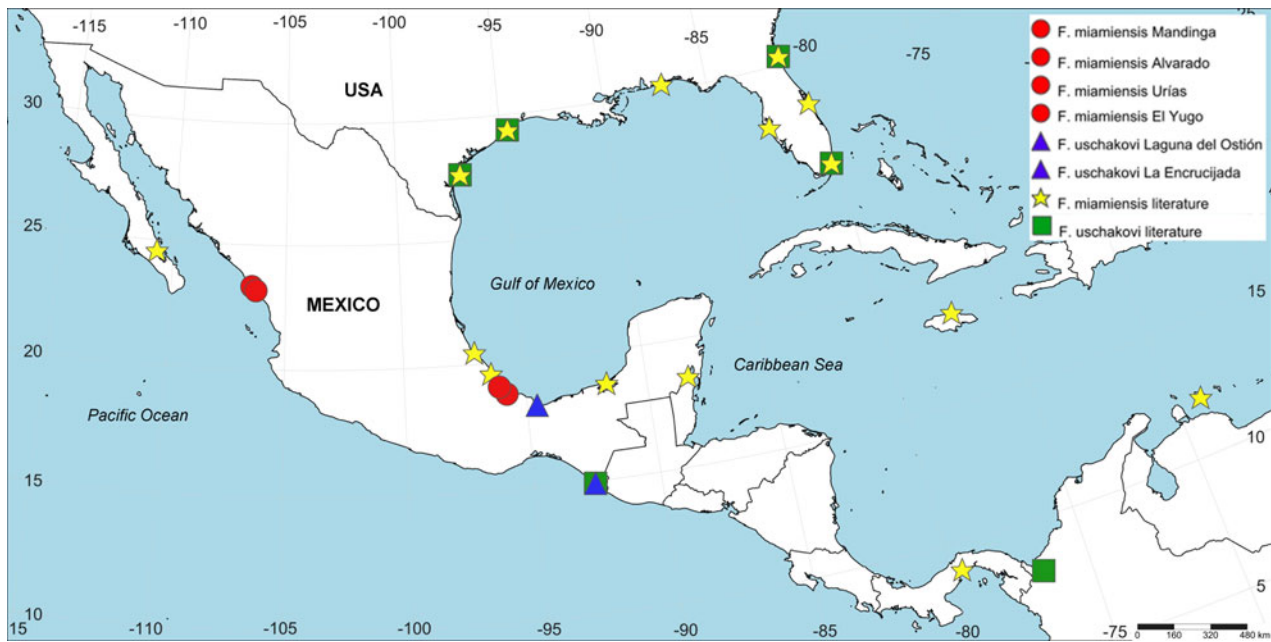


Fig. 1. Amphi-American distribution of *Ficopomatus miamiensis* (red circles represent records from the present study, yellow stars – records from literature) and *F. uschakovi* (blue triangles records from the present study, green squares – records from literature).

Table 1. Measurements of *Ficopomatus miamiensis* from Western Atlantic and Eastern Pacific populations

Measurement	Atlantic population (Veracruz, Mandinga, this study)	Pacific population (Mazatlán, this study)
Total body length	7.35 mm (6.17 ± 2.92 mm, N = 8, r: 3.1–11.4 mm)	13.61 mm (12.52 ± 4.13 mm, N = 10, r: 8.7–20.1 mm)
Number of left radioles	7.37 radioles (7.34 ± 0.51 radioles, N = 8, r: 7–8 radioles)	8.2 radioles (8.15 ± 0.63 radioles, N = 10, r: 7–9 radioles)
Number of right radioles	7.37 radioles (7.34 ± 0.51 radioles, N = 8, r: 7–8 radioles)	8.2 radioles (8.15 ± 0.63 radioles, N = 10, r: 7–9 radioles)
Insertion left	N = 10	N = 10
Peduncle plus operculum length	1.38 mm (1.25 ± 0.51 mm, N = 8, r: 1–2.4 mm)	2.63 mm (2.53 ± 0.54 mm, N = 10, r: 1.8–3.8 mm)
Opercular diameter	0.43 mm (0.43 ± 0.05 mm, N = 8, r: 0.4–0.5 mm)	0.58 mm (0.56 ± 0.10 mm, N = 10, r: 0.5–0.7 mm)
Thorax length	1.65 mm (1.59 ± 0.33 mm, N = 8, r: 1.2–2.2 mm)	2.56 mm (2.49 ± 0.43 mm, N = 10, r: 1.9–3.3 mm)
Thorax width	0.51 mm (0.50 ± 0.08 mm, N = 8, r: 0.4–0.7 mm)	1 mm (0.94 ± 0.27 mm, N = 10, r: 0.7–1.7 mm)
Number of thoracic chaetigers	7 (including collar chaetiger), N = 8	7 (including collar chaetiger), N = 10

Table 2. Measurements of *Ficopomatus uschakovi* from Western Atlantic and Eastern Pacific populations

Measurement	Atlantic population (Barrillas, this study)	Pacific population (La Encrucijada: Bastida-Zavala & García-Madriral, 2012)
Total body length	6.46 mm (5.99 ± 1.93 mm, N = 9, r: 4–9.8 mm)	6.7 mm (5.2 ± 1 mm, N = 10, r: 4–6.7 mm)
Number of left radioles	6.5 radioles (6.34 ± 1.08 radioles, N = 10, r: 5–8 radioles)	9 radioles (7.4 ± 0.8 radioles, N = 10, r: 6–9 radioles)
Number of right radioles	6.5 radioles (6.34 ± 1.08 radioles, N = 10, r: 5–8 radioles)	8 radioles (8 ± 0.7 radioles, N = 10, r: 7–9 radioles)
Insertion left	N = 10	N = 10
Peduncle plus operculum length	1.2 mm (1 ± 0.4 mm, N = 10, r: 0.9–1.4 mm)	1.8 mm (1.6 ± 0.4 mm, N = 9, r: 1–1.9 mm) (as operculum length)
Opercular diameter	0.28 mm (0.45 ± 0.10 mm, N = 8, r: 0.23–0.6 mm)	0.6 mm (0.6 ± 0.1 mm, N = 9, r: 0.5–0.8 mm)
Rows of opercular spines	1 row (N = 8, r: 0–3 rows)	r: 1–4, N = ?
Thorax length	1.28 mm (1.23 ± 0.22 mm, N = 10, r: 0.8–1.5 mm)	2 mm (1.7 ± 0.2 mm, N = 10, r: 1.4–2 mm)
Thorax width	0.49 mm (0.48 ± 0.05 mm, N = 10, r: 0.4–0.6 mm)	0.7 mm (0.6 ± 0.1 mm, N = 10, r: 0.5–0.7 mm)
Number of thoracic chaetigers	7 (including collar chaetiger), N = 10	7 (including collar chaetiger), N = 10

Macrogen TM, South Korea for purification and standard Sanger sequencing. Sequences were edited and aligned using Geneious. A BLAST search confirmed the correct gene regions had been amplified (Altschul *et al.*, 1990) and the new sequences were submitted to GenBank (Table 3).

The analysed dataset included 13 Cytb published sequences of *Ficopomatus enigmaticus*, *F. macrodon*, *F. cf. uschakovi* and *F. miamiensis* available to date in GenBank as well as three new sequences from Tropical America (Table 3). *Galeolaria caespitosa* was used as an outgroup.

The phylogenetic relationships were inferred using maximum likelihood analysis in IQ-TREE (Minh *et al.*, 2020). Nucleotide substitution model selected using the Bayesian information criterion in ModelFinder (Kalyaanamoorthy *et al.*, 2017) was HKY + F + I + G4. Branch support was estimated using 1000 ultrafast bootstraps (Hoang *et al.*, 2018).

Results

Taxonomy

Serpulidae Rafinesque, 1815

Genus *Ficopomatus* Southern, 1921

***Ficopomatus miamiensis* (Treadwell, 1934)**

Figures 1–4, Table 1

Sphaeropomatus miamiensis Treadwell, 1934: 339–341, figs 1–5, 9 (Miami River, FL, USA).

Mercierellopsis prietoi Rioja, 1945: 411–417, plates 1, 2 (Mexico, Tecolotla (Gulf of Mexico)).

Ficopomatus miamiensis. – Hartman, 1956: 300 (Indian and Miami Rivers, Florida). – ten Hove & Weerdenburg, 1978: 106–109, figs 1f–i, 3c, 4h–i, q, v–w, ee–ii, xx, 5a–b (Florida, Louisiana, Jamaica, Barbados, Curaçao, Belize, Panama (canal zone)). – Lacalli, 1976: 301–303 (larval development). – Bastida-Zavala, 2008: 19, 21, figs 5B–D (Estero de Urías, Sinaloa, Mexico and Miraflores, Panama). – Tovar-Hernández *et al.*, 2009, 327–328, Figs 3g–i, 6a, 7a–c (El Confite Estuary,

Sinaloa, Mexico). – Ruiz Guerrero & López-Portillo, 2014: 1316, 2017: 752 (La Mancha, Veracruz, Mexico, ecology). – Tovar-Hernández *et al.*, 2014: 386, fig 2i (La Paz, Baja California Sur, Mexico). – Bastida-Zavala *et al.*, 2017: 19–21, figs 2I–K, 3 (Jacksonville, Indian River, Biscayne Bay, Tampa Bay, Pensacola, FL; Galveston and Corpus Christi TX, USA; Chetumal, Mexico). – Miranda-Salinas *et al.*, 2016: 10 (Isla del Carmen, Campeche, Mexico).

Examined material

Atlantic Ocean, Gulf of Mexico, Mexico, Veracruz

ECOSUR-OH-P-1116 (1 spec), UANL 8118 (28 spec), AM (W.43523, W.43664, W.43665, W.43666, W.43667, W.43668, W.43669, W.43670, W.43671, W.43672, W.43673) (11 spec): Mandinga, Laguna Grande, Station 26, 19°2'20.64"N 96°4'24.24"W, on oyster *C. virginica*, 0.5 m deep, 10.74 ppt, 26.63°C, 4.31 mg O₂/l, 10 December 2012, legit JM. Aguilar & TF. Villalobos. Fixed in 96% ethanol.

ECOSUR-OH-P1114 (1 spec), ECOSUR-OH-P1115 (1 spec), ECOSUR-OH-P1117 (1 spec), ECOSUR-P3240 (28 spec), UANL 8119 (12 spec): Mandinga, Laguna Grande, Station 27, 19°01.847'N 96°04.845'W, on mangrove roots, 0.5 m deep, 10.87 ppt, 27.23°C, 5.78 mg O₂/l, 10 December 2012, legit JM. Aguilar & TF. Villalobos. Fixed in 96% ethanol.

UANL 8120 (30 spec): Mandinga, Laguna Grande, Station 28, 19°01.916'N 96°04.135'W, on oyster *C. virginica*, 0.5 m deep, 11.41 ppt, 27.24°C, 6.32 mg O₂/l, 10 December 2012, legit JM. Aguilar, TF. Villalobos & MA. Tovar. Fixed in 96% ethanol.

ICML-EMU 13,276 (3 spec): Alvarado, 18°44'1.26"N 95°47'1.2"W, on wooden dock, 0.5 m deep, salinity, temperature and dissolved oxygen not determined, 6 December 2012, legit AD. Vera & JM. Aguilar. Fixed in formalin.

ICML-EMU 13277 (8 spec): Alvarado, 18°45'20.34"N 95°46'29.04"W, on car battery, 1 m deep, salinity, temperature and dissolved oxygen not determined, 6 December 2012, legit JM. Aguilar. Fixed in formalin.

Table 3. Terminals used in phylogenetic analysis with registration numbers and collection localities

Species	Registration number	Collection locality	Cytb	Source
<i>Ficopomatus miamiensis</i>	SAM E3617	FL, USA	KP863779	Styan <i>et al.</i> (2017)
<i>Ficopomatus miamiensis</i>	OP832408	Gulf of Mexico	To add	This study
<i>Ficopomatus miamiensis</i>	OP832410	Gulf of Mexico	To add	This study
<i>Ficopomatus miamiensis</i>	OP832409	Gulf of California	To add	This study
<i>Ficopomatus macrodon</i>	SAM E3618	Thailand	KP863778	Styan <i>et al.</i> (2017)
<i>Ficopomatus enigmaticus</i>	–	Vic, Australia	KP863745	Styan <i>et al.</i> (2017)
<i>Ficopomatus enigmaticus</i>	–	WA, Australia	KP863762	Styan <i>et al.</i> (2017)
<i>Ficopomatus enigmaticus</i>	–	CA, USA	MK334104	Yee <i>et al.</i> (2019)
<i>Ficopomatus enigmaticus</i>	–	Vic, Australia	KP863749	Styan <i>et al.</i> (2017)
<i>Ficopomatus enigmaticus</i>	–	Vic, Australia	KP863764	Styan <i>et al.</i> (2017)
<i>Ficopomatus enigmaticus</i>	–	Spain	MT215015	Grosse <i>et al.</i> (2021)
<i>Ficopomatus enigmaticus</i>	–	CA, USA	MK334059	Yee <i>et al.</i> (2019)
<i>Ficopomatus cf. uschakovi</i>	–	NSW, Australia	KP863776	Styan <i>et al.</i> (2017)
<i>Ficopomatus cf. uschakovi</i>	–	NSW, Australia	KP863775	Styan <i>et al.</i> (2017)
<i>Ficopomatus cf. uschakovi</i>	–	NSW, Australia	KP863770	Styan <i>et al.</i> (2017)
<i>Ficopomatus cf. uschakovi</i>	–	NSW, Australia	KP863777	Styan <i>et al.</i> (2017)
<i>Galeolaria caespitosa</i>	–	WA, Australia	FJ646547	Halt <i>et al.</i> (2009)

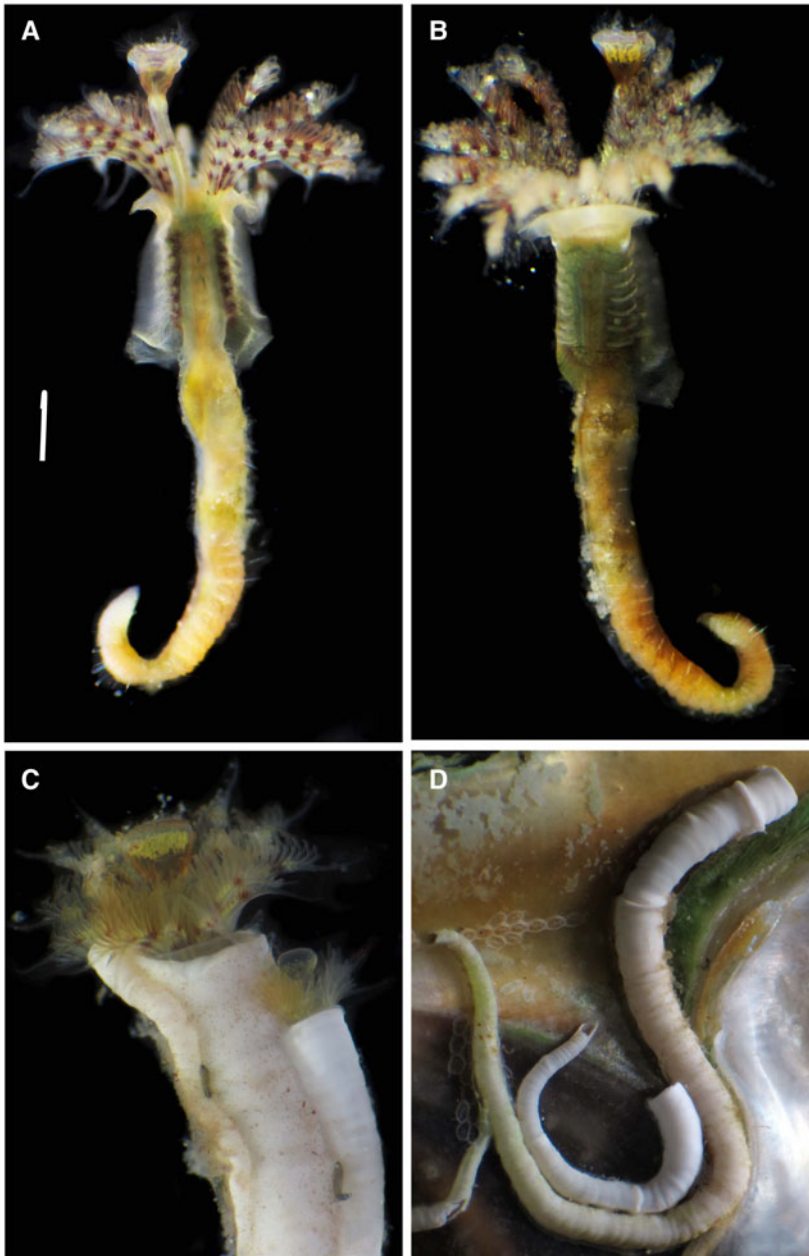


Fig. 2. *Ficopomatus miamiensis* from the southern Gulf of Mexico, live worms: (A) body, dorsal view; (B) same, ventral view; (C) radiolar crowns and opercula; (D) tubes.

ICML-EMU 13278 (23 spec): Alvarado, 18°46'32.76"N 95°46'54.60"W, on a crown-shaped plastic wire, 6 December 2012, 1 m deep, salinity, temperature and dissolved oxygen not determined, legit AD. Vera & JM. Aguilar. Fixed in formalin.

UANL 8124 (38 spec): Del Yugo Estuary, 23°18'9.40"N 106°28'59.59"W, on wooden dock pilings and rocks, 9 October 2014, 0.5 m deep, salinity, temperature and dissolved oxygen not determined. Legit MA. Tovar. Fixed in 96% ethanol.

Pacific Ocean, Mexico, Gulf of California, Sinaloa

ECOSUR-OH-P1104 (1 spec), ECOSUR-OH-P1105 (1 spec), ECOSUR-OH-P1106 (1 spec), ECOSUR-OH-P1107 (1 spec), ECOSUR-OH-P1108 (1 spec), ECOSUR-P3241 (3 spec), UANL 8121 (17 spec), ICML-EMU 13279 (38 spec). Shrimp Farm, Urías Estuary, 23°09'30.29"N 106°17'58.35"W, on bivalves covering dock pilings, 5 August 2014, 0.5 m deep, 42 ppt, 29°C, dissolved oxygen not determined. Legit MA. Tovar. Fixed in 96% ethanol.

AM (W.43522, W.43654, W.43655, W.43656, W.43657, W.43658, W.43659, W.43660, W.43661, W.43662, W.43663) (11 spec). El Confitte Estuary, 23°0.9'32.1"N 106°18'14.2"W, on mangrove roots, 30 April 2008, 0.3 m deep, salinity, temperature and dissolved oxygen not determined, legit MA. Tovar & J. Salgado. Fixed in 96% ethanol.

Diagnosis

Tubes gregarious or solitary, white (Figures 2C, 4E, G, H), with 3–5 peristomes, lacking keels or alveoli (Figure 2D). Operculum spherical, smooth, without spines (Figure 3A–D). Collar entire (Figure 2B), collar chaetae coarsely serrated (Figure 3E–F). Thoracic membrane not fused dorsally (Figure 2A), ventrally united to form a short apron (Figure 2B). Thorax with limbate chaetae (Figure 3H) and saw-shaped uncini with 6–8 teeth. Abdomen with true trumpet-shaped chaetae. Anterior abdominal uncini saw to rasp-shaped (Figure 3I), with 8–9 teeth visible in profile. Posterior abdominal uncini rasp-shaped and smaller than anterior ones. Measurements of body and radiolar structures from Atlantic and Pacific populations are shown in Table 1.

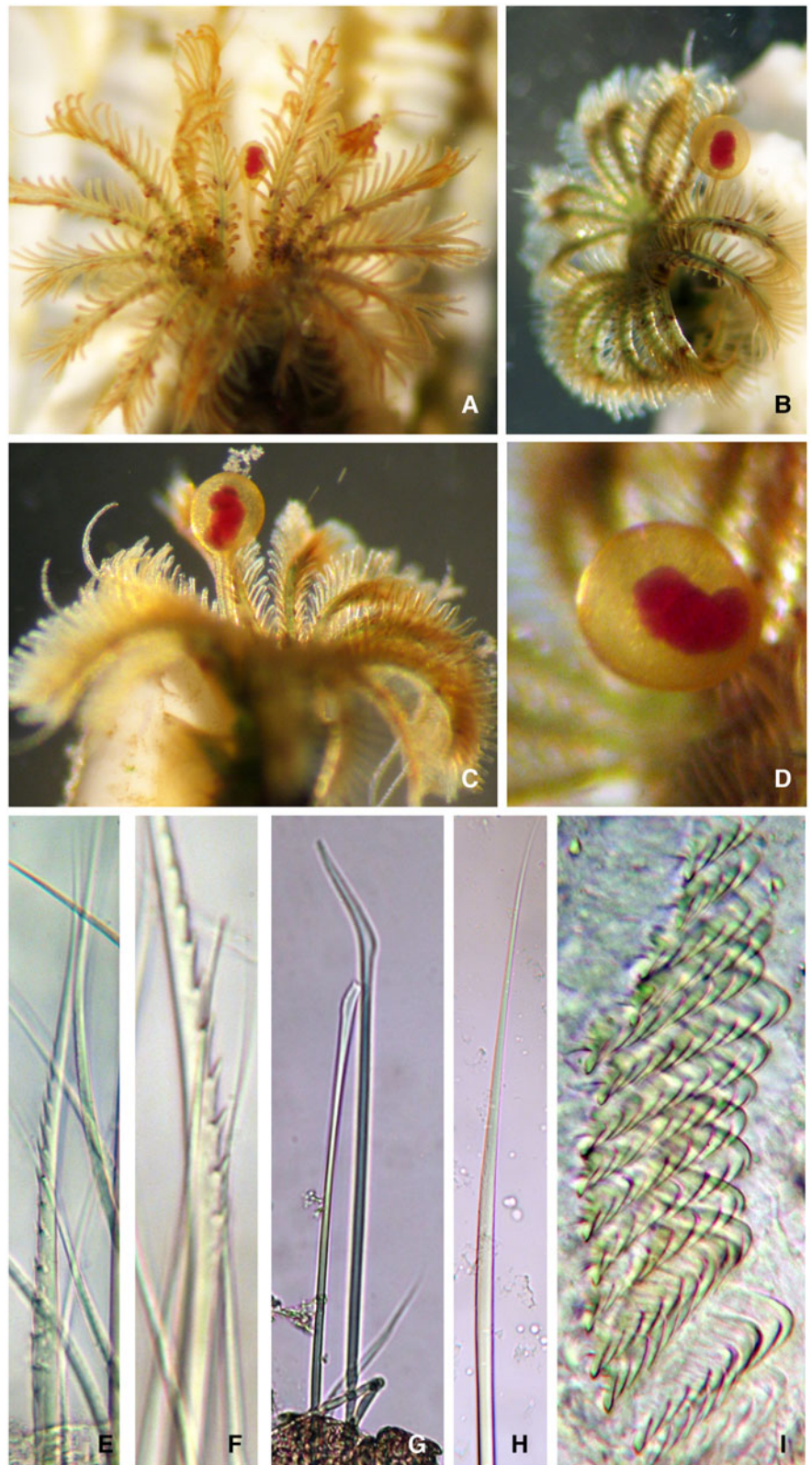


Fig. 3. *Ficopomatus miamiensis* from the southern Gulf of California: (A–C) radiolar crowns of live worms, (D) detail of operculum showing the internal blood vessel, (E–F) coarsely serrated collar chaetae, (G) abdominal chaeta, (H) thoracic chaeta, (I) saw-shaped anterior abdominal uncini.

Molecular results

The results of maximum likelihood analysis (Figure 5) placed sequences of *F. miamiensis* from Gulf of Mexico and Gulf of California into a perfectly supported monophyletic clade (100%) with *F. miamiensis* previously collected in Florida. The *F. miamiensis* clade formed the sister group to the clade (91.8%) including *F. macrodon* from Thailand and the *F. cf. uschakovi* from Southern NSW, Australia (100%). The *Ficopomatus enigmaticus* clade was well supported (98.7%) and

included three well-supported clades including specimens from Australia, California and Spain (Balearic Islands).

Remarks

We found no phenotypic differences between specimens of *F. miamiensis* from the Atlantic and the Pacific coasts of Mexico (also see Tovar-Hernández *et al.*, 2009 (Figs 3g–i, 6a, 7a–c), Tovar-Hernández *et al.*, 2012 (text figures on pages 12–13), Tovar-Hernández & Yáñez-Rivera, 2012 (Figures 1, 5–6)). This



Fig. 4. *Ficopomatus miamiensis* reefs in a shrimp farm from the southern Gulf of California: (A, D) empty pond, soil covered with reefs of tubeworms, (B) reefs at border of a pond, (C) reef fragment removed from a wood piling, (E, G) detail of a reefs, (F) aquaculture infrastructure covered by tubeworms, (H) detail of a colony, (I) tubeworms on mangrove roots.

species is easy to identify by its smooth spherical operculum lacking spines (Tovar-Hernández *et al.*, 2009). The examined population of the Atlantic side of Mexico has a larger average body size than that from the Pacific population (7.35 vs 13.61 mm, Table 1). It might be because the Pacific population was collected in culture ponds of a shrimp farm where the food availability is higher than in natural habitats (oyster banks) of the Atlantic population.

Like all species of the genus, *F. miamiensis* worms are either dioecious (or likely protandric hermaphrodites) lacking sexual dimorphism, their oocytes have asynchronous development and vitellogenesis is extra-ovarian (Lacalli, 1976; reviewed in Dittmann *et al.*, 2009). External fertilization takes place in the water column and typical planktotrophic larval development from early trochophore to settlement takes place in 13 days at 27°C (Tovar-Hernández *et al.*, 2009; Tovar-Hernández & Yáñez-Rivera, 2012).

Ficopomatus uschakovi (Pillai, 1960)

Figures 1, 6–7, Table 2

Neopomatus uschakovi Pillai, 1960: 28–32, fig. 10H, 11A–H, 12A–H, plate I, figs 1–2 (Panadura River estuary, Madu Gamga estuary at Balapitiya and Ratgama Lake, Donanduwa, Sri Lanka). – Hartman, 1965: 80 (catalogue). – Pillai, 1965: 172 (Surabaya and Madura Island, East Java); 1971: 118–123, 127, fig. 9G, 10 (Hikkaduwa and Panadura, Sri Lanka). – Hartmann-Schröder, 1971: 7–27, fig. 2, 3, 5, 7b–d, 11–14 (Nambucca River, New South Wales; Brisbane, Queensland, Australia). – Zibrowius, 1973: 64 (West coast of Africa).

Mercierella enigmatica (non Fauvel, 1923). – Fauvel, 1931: 1067, 1932: 249, 1933: 185. – Dew, 1959: 31, fig. 22. –

Straughan, 1966: 143–144, fig. 2–3, 1967: 204, 1968: 59–64, plates 1–5 (in part, plates 1, 2, 3A are *F. uschakovi* fide ten Hove & Weerdenburg, 1978), 1971: 171–173, 1972 (along entire text, ecological studies).

Neopomatus uschakovi var. *lingayanensis* Pillai, 1965: 170–172, fig. 23A–I (Lingayan Gulf, Luzon Island, Philippines).

Neopomatus similis Pillai, 1960: 32–33, fig. 12 I–M, plate II, fig. 1 (Negombo Lagoon, Maha Alamba, Pitipana, Sri Lanka). – Hartman, 1965: 80 (catalogue).

Neopomatus similis var. *rugosus* Pillai, 1960: 33–35, plate II, fig. 2 (Negombo Lagoon, Sri Lanka). – Hartman, 1965: 80 (catalogue).

Ficopomatus uschakovi. – ten Hove & Weerdenburg, 1978: 109–113, fig. 2a–d, 3a, f–k, 4j–n, r, x–z, 5d (Panadura River Estuary, Maha Alamba, Ratgama Lake (Sri Lanka), Madras (India), Java (Indonesia), Luzon (Philippines), Guadalcanal (Solomon Islands), Northern New South Wales and Queensland (Australia), Lagos (Nigeria), Abidjan (Ivory Coast), Noordwijk (the Netherlands). – Bastida-Zavala & García-Madrugal, 2012: 48–52, fig. 1A–E, 2A–I (La Encrucijada, Chiapas, Mexico). – Liñero-Arana & Díaz-Díaz, 2012: 235–237, figs 1a–j (Caño Morocoto, Venezuela). – Arteaga-Flórez *et al.*, 2014: 5–9, fig. 2A–J (Golfo de Urabá, Caribbean Colombia). – Bastida-Zavala *et al.*, 2017: 21–22, figs 2L–O, 3 (Florida: Jacksonville, Biscayne Bay; Texas: Galveston, Corpus Christi, USA).

Examined material

Atlantic Ocean, Gulf of Mexico, Mexico, Veracruz State

AM W.43524, W.43674, W.43675, W.43676 (4 spec), ECOSUR-OH-P1109 (1 spec), ECOSUR-OH-P1110 (1 spec), ECOSUR-OH-P1111 (1 spec), ECOSUR-OH-P1112 (1 spec),

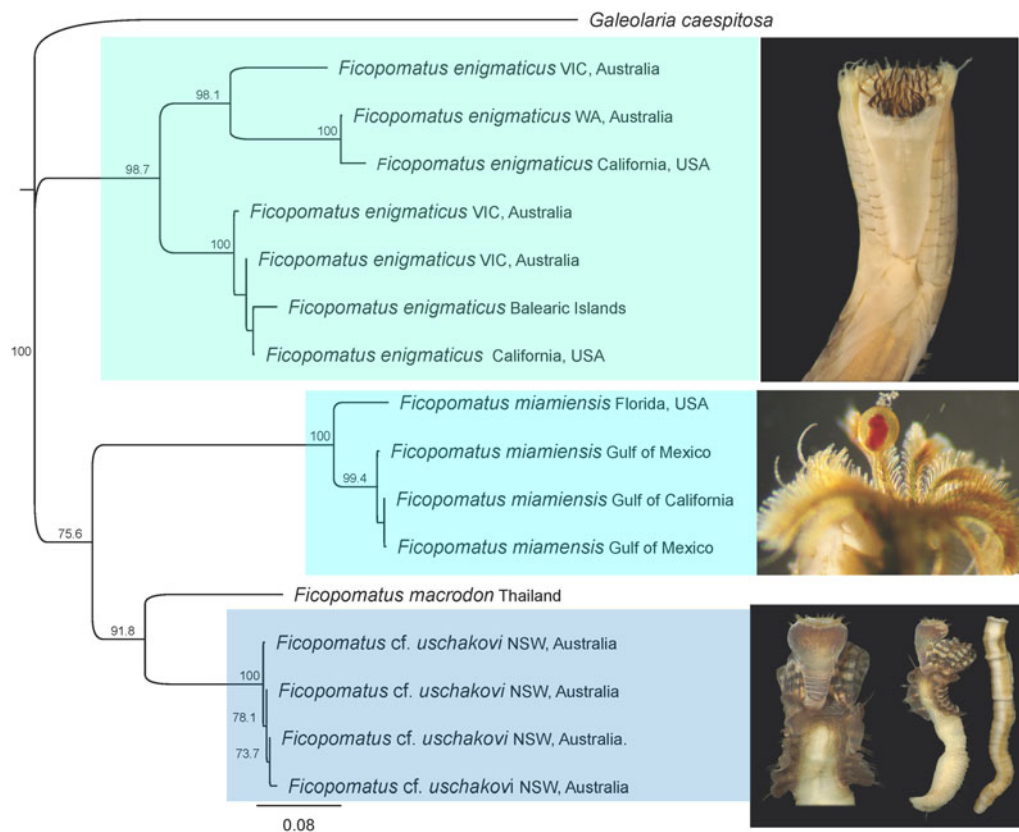


Fig. 5. Maximum likelihood phylogram resulting from the analysis of 16 Cytb sequences of *Ficopomatus* rooted with *Galeolaria caespitosa*. Numbers above branches are bootstrap values from ML analysis. Only bootstrap values over 70 are shown.

ECOSUR-OH-P1113 (1 spec), ECOSUR-P3242 (4 spec), UANL 8122 (41 spec): Barrillas, Laguna del Ostión, Station 5, 18° 11'38.8"N 94°35'51.27"W, mangrove roots, 0.5 m deep, salinity, temperature and dissolved oxygen not determined, 5 December 2012, legit J. Cruz. Fixed in 96% ethanol.

UANL 8123 (15 spec): Granja Sociedad Cooperativa, Station 4, 18°11'20.15"N 94°35'56.97"W, on oyster *C. virginica*, 5 December 2012, 0.5 m deep, salinity, temperature and dissolved oxygen not determined, legit J. Cruz. Fixed in formalin.

Pacific Ocean, Mexico, Chiapas State

ECOSUR-OH-P1099 (1 spec), ECOSUR-OH-P1100 (1 spec), ECOSUR-OH-P1101 (1 spec), ECOSUR-OH-P1102 (1 spec), ECOSUR-OH-P1103 (1 spec), ECOSUR-P3243 (1 jar with many tubes attached to mangrove roots), UANL 8125 (1 jar): Reserva de la Biosfera La Encrucijada, Barra San Juan, 14°55'16.78"N 92°37'18.40"W, on mangrove roots, 0.5 m deep, salinity, temperature and dissolved oxygen not determined, 5 July 2014, legit G. Mejía & Y. Siu. Fixed in 96% ethanol.

Diagnosis

Tubes gregarious or solitary, red in live material (Figure 6A–C), changing to brown or orange in preserved material. Tube with prominent to shallow peristomes or only low growth rings. Alveoli absent, a keel sometimes present in specimens from southern Gulf of Mexico (Figure 6C). Operculum spherical to oval in shape, with flat, slightly convex or slightly concave horny endplate (Figure 7B–E). Opercula with 1–5 concentric rows of spines (Figure 7B–E); the rows sometimes incomplete or converging with other rows. Collar entire (Figure 7A). Collar chaetae include coarsely serrated chaetae and narrowly limbate chaetae (Figure 7H). Thoracic membranes fused dorsally (Figure 6D–E), ventrally forming a small apron (Figure 7A).

Thorax with limbate chaetae (Figure 7G) and saw-shaped uncini with 6–7 teeth (Figure 7I, K). Abdomen with true trumpet-shaped chaetae (Figure 7F). Anterior abdominal uncini rasp-shaped (Figure 7J) and partly saw-to-rasp-shaped with 9 teeth. Measurements of body and radiolar structures from Atlantic and Pacific populations are given in Table 2.

Remarks

Specimens identified here as *F. uschakovi* show a distinctive opercular variation, from an operculum being spherical to oval in shape, with a slightly convex, flat or slightly concave horny plate and 1–5 concentric rows of spines, these rows are sometimes incomplete or converge with other rows. This remarkable variation was also noted by Bastida-Zavala & García Madrigal (2012) to all descriptions from all American *F. uschakovi* records.

Unfortunately, attempts to amplify either cytochrome oxidase I (COI) (Beatriz Yáñez Rivera, Luis Fernando Carrera, pers. comm.) or Cytb fragments of *F. uschakovi* from Mexican Pacific (La Encrucijada) were not successful, perhaps due to the damage of DNA as worms were fixed within their tubes and stored in a hot place for a month after sampling.

Discussion

This study demonstrated that non-native *F. miamiensis* and *F. uschakovi* are established on both coasts of Mexico. However, our understanding of taxonomic status, invasive pathways, and ecological impact differs for these two species.

Ficopomatus miamiensis is an apparently single species (as evidenced by morphological and preliminary molecular data here) with the Caribbean native range introduced to and established in the Pacific localities within the last 40 years. According to ten Hove & Weerdenburg (1978), *Ficopomatus miamiensis* was



Fig. 6. *Ficopomatus uschakovi* from Mexico: (A) tubes on mangrove roots; (B) tubes on oyster *C. virginica* shells; (C) detail of tubes; (D–E) thoracic membranes, dorsal views, in (E) arrow points to fused membrane. (A–D) Specimens from the southern Gulf of Mexico, (E) specimen from the southern Gulf of California.

originally restricted to tropical and sub-tropical localities along the Atlantic coast of North and Central America and the Caribbean. The authors reported an isolated locality at the Pacific end of the Panama Canal, which could have been the initial point of introduction to the Pacific Ocean. Alternatively, the successful invasion of *F. miamiensis* to the Gulf of California was attributed to shrimp aquaculture practices four decades ago, when white shrimp (*Litopenaeus vannamei*) larvae were imported from laboratories in Florida to the farms in the Gulf of California in a time when aquaculture practices were not as controlled as they are now (Tovar-Hernández & Yáñez-Rivera, 2012).

In the southern Gulf of Mexico, which apparently constitutes a part of its native range, *F. miamiensis* inhabits coastal lagoons, often being attached to mangrove roots and oyster (*Crassostrea virginica*) shells but does not form large aggregations. In the southern Gulf of California, where it is considered an introduced species, *F. miamiensis* specimens build thousands of small reefs

(20–80 cm diameter) per hectare in shrimp farm ponds during every culture cycle (Figure 4A–B, D–E, G–H). The tubes cover any submerged object such as ropes and wood pilings (Figure 4C), but they also grow on mangrove roots in aquaculture ponds (Figure 4I: dry tubes once ponds are drained) (Tovar-Hernández & Yáñez-Rivera, 2012).

The presence of the introduced *F. miamiensis* does not seem to bother aquaculture owners as the worms do not negatively affect shrimp production. Moreover, it is considered a beneficial filter feeder that cleans the water column of shrimp faeces and wasted shrimp food (purina pellets). Once the culture cycle is over and ponds are drained, *Ficopomatus* tube aggregations are removed, but when the ponds are re-filled to start a new culture cycle, larvae of *F. miamiensis* re-colonize the farm ponds (Tovar-Hernández & Yáñez-Rivera, 2012).

Ecological impacts of *F. miamiensis* in the estuary El Confito in the southern Gulf of California are unknown. This tubeworm is

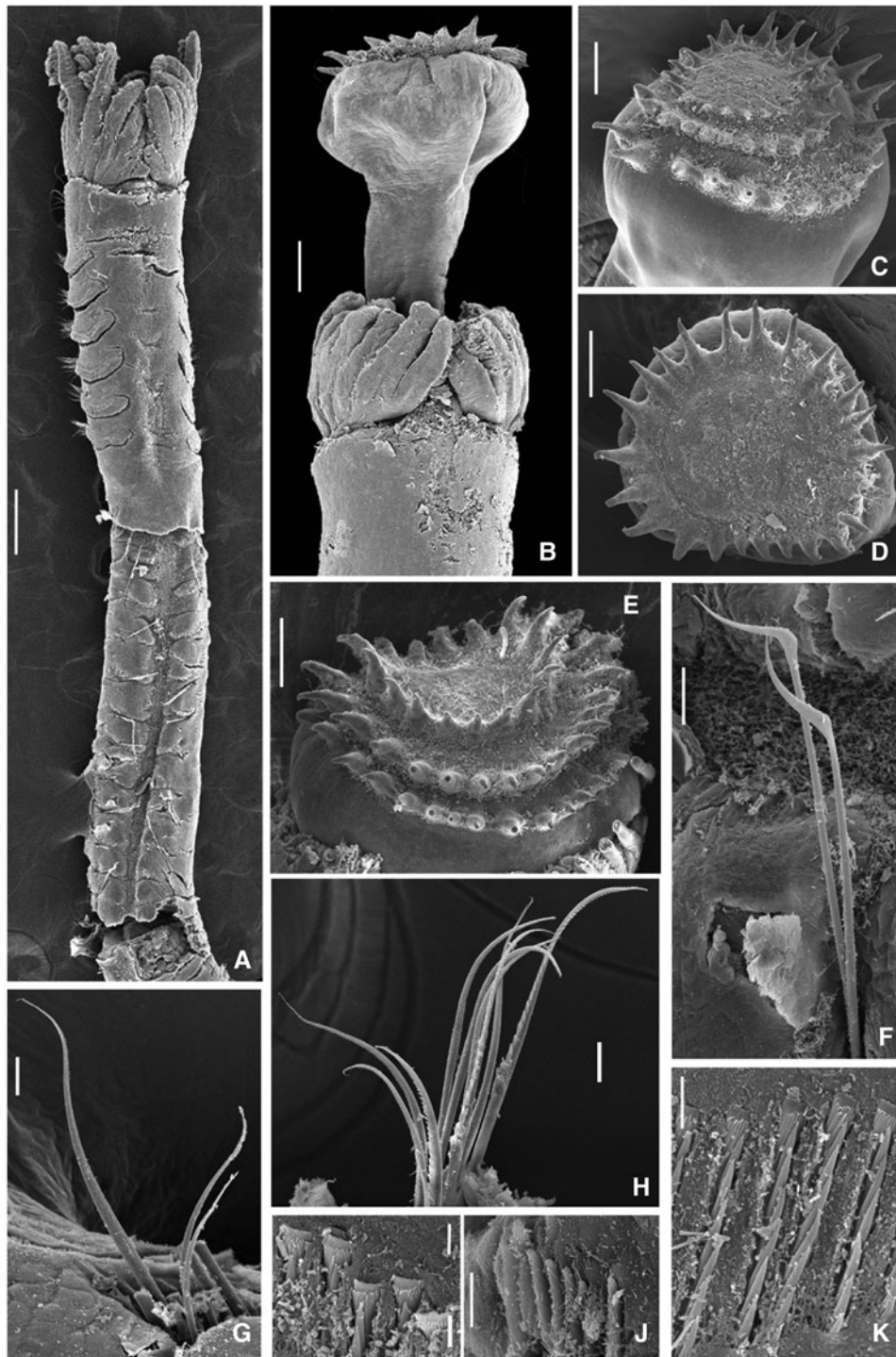


Fig. 7. *Ficopomatus uschakovi* from southern Gulf of Mexico. SEM images: (A) body, ventral view; (B) radiolar crown and operculum; (C–E) opercula, different views; (F) trumpet chaetae from abdomen; (G) chaetae from last thoracic segment; (H) collar chaetae; (I) pegs of uncini from mid-thorax; (J) uncini from anterior abdomen; (K) uncini from mid-thorax. Scale bars: A, 250 μ m; B–E, 100 μ m; F, 30 μ m; G, 20 μ m; H, 15 μ m; I, 2 μ m; J, 10 μ m; K, 3 μ m.

among the six dominant species (along with mussels, barnacles, oysters and a crab) present throughout the year on mangrove roots. The populations of this species show a remarkable 70% increase in abundance in November/December (Salgado-Barragán, 2002), which coincides with the end of culture cycles in October when nutrient-rich water of ponds, containing larvae of *F. miamiensis*, is directly discharged to the nearest estuary. Larvae of *F. miamiensis* subsequently settle in large numbers on mangrove roots (Tovar-Hernández & Yáñez-Rivera, 2012). Even though economic and ecological impacts of *F. miamiensis* are unknown, it is included in the list of invasive for Mexico species

(Diario Oficial de la Federación, 2016), whose introduction is forbidden in natural protected areas and critical habitats for wildlife conservation as well as in refuge areas to protect native aquatic species.

Unlike *F. miamiensis*, specimens of *F. uschakovi* show significant morphological variability suggesting that the nominal species might be an unresolved complex of multiple species, some of which are highly invasive. Thus, as in *F. enigmaticus* where the existence of cryptic species has been demonstrated with genetic data (Styan *et al.*, 2017; Yee *et al.*, 2019; Grosse *et al.*, 2021), multiple species within *F. uschakovi* are also likely to be revealed with

DNA data. Unfortunately, no published sequences of nominal *F. uschakovi* are currently available from any locality, except for *F. cf. uschakovi* from temperate Southern NSW, Australia in Styan *et al.* (2017). These animals are morphologically distinct from *F. uschakovi sensu stricto* in having thoracic membranes free, not fused dorsally, suggesting the existence of an undescribed species with *F. uschakovi* opercular morphology in temperate Australia.

Ficopomatus uschakovi was originally described from Sri Lanka, but its native range in Southeast Asia is unknown. It is clearly a highly invasive taxon that was first introduced to America about a decade ago, but introductory pathways are unknown. In the Biosphere Reserve 'La Encrucijada' (Southern Mexican Pacific) the nearest port is 70 km away and there are no shrimp farms that support the hypothesis of ships/marine traffic or aquaculture activities as pathways of introduction (Bastida-Zavala & García-Madrugal, 2012). The nominal species has been reported in Tropical America forming small patches attached to mangrove roots (de Assis *et al.*, 2008; Bastida-Zavala & García-Madrugal, 2012; Arteaga-Flórez *et al.*, 2014) and found in discrete groups under rocks (Liñero-Arana & Díaz-Díaz, 2012). Either ecological or economic impacts of this invader are unknown, except for the fact that fishing boats in the southern Mexican Pacific require frequent cleaning of *F. uschakovi* tube encrustations (Bastida-Zavala & García-Madrugal, 2012).

Molecular genetics studies are needed to clarify the *F. uschakovi* taxonomic status and invasive pathways. In particular, specimens from the type locality (Sri Lanka) and other reportedly native localities in Southeast Asia need to be sequenced and compared with the sequences obtained from specimens collected along American coasts. Further ecological studies are needed to evaluate potential impacts of these invasive species on native biota and economic activities.

Data Availability Statement

The authors confirm that the data supporting the findings of this study are available within the article.

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Author contributions. MATH, conceptualization; funding acquisition; sampling; writing; original draft preparation, review and editing. JAdLG: analysis; writing; drafting the work; editing and final approval of version to be published. EK: analysis; funding acquisition; writing, review and editing.

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Conflict of interest. The authors declare none.

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