



Review of the geographic distribution of *Hoffmannola hansii* (Gastropoda: Pulmonata) in the Mexican Pacific

Revisión del ámbito de distribución geográfica de *Hoffmannola hansii* (Gastropoda: Pulmonata) en el Pacífico mexicano

Omar Hernando Avila-Poveda^{1✉}, Quetzalli Yasú Abadia-Chanona², Raúl Herrera-Fragoso³ and Benoît Dayrat⁴

¹División de Estudios de Posgrado, Universidad del Mar, 70902 Puerto Ángel, Oaxaca, Mexico.

²Licenciatura en Biología Marina, Universidad del Mar, 70902 Puerto Ángel, Oaxaca, Mexico. Present address: Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional, 23096 La Paz, Baja California Sur, Mexico.

³Universidad La Salle-Nezahualcóyotl. Av. Bordo de Xochiaca, 57300 Nezahualcóyotl, Estado de México, Mexico.

⁴Department of Biology, Pennsylvania State University. University Park, 16802 PA, USA.

✉ oavila@colombia.com

Abstract. *Hoffmannola hansii* (Mexican intertidal leather slug) is traditionally reported as an endemic species to the Gulf of California, Mexico. However, its presence in the southern Mexican Pacific has been mentioned in regional checklists and reports. Here we provide new records of *H. hansii* populations from at least 3 locations from Oaxaca, Mexico. The anatomical characteristics useful for *H. hansii* identification are described for both, living and preserved specimens. Specimen's reports from the Gulf of California to Oaxaca, Mexico, are mentioned, yielding a revised distribution throughout the Mexican Pacific. A map with the wider geographic distribution of *H. hansii* is also updated. Therefore, this species is not "endemic" to the Gulf of California, but is distributed throughout the Mexican Pacific. However its distribution is discontinuous with the possible existence of 2 cryptic species geographically separated by the Sinaloan gap: 1 in the North (Gulf of California) and 1 in the South. Additional work is needed to explore in more detail the complete geographical range of *H. hansii* populations on the entire Mexican Pacific Coast.

Key words: Mollusca, Onchidiidae, non-endemic, Oaxaca, Gulf of California, Tropical Eastern Pacific (TEP), geographical range, cryptic species.

Resumen. *Hoffmannola hansii* (babosa de cuero intermareal mexicana) es tradicionalmente registrada como una especie endémica del golfo de California, México. Sin embargo, su presencia en el sur del Pacífico mexicano ha sido mencionada en listas de control y en informes regionales. Ofrecemos nuevos registros de poblaciones de *H. hansii* de al menos 3 localidades de Oaxaca, México. Las características anatómicas que ayudan a identificar a *H. Hansii* se describen para ejemplares vivos y conservados. Se mencionan los ejemplares desde el golfo de California hasta Oaxaca, México, proporcionando una distribución ampliada a lo largo del Pacífico mexicano. Un mapa con la distribución geográfica de *H. Hansii* también se actualiza. Por lo tanto, esta especie no es endémica del golfo de California, sino que está bien distribuida en el Pacífico mexicano. Sin embargo, su distribución es discontinua, con la posible existencia de 2 especies crípticas geográficamente separadas por la brecha sinaloense: una en el Norte (golfo de California) y otra en el Sur. Sigue siendo necesario realizar trabajo adicional para explorar en mayor detalle la distribución geográfica completa de las poblaciones de *H. hansii* en toda la costa del Pacífico mexicano.

Palabras clave: Mollusca, Onchidiidae, no endémico, Oaxaca, golfo de California, Pacífico Oriental Tropical (POT), ámbito geográfico, especies crípticas.

Introduction

Currently, the Onchidiidae (Mollusca: Gastropoda: Pulmonata) is classified within the pulmonate gastropods (Holznagel et al., 2010; Wu et al., 2010; Dayrat et al., 2011a). However, its phylogenetic position has been

heavily debated during the last 8 decades. Authors have considered them as opisthobranchs (Fretter, 1943; Boettger, 1954; Marcus, 1965; Marcus and Marcus, 1967; 1970), pulmonates (Brettnall, 1919; Baker, 1938; Baker, 1955; Ghiselin, 1965; Solem, 1978; Britton, 1984; Barker, 2001; Grande et al., 2004; Dayrat, 2009; Dayrat et al., 2011a,b), euthyneurans (Marcus and Burch, 1965; Selmi et al., 1988; Winnepenninckx et al., 1998; Dayrat and Tillier,

2000; 2002; 2003), or even as a separate Order Onchidiida (Starobogatov, 1976) and Silicodermatae (Labbé, 1934). Regardless, Onchidiidae remains a poorly-known taxon in many regards, especially in species diversity and distribution.

The most interesting aspect of the geographic range for Onchidiidae is that almost all the genera are exclusively found in tropical and subtropical areas from the Indo-West Pacific (Brettnall, 1919; Stringer, 1969; Wu et al., 2010) and the Mediterranean Sea (Barletta and Ghisotti, 1978), excepting 4 nominal *Onchidella* species and 2 nominal *Hoffmannola* species (i.e., *H. hansii* and *H. lesliei*) that are restricted to the tropical Eastern Pacific (Dayrat, 2009; Dayrat et al., 2011b). *Onchidella* has an extensive geographical range in all the tropical Eastern Pacific; while *Hoffmannola hansii* is restricted to the Northern Gulf of California and *Hoffmannola lesliei* to the Galapagos (e.g., Marcus and Marcus, 1967, 1970; Keen, 1971; Hendrickx et al., 2005; Dayrat, 2009; Dayrat et al., 2011a).

Hoffmannola hansii Marcus and Marcus, 1967 (for nomenclatural information, see, Dayrat et al., 2011b) has been known by its description as “endemic” commonly found in the rocky, intertidal communities of the Gulf of California, Mexico, across shores from Baja California Norte, Sonora, and Sinaloa (Marcus and Marcus, 1967, 1970; Keen, 1971; Hendrickx et al., 2005; Zamora-Silva and Naranjo-García, 2008; Dayrat, 2009; ASDM, 2011; Dayrat et al., 2011a). Nevertheless, various publications, reports, and regional checklists (none of which citing any deposited material) have mentioned *H. hansii* in other Mexican states and localities outside the Gulf of California and further south into the Mexican Pacific, such as, Jalisco (Esqueda-González, 1995; Esqueda et al., 2000), Jalisco, Colima and Michoacán (Holguín-Quñones and González-Pedraza, 1994), Michoacán (Villaseñor-Gómez, 2005), Guerrero (Flores-Garza et al., 2005; 2007; Flores-Rodríguez et al., 2001, 2003, 2007, 2012; Flores-Rodríguez, 2004; Valdés-González et al., 2004) and Oaxaca (Rodríguez-Palacios et al., 1988; León-Herrera, 2000; 2001; Ramírez-González, 2008). Although they did not cite any actual specimens, those publications suggest that *H. hansii* may not be endemic to the Gulf of California.

The present study provides a review of the geographic distribution of *H. hansii* from available original literature (e.g., reports, grey literature, and regional checklists), several online databases of museum collections and specimens collected by our group Oaxaca, Mexico.

Material and methods

Specimens of different sizes of *H. hansii* were found while sampling for *Chiton (Chiton) articulatus* at Oaxaca

(Avila-Poveda, 2013; Avila-Poveda and Abadia-Chanona, 2013). They were living next to 2 other species of mollusks (*Chiton (Chiton) articulatus* and/or *Plicopurpura pansa*) within crevices at high tide, or by themselves on the surface of rocks during low tide (Fig. 1). Several specimens of *H. hansii* were collected (n= 18, 14 ≤ TL ≤ 48 mm, total length, Fig. 2), in March, April, August, and October 2011 from 3 localities in Oaxaca, Mexico: 1) Puerto Angel (15°39' N, 96°29' W); 2) El Faro, Puerto Angel (15°39' N, 96°30' W), and 3) Conejos Bay, Huatulco (15°46' N, 96°04' W).

Three specimens (45 ± 3 mm TL, Fig. 3) were relaxed and allowed to extend for 1 h, with gradual additions of tap water to the seawater, until the salinity reached half the salinity of the seawater of the sampling site (i.e., 50:50 in volume: Avila-Poveda, 2013) and accelerating the relaxation process by adding few milliliters of 10% ethanol (after Lincoln and Sheals, 1979). Later, specimens were fixed in 10% neutral formalin-saline solution in seawater for 2 weeks and subsequently preserved in 70% ethanol (Avila-Poveda and Baqueiro-Cárdenas, 2009). Other specimens were preserved in 95% ethanol for future molecular work (Dayrat lab). The external and internal morphologies were studied under a dissecting microscope.

Specimens were (or shortly will be) deposited in museums in the region: 1) Laboratorio de Sistemática de Invertebrados Marinos (LABSIM), Universidad del Mar, Puerto Angel, Oaxaca, Mexico; 2) California Academy of Sciences (CAS), San Francisco, California, USA; 3) Santa Barbara Museum of Natural History (SBMNH), Santa Barbara County, California, USA; 4) Scripps Institution of Oceanography (SIO), San Diego, California, USA; 5) Arizona-Sonora Desert Museum (ASDM), Tucson, Arizona, USA; 6) Smithsonian National Museum of Natural History (NMNH), NW Washington, D.C., USA.

A checklist and a map of the geographic distribution of *H. hansii* were developed, based on records found for this species in scientific databases and web sites (e.g., BHL, BioStor, JSTOR, among many others), available original literature (e.g., reports and checklists), online databases of museum collections (e.g., ASDM, CAS, LABSIM, NMNH, SBMNH, SIO) and with the samples collected by our group Oaxaca, Mexico.

Results

The most important anatomical characters observed that help to identify the species are (for additional information, see: Dayrat et al., 2011b): 1) the total length of live specimens ranges from 14 mm to 48 mm (Fig. 3A) while preserved material is on average 25% shorter (e.g., the largest live specimen of 48 mm long measures

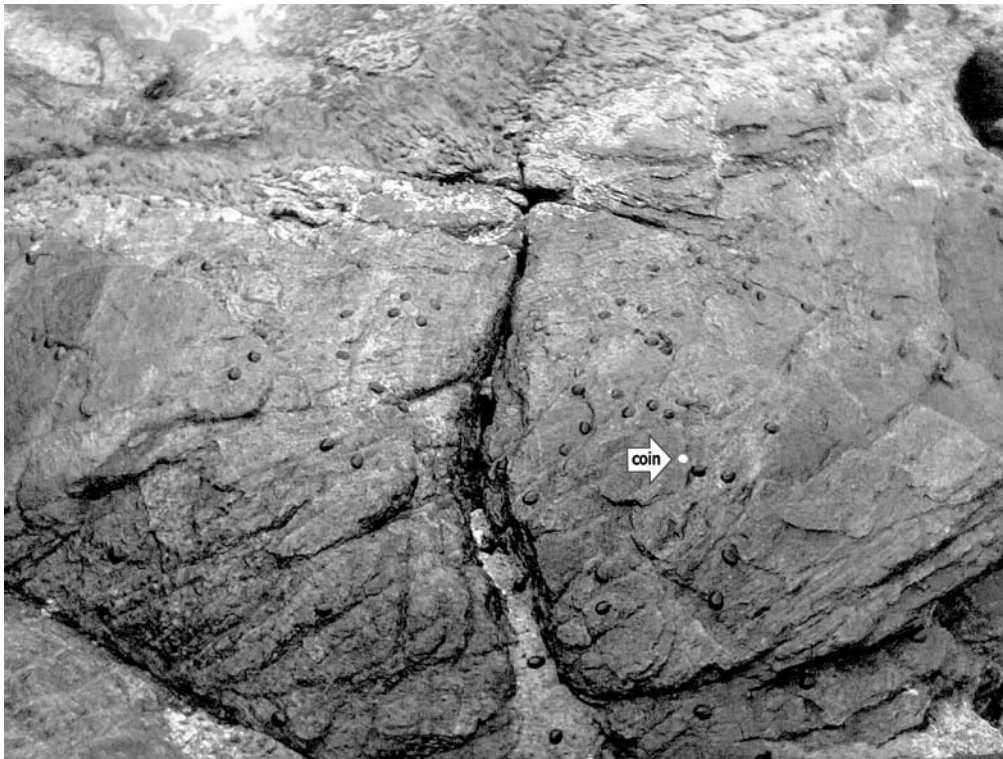


Figure 1. *Hoffmannola hansii*. Live animals (~50 specimens in picture) observed in the rocky intertidal of El Faro, Puerto Angel, Oaxaca, Mexico (15°39'N-96°30'W), USNM 1155112. The arrow indicates a 2 pesos Mexican coin (23 mm diameter).

only 33 mm once preserved; see, Fig. 3B); exceptionally, we observed specimens in the field that were longer than 48 mm, but in areas with difficult access; 2) the total width of the hyponotum (left and right side, H) relative to the width of the pedal sole (S) is around the third or fourth part (i.e., $H \ll S$) with H-S-H of 5-16/22-5 mm



Figure 2. Preserved specimens of different sizes of *Hoffmannola hansii*. The viscous fluid secreted by the marginal gland (repugnatorial gland) is observed in the periphery of each specimen.

for live organisms, while these are 4-13/18-4 mm for the same preserved organisms; 3) there are generally about 14 marginal glands on the left and about 15 on the right; 4) the visceral cavity is divided in 2 by a septum (which actually is a characteristic of *Hoffmannola*).

During the sampling months (i.e., March, April, August, and October), early life stages of various species of intertidal mollusks such as *Chiton (Chiton) albolineatus*, *Chiton (Chiton) articulatus*, *Echinolittorina aspera*, *Echinolittorina modesta*, *Plicopurpura pansa*, *Nerita scabricosta*, and *Hoffmannola hansii*, among many others mollusks, were observed in large stocks that resembled a nursery.

A geographic distribution of *H. hansii* specimens was found available broadly over the Mexican Pacific, and not just restricted to the Gulf of California (Table 1; Fig. 4).

Discussion

The checklist and map presented here show many more records of *Hoffmannola hansii* towards the Mexican south Pacific (records No. 13 to 36, total 24; Table 1; Fig. 4) than northern locations, where it has been termed as “endemic”

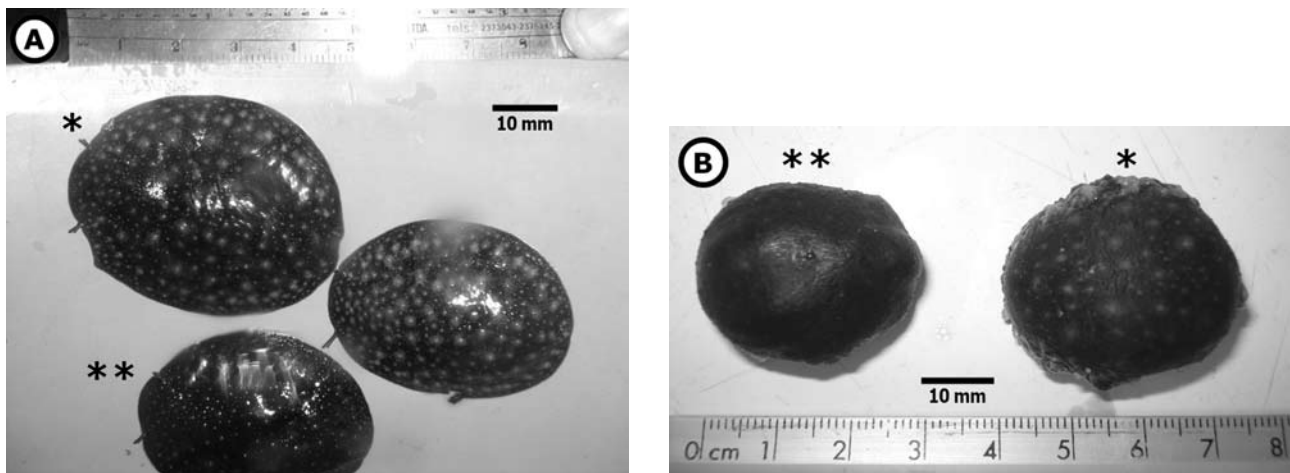


Figure 3. *Hoffmannola hansii*. Live animals (A); and fixed and preserved individuals used for dissection (B). Collected at El Faro, Puerto Angel, Oaxaca, Mexico (15°39'N-96°30'W). Same number of asterisks indicates the same specimen.

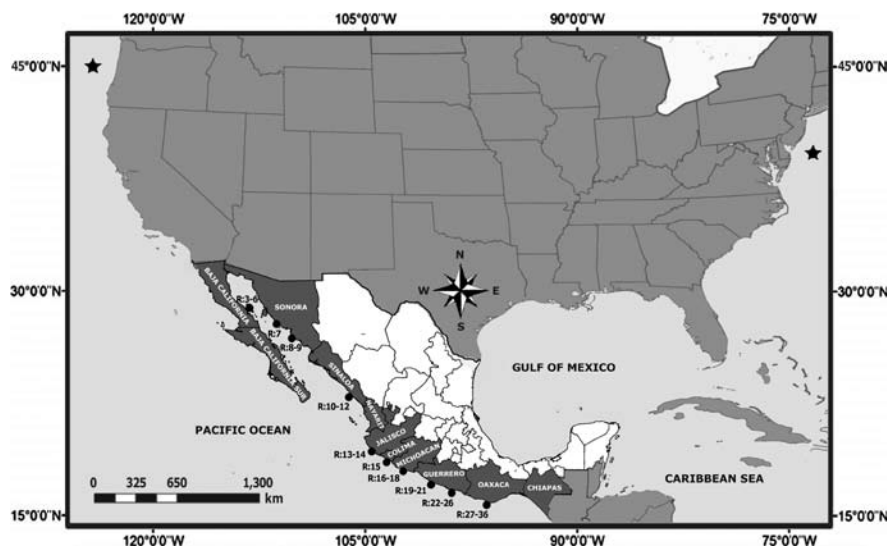


Figure 4. Geographical distribution of *Hoffmannola hansii* along the Tropical Eastern Pacific. Records (R) according to Table 1. A star (*) marks 2 questionable localities, outside the Tropical Eastern Pacific (catalog numbers USNM 771808 and USNM 710013; NMNH 2011).

to the Gulf of California ((records No. 3 to 12, total 10: Table 1; Fig. 4). Thus, *H. hansii* has been previously recorded in Jalisco (Esqueda et al., 2000), Jalisco, Colima and Michoacán (Holguín-Quñones and González-Pedraza, 1994), Michoacán (Villaseñor-Gómez, 2005), Guerrero (Flores-Garza et al., 2005; 2007; Flores-Rodríguez et al., 2001, 2003, 2007, 2012; Flores-Rodríguez, 2004; Valdés-González et al., 2004) and Oaxaca (Rodríguez-Palacios et al., 1988; León-Herrera, 2000; 2001; Ramírez-González, 2008).

Based on information presented here, the localities of Puerto Angel, El Faro, and Conejos Bay of Huatulco, all in the state of Oaxaca, Mexico, should be incorporated into the species geographical distribution, as well as the states of Jalisco, Colima, Michoacán, and Guerrero, in Mexico, where *H. hansii* (Mexican intertidal leather slug) has been mentioned from the rocky intertidal.

In any case, *H. hansii* is not endemic to the Gulf of California, but is distributed throughout the Mexican Pacific, although its distribution is quite discontinuous.

Table 1. Records of *Hoffmannola hansii* along the Tropical Eastern Pacific. Coordinates were taken from each original source. Dashed lines indicate unavailable data. Data was organized according to geographical coordinates and area according to country, state, region, and locality. *R*, is the progressive record for each locality. The gray shadow helping to distinguish each group by state

<i>R</i>	<i>Catalog number</i>	<i>Coordinates</i>	<i>Geographical area and locality</i>	<i>Year of collection</i>	<i>Sources</i>
1	USNM 771808	45°N-125°W	USA, Washington, Fort Canby State Park ***	1970	NMNH 2011
2	USNM 710013	41°N-71°W	USA, New Hampshire, Pitsfield ***	1974	NMNH 2011
3	USNM 678419	29°N-113°W	Mexico, Baja California, Gulf of California, San Agustín	1967*	NMNH 2011, Marcus and Marcus 1967
4	----	29°N-113°W	Mexico, Baja California, Gulf of California, Angel de la Guarda Island	----	ASDM 2011, Hendrickx et al. 2005
5	----	29°N-113°W	Mexico, Baja California, Gulf of California, Angel de la Guarda Island	----	Keen 1971
6	----	29°N-113°W	Mexico, Baja California, Gulf of California, San Agustín	1966	Marcus and Marcus 1970
7	----	28°N-111°W	Mexico, Sonora, Gulf of California, Kino Bay	----	Keen 1971
8	USNM-753651	27°N-110°W	Mexico, Sonora, Gulf of California, El Sahuaral	1966	NMNH 2011
9	USNM 753653	27°N-110°W	Mexico, Sonora, Gulf of California, El Sahuaral	1966	NMNH 2011
10	CAS-81809	23°N-106°W	Mexico, Sinaloa, Gulf of California, Gaviotas Beachs	1953	CAS 2011
11	CNMO 1783 **	23°N-106°W	Mexico, Sinaloa, Gulf of California, Cerro Crestón Beachs	1987	Zamora-Silva and Naranjo-García 2008
12	----	23°N-106°W	Mexico, Sinaloa, Gulf of California, Mazatlán	----	ASDM 2011, Hendrickx et al. 2005
13	CMLE †	19°13'N- 104°42'W	Mexico, Jalisco, Melaque	1987-1989	Holguín-Quiñones and González-Pedraza 1994
14	----	19°14'N- 104°46'W	Mexico, Jalisco, Cuastecomate Bay, La Calechosa	1993-1994	Esqueda-González 1995, Esqueda et al. 2000
15	CMLE †	19°06'N-104°20'W	Mexico, Colima, Las Hadas, Club de Yates Beach	1987-1989	Holguín-Quiñones and González-Pedraza 1994
16	----	18°N-103°W	Mexico, Michoacán	----	Villaseñor-Gómez 2005
17	CMLE †	18°20'N-103°30'W	Mexico, Michoacán, Faro de Bucerías town	1987-1989	Holguín-Quiñones and González-Pedraza 1994
18	CMLE †	18°16'N-103°20'W	Mexico, Michoacán, Maruata town	1987-1989	Holguín-Quiñones and González-Pedraza 1994
19	CMLEICS §,b	17°47'N-101°44'W	Mexico, Guerrero, Troncones Beach	2000/2001/2005	a, b, d, e, g
20	----	17°32'N-101°26'W	Mexico, Guerrero, Barra de Potosí Beach	2000/2001/2005	a, d, e, g
21	----	17°15'N-101°01'W	Mexico, Guerrero, Tlacyunque Beach	2000/2001/2005	a, d, e, g
22	----	16°49'N-99°54'W	Mexico, Guerrero, La Roqueta-"Palmitas" Island	2000/2001/2005	a, e, g, h
23	----	16°42'N-99°54'W	Mexico, Guerrero, La Roqueta-"Zoológico" Island	2000/2001/2005	a, e, e, g, h

Table 1. Continues

24	----	16°33'N-98°46'W	Mexico, Guerrero, Las Peñitas Beach	2000/2001/2005	a, e, g
25	----	16°32'N-98°54'W	Mexico, Guerrero, Ventura Beach	2000/2001/2005	a, e, f, g
26	----	16°19'N-98°34'W	Mexico, Guerrero, Punta Maldonado Beach	2000/2001/2005	a, e, g
27	----	15°46'N-96°05'W	Mexico, Oaxaca, Tangelunda Bay	----	León-Herrera 2001, 2000
28	----	15°46'N-96°04'W	Mexico, Oaxaca, Conejo Beach	2011	This study
29	----	15°45'N-96°07'W	Mexico, Oaxaca, Violín Beach	----	León-Herrera 2001, 2000
30	----	15°45'N-96°07'W	Mexico, Oaxaca, Arroyo Beach	----	Ramírez-González 2008, León-Herrera 2001, 2000
31	----	15°44'N-96°07'W	Mexico, Oaxaca, India Beach	----	León-Herrera 2001, 2000
32	----	15°43'N-96°10'W	Mexico, Oaxaca, Cacaluta Island	2005	Ramírez-González 2008
33	----	15°41'N-96°26'W	Mexico, Oaxaca, Tijera Bay	----	León-Herrera 2001, 2000
34	USNM 1155112	15°39'N-96°30'W	Mexico, Oaxaca, Puerto Ángel, El Faro	2011	This study
35	UMAR-Gast-001 [^]	15°39'N-96°29'W	Mexico, Oaxaca, Puerto Ángel town	2011	This study
36	----	15°39'N-96°29'W	Mexico, Oaxaca, Puerto Ángel	----	Rodríguez-Palacios et al. 1988, León-Herrera 2001, 2000

^a Flores-Rodríguez et al., 2012

^b Flores-Rodríguez et al., 2007

^c Flores-Rodríguez et al., 2003

^d Flores-Rodríguez et al., 2001

^e Flores-Rodríguez 2004,

^f Flores-Garza et al. 2007,

^g Flores-Garza et al. 2005,

^h Valdés-González et al. 2004,

* Collected date only mentioned by Marcus and Marcus (1967)

** Colección Nacional de Moluscos (CNMO), Instituto de Biología, Universidad Nacional Autónoma de México (UNAM).

*** Questionable localities, outside of the Tropical Eastern Pacific Region, possible errors. Feedback was sent to NMNH for its review.

§ Colección de Moluscos del Laboratorio de Investigación en Ecología Costera y Sustentabilidad (CMLIECS), Unidad Académica de Ecología Marina, Universidad Autónoma de Guerrero, Mexico.

† Colección de Moluscos del Laboratorio de Ecología (CMLE), Escuela Nacional de Ciencias Biológicas, Mexico.

[^] Colección Científica de Invertebrados, Laboratorio de Sistemática de Invertebrados Marinos (LABSIM), Universidad del Mar, campus Puerto Ángel, Oaxaca, Mexico.

However, *H. hansii* requires rocky shores to live and large parts of the coast between the Gulf of California and southern Mexico are sandy beaches, especially the Sinaloan gap (Hastings, 2000). However, additional work is still needed to explore in more detail the complete geographical range of *H. hansii* populations on the entire Mexican Pacific Coast.

Currently, as only morphological data are available and as populations from the Gulf of California and those from Oaxaca are not distinguishable, it is more parsimonious to regard them all as part of the same species, *H. hansii*. However, it cannot be excluded that molecular data could reveal the existence of 2 cryptic but separate species, one in the North (Gulf of California) and one in the South, both separated geographically by the long Sinaloan gap. Various types of patterns of distribution have been found by authors for rocky, intertidal species from the tropical Eastern Pacific (e.g., Hastings, 2000; Wares, 2001; Craig et al., 2006; Pitombo and Burton, 2007; Wares et al., 2009). Both onchidiid species, *H. hansii* and *Onchidella binneyi* (also distributed all along the Mexican Pacific), seem ideal candidates for such population studies (Dayrat et al. 2011b).

On the other hand, some errors were unveiled in the literature as well as online databases. Two museum records for *H. hansii* (NMNH 2011: USNM 771808 and USNM 710013) are likely to be incorrect, or at least questionable, since they are outside of the tropical Eastern Pacific and even in a different region of the Western Atlantic (Fig. 4). Feedback has been sent to NMNH Customer Service for its review (Avila-Poveda, pers. comm.).

Acknowledgments

This work was personally assured by Avila-Poveda OH with SNI-Conacyt stimulus (record No. 44175, from January to July 2012). Avila-Poveda OH gives special thanks for the family grant that covered his stay in the location during the course of this study. Thanks to Saúl Jaime Serrano-Guzmán for transporting the specimens to Benoît Dayrat at the School of Natural Sciences, University of California at Merced, California, USA. Thanks to Francisco Benitez-Villalobos for transporting and depositing some specimens in the NMNH (USNM 1155112). All rare references were downloaded via the Biodiversity Heritage Library (<http://www.biodiversitylibrary.org/>), Bioline International (<http://www.bioline.org.br/>), BioStor (<http://biostor.org/>), and Internet Archive (<http://www.archive.org/>).

Literature cited

ASDM (Arizona-Sonora Desert Museum). 2011. Macrofauna golfo invertebrate database <http://www.desertmuseum.org/>

- center/seaofcortez/searchdb.php; last access: 5.IV.2011.
- Avila-Poveda, O. H. 2013. Annual change in morphometry and in somatic and reproductive indices of *Chiton articulatus* adults (Mollusca: Polyplacophora) from Oaxaca, Mexican Pacific. *American Malacological Bulletin* 31:65-74.
- Avila-Poveda, O. H. and Q. Y. Abadia-Chanona. 2013. Emergence, development, and maturity of the gonad of two species of chitons “sea cockroach” (Mollusca: Polyplacophora) through the early life stages. *PLoS ONE* 8(8): e69785. doi:10.1371/journal.pone.0069785
- Avila-Poveda, O. H. and E. R. Baqueiro-Cárdenas. 2009. Reproductive cycle of *Strombus gigas* Linnaeus 1758 (Caenogastropoda: Strombidae) from Archipelago of San Andres, Providencia and Santa Catalina, Colombia. *Invertebrate Reproduction and Development* 53:1-12.
- Baker, H. B. 1955. Heterurethrous and Aulacopod. *The Nautilus* 68:109-112.
- Baker, H. B. 1938. Nomenclature of Onchidiidae. *The Nautilus* 51:85-88.
- Barker, G. M. 2001. Gastropods on land: phylogeny, diversity and adaptive morphology. *In* The biology of terrestrial molluscs, G. M. Barker (ed.). CABI Publishing, London. p. 1-146.
- Barletta, G. and F. Ghisotti. 1978. Primo rinvenimento di una forma della famiglia Onchidiidae nel Golfo di Genova e in Tunisia (Gastropoda: Soleolifera). *Bollettino di Zoologia* 45:253-256. [Renamed as: Italian Journal of Zoology].
- Boettger, C. R. 1954. Die systematik der euthyneuren Schnecken. *Verhandlungen der Deutschen Zoologischen Gesellschaft in Tübingen* 18:253-280.
- Brettnall, B. W. 1919. Onchidiidae from Australia and the South-Western Pacific Islands. *Records of the Australian Museum* 12:303-328.
- Britton, K. M. 1984. The onchidiacea (Gastropoda, Pulmonata) of Hong Kong with a worldwide review of the genera. *Journal of Molluscan Studies* 50:179-191.
- CAS “California Academy of Sciences”. 2011. Search the Collections Catalog. http://research.calacademy.org/redirect?url=http://researcharchive.calacademy.org/research/izg/iz_coll_db/index.asp; last access: 28.III.2011.
- Craig, M. T., P. A. Hastings, D. J. Pondella, D. R. Robertson and J. A. Rosales-Casián. 2006. Phylogeography of the flag crab *Epinephelus labriformis* (Serranidae): implications for the biogeography of the Tropical Eastern Pacific and the early stages of speciation in a marine shore fish. *Journal of Biogeography* 33:969-979.
- Dayrat, B., M. Conrad, S. Balayan, T. R. White, C. Albrecht, R. Golding, S. R. Gomes, M. G. Harasewych and A. M. de-Frias-Martins. 2011a. Phylogenetic relationships and evolution of pulmonate gastropods (Mollusca): New insights from increased taxon sampling. *Molecular Phylogenetics and Evolution* 59:425-437
- Dayrat, B., S. Zimmermann and M. Raposa. 2011b. Taxonomic revision of the Onchidiidae (Mollusca: Gastropoda: Pulmonata) from the Tropical Eastern Pacific. *Journal of Natural History* 45:939-1003.
- Dayrat, B. 2009. Review of the current knowledge of the

- systematics of Onchidiidae (Mollusca: Gastropoda: Pulmonata) with a checklist of nominal species. *Zootaxa* 2068:1-26.
- Dayrat, B. and S. Tillier. 2003. Goals and limits of phylogenetics: the Euthyneuran gastropods. *In* Molecular systematics of mollusks, C. Lydeard and D. Lindberg (eds.). Smithsonian Institution Press, Washington D. C. p. 161-184.
- Dayrat, B. and S. Tillier. 2002. Evolutionary relationships of euthyneuran gastropods (Mollusca): a cladistic re-evaluation of morphological characters. *Zoological Journal of the Linnean Society* 135:403-470.
- Dayrat, B. and S. Tillier. 2000. Taxon sampling, character sampling and systematics: how gradist presuppositions created additional ganglia in gastropod euthyneuran taxa. *Zoological Journal of the Linnean Society* 129:403-418.
- Esqueda-González, M. C. 1995. Moluscos de la bahía de Cuastecomate, Jalisco, México. (Clases: Gastropoda y Bivalvia). B. Sc. Thesis. Facultad de Biología, Universidad de Guadalajara. Zapopán. 122 p
- Esqueda, M. C., E. Ríos-Jara, J. E. Michel-Morfin and V. Landa-Jaime. 2000. The vertical distribution and abundance of gastropods and bivalves from rocky beaches of Cuastecomate Bay, Jalisco, Mexico. *Revista de Biología Tropical* 48:765-775
- Flores-Garza, R., P. Flores-Rodríguez, S. García-Ibáñez and A. Valdés-González. 2007. Demografía del caracol *Plicopurpura pansa* (Neotaenioglossa: Muricidae) y constitución de la comunidad malacológica asociada en Guerrero, México. *Revista de Biología Tropical* 55:867-878.
- Flores-Garza, R., P. Flores-Rodríguez, S. García-Ibáñez, A. Valdés-González and D. Arana-Salvador. 2005. Estructura de la población de *Plicopurpura patula pansa* (gould, 1853) (Neotaenioglossa: Muricidae) y malacofauna asociada en el litoral rocoso del Estado de Guerrero. XVIII Congreso Nacional de Zoología, Monterrey, Nuevo León, Mexico, October 4-7, 2005. [Abstract 0272].
- Flores-Rodríguez, P. 2004. Estructura de la comunidad de moluscos del mesolitoral superior en playas de facie rocosa del estado de Guerrero, México. Ph.D. Thesis, Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León. San Nicolás de los Garza. 207 p.
- Flores-Rodríguez, P., R. Flores-Garza, S. García-Ibáñez, A. Valdés-González, J. Violante-González, E. Santiago-Cortés, L. Galeana-Rebolledo and C. Torreblanca-Ramírez. 2012. Mollusk species richness on the rocky shores of the state of Guerrero, Mexico, as affected by rains and their geographical distribution. *Natural Resources* 3:248-260
- Flores-Rodríguez, P., R. Flores-Garza, S. García-Ibáñez and A. Valdés-González. 2007. Variación en la diversidad malacológica del mesolitoral rocoso en Playa Troncones, La Unión, Guerrero, México. *Revista Mexicana de Biodiversidad* 78:33S-40S.
- Flores-Rodríguez, P., R. Flores-Garza, S. García-Ibáñez and A. Valdés-González. 2003. Riqueza y diversidad de la malacofauna del mesolitoral rocoso de la Isla La Roqueta, Acapulco, Guerrero, México. *Ciencia, Universidad Autónoma de Guerrero* 11:5-14.
- Flores-Rodríguez, P., R. Flores-Garza, S. García-Ibáñez and A. Valdés-González. 2001. Malacofauna y estructura trófica del mesolitoral rocoso en la Costa Grande, Guerrero, México. VIII Reunión Nacional de Malacología y Conquiliología (Renamac), Ciudad Victoria, Tamaulipas, Mexico, September 25-28, 2001 [Abstract 32].
- Fretter, V. 1943. Studies in the functional morphology and embryology of *Onchidella celtica* (Forbes and Hanley) and their bearing on its relationships. *Journal of the Marine Biological Association of the United Kingdom* 25:685-720.
- Ghiselin, M. T. 1965. Reproductive function and the phylogeny of opisthobranch gastropods. *Malacologia* 3:327-378.
- Grande, C., J. Templado, J. L. Cervera and R. Zardoya. 2004. Phylogenetic relationships among Opisthobranchia (Mollusca: Gastropoda) based on mitochondrial *cox 1*, *trnV*, and *rrnL* genes. *Molecular Phylogenetics and Evolution* 33:378-388.
- Hastings, P. A. 2000. Biogeography of the Tropical Eastern Pacific: distribution and phylogeny of chaenopsid fishes. *Zoological Journal of the Linnean Society* 128:319-335.
- Hendrickx, M. E., R. C. Brusca and L. T. Findley. 2005. Listado y distribución de la macrofauna del golfo de California, México. Parte 1. Invertebrados. Arizona-Sonora Desert Museum, Tucson. 429 p.
- Holguín-Quñones, O. E. and A. C. González-Pedraza. 1994. Moluscos de la franja costera de Michoacán, Colima y Jalisco, México. Instituto Politécnico Nacional, México, D. F. 150 p.
- Holznagel, W. E., D. J. Colgan and C. Lydeard. 2010. Pulmonate phylogeny based on 28S rRNA gene sequences: A framework for discussing habitat transitions and character transformation. *Molecular Phylogenetics and Evolution* 57:1017-1025
- Keen, A. M. 1971. Sea shell of Tropical West America. Marine mollusks from Baja California to Peru. Second Edition, Stanford University Press, California. 1063 p.
- Labbé, A. 1934. Les silicodermés (Labbé) du Museum d'Histoire Naturelle de Paris. Première partie: Classification, formes nouvelles ou peu connues. *Annales de l'Institut Océanographique de Monaco* 14:173-246.
- León-Herrera, M. G. 2001. Abundancia y diversidad de moluscos intermareales en seis playas rocosas del litoral Oaxaqueño. B. Sc. Thesis. Facultad de Biología Marina, Universidad del Mar. Puerto Ángel. 94 p.
- León-Herrera, M. G. 2000. Listado taxonómico de las especies de moluscos en la zona central del litoral Oaxaqueño. *Ciencia y Mar* 12:49-51.
- Lincoln, R. J. and J. G. Sheals. 1979. Invertebrate animals: collection and preservation. British Museum and Cambridge University Press. London. 150 p.
- Marcus, E. B. R. and E. Marcus. 1970. Some gastropods from Madagascar and West Mexico. *Malacologia* 10:181-223.
- Marcus, E. B. R. and E. Marcus. 1967. American Opisthobranch Mollusks. *Studies in Tropical Oceanography* 6:1-256.
- Marcus, E. 1965. Some Opisthobranchia from Micronesia. *Malacologia* 3:263-286.
- Marcus, E. and J. R. Burch. 1965. Marine Euthyneuran

- gastropoda from eniwetok atoll, Western Pacific. *Malacologia* 3:235-262.
- NMNH (Smithsonian National Museum of Natural History). 2011. Invertebrate zoology collections Search. <http://collections.nmnh.si.edu/search/iz/>; last access: 25.II.2011.
- Pitombo, F. B. and R. Burton. 2007. Systematics and biogeography of Tropical Eastern Pacific *Chthamalus* with descriptions of two new species (Cirripedia, Thoracica). *Zootaxa* 1574:1-30.
- Ramírez-González, A. 2008. Caracterización de Mollusca en la isla y en la bahía Cacaluta. In *Diagnóstico de los recursos naturales de la bahía y micro-cuenca del río Cacaluta, Municipio de Santa María Huatulco, Oaxaca*, J. M. Domínguez-Licona (ed.). Universidad del Mar, Huatulco. p. 211-242.
- Rodríguez-Palacios, C. A., L. M. Mitchell-Arana, G. Sandoval-Díaz, P. Gómez and G. Green. 1988. Los moluscos de las bahías de Huatulco y Puerto Ángel, Oaxaca. *Distribución, diversidad y abundancia*. Universidad y Ciencia 5:85-94.
- Selmi, M. G., F. Giusti and G. Manganelli. 1988. The fine structure of the mature spermatozoon of *Onchidella celtica* (Cuvier) (Mollusca: Gastropoda) and its phylogenetic implications. *Journal of Ultrastructure and Molecular Structure Research* 99:107-123.
- Solem, A. 1978. Classification of the land Mollusca. In *Pulmonates: systematics, evolution and ecology*, Vol. 2A, V. Fretter and J. Peake (eds.). Academic Press, New York. p. 49-97.
- Starobogatov, Y. I. 1976. Composition and taxonomic position of marine pulmonate mollusks. *Soviet Journal of Marine Biology* 4:206-212.
- Stringer, B. L. 1969. The species of New Zealand Onchidiidae (mollusca, gastropoda) and their distribution. *New Zealand Journal of Marine and Freshwater Research* 3:29-45
- Valdés-González, A., P. Flores-Rodríguez, R. Flores-Garza and S. García-Ibáñez. 2004. Molluscan communities of the rocky intertidal zone at two sites with different wave action on isla La Roqueta, Acapulco, Guerrero, Mexico. *Journal of Shellfish Research* 23:875-880.
- Villaseñor-Gómez, L. E. 2005. La biodiversidad en Michoacán: estudio de estado. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Secretaría de Urbanismo y Medio Ambiente, Universidad Michoacana de San Nicolás de Hidalgo, Mexico D. F. 760 p.
- Wares, J. P. 2001. Patterns of speciation inferred from mitochondrial DNA in North American *Chthamalus* (Cirripedia: Balanomorpha: Chthamaloidea). *Molecular Phylogenetics and Evolution* 18:104-116.
- Wares, J. P., M. S. Pankey, F. Pitombo, L. G. Daglio and Y. Achituv. 2009. A "shallow phylogeny" of shallow barnacles (*Chthamalus*). *Plos One* 4: e5567. doi:10.1371/journal.pone.0005567
- Winnepenninckx, B., G. Steiner, T. Backeljau and R. De-Wachter. 1998. Details of gastropod phylogeny inferred from 18S rRNA sequences. *Molecular Phylogenetics and Evolution* 9:55-63.
- Wu, W. J., B. Shen, C. Chen, H. D. Shen, L. L. Wei, L. Wang and K. Li. 2010. Preliminary classification and phylogenetic relationship among onchidiidae in China inferred from 18S rRNA partial sequence. *Zoological Research* 31:381-386.
- Zamora-Silva, A. and E. Naranjo-García. 2008. Los opistobranquios de la Colección Nacional de Moluscos. *Revista Mexicana de Biodiversidad* 79:333-342.