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A review on the diversity and distribution of opisthobranch gastropods from Peru, with the addition of three new records

(Gastropoda, Heterobranchia)

Roberto A. Uribe, Katia Nakamura, Aldo Indacochea, Aldo S. Pacheco, Yuri Hooker & Michael Schrödl

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Although the diversity of marine molluscs along the Humboldt Current ecosystem is relatively well known, some groups such as opisthobranch sea slugs and snails (Gastropoda, Heterobranchia) have received little attention. Herein, we critically review and update the taxonomical composition of Acteonoidea, Nudipleura, Euopisthobranchia and marine panpulmonates Sacoglossa and Acochlida from coastal Peruvian waters. Our checklist comprises a total of 56 species belonging to 30 families. The nudibranch species *Tritonia* sp., *Tyrinna nobilis* and *Diaulula variolata* are reported for the first time in the Peruvian coast. We also add new collection localities for 19 species, including *Bulla punctulata*, *Navanax aenigmaticus*, *Haminoea peruviana*, *Aplysia juliana*, *Dolabrifera dolabrifera*, *Elysia diomedea*, *Elysia hedgpethi*, *Doris fontainei*, *Baptodoris peruviana*, *Polycera alabe*, *Felimare agassizii*, *Doto uva*, *Dendronotus* cf. *venustus*, *Flabellina cynara*, *Fiona pinnata*, *Spurilla* cf. *neapolitana*, *Phidiana lottini*, *Bajaeolis bertschi* and *Glaucus atlanticus*. The species *Bulla punctulata*, *H. peruviana*, *F. cynara* and *A. juliana*, which are usually distributed in the Tropical East Pacific, are now reported also from the Warm Temperate Southeastern Pacific Province. Earlier records of thecosome pteropods and several more or less adequately described *Aplysia* species still need taxonomic revision. Several benthic Peruvian opisthobranch species assumed to show wide or even circumtropical distributions are likely to be part of species complexes. Integrative approaches including molecular species characterization and intensified field work are necessary to enhance the knowledge on the diversity of opisthobranchs from Peru.

Roberto A. Uribe, Programa de Doctorado en Ciencias Aplicadas Mención Sistemas Marinos Costeros LAMSEC, Universidad de Antofagasta, Avenida Angamos 601, PO Box 170, Antofagasta, Chile

Katia Nakamura, Centro para la Sostenibilidad Ambiental, Universidad Peruana Cayetano Heredia, Lima, Peru

Aldo Indacochea, Facultad de Biología Marina y Econegocios, Universidad Cientifica del Sur, Lima, Peru

Aldo S. Pacheco, Instituto de Investigaciones Oceanológicas, CENSOR laboratory, Universidad de Antofagasta, Antofagasta, Chile; e-mail: babuchapv@yahoo.com

Yuri Hooker, Laboratorio de Biología Marina, Universidad Peruana Cayetano Heredia, Lima, Peru

Michael Schrödl, SNSB – Zoologische Staatssammlung München, Münchhausenstr. 21, 81247 München; and Ludwig-Maximilians-Universität München, Germany

Introduction

The coast of Peru encompasses ~2500 km of shoreline (3°23'–18°21'S) on the northern branch of the highly productive Humboldt Current Upwelling Ecosystem (Ramírez et al. 2003, Zavalaga et al. 2009) and along the Warm Temperate Southeastern Pacific Province (WTSPP) (sensu Spalding et al. 2007). This extensive coastal line is geomorphologically complex with protected bays interspersed by headlands, rock cliffs and extensive sandy beaches. Such heterogeneity leads to the formation of several types of marine benthic habitats (Tarazona et al. 2003). From an oceanographic perspective, two well defined current systems are present: the cold, nutrient-rich upwelling system that flows northward from northern Chile up to ~6 °S, and the warm and less productive equatorial system with a poleward direction from the equator down to ~6 °S (Ramírez et al. 2003). As a result of these oceanographic and geomorphological characteristics together with ecological factors the Peruvian coast holds a rich and diverse mollusc fauna in habitats ranging from the intertidal to the continental shelf. The last reviews on marine mollusc diversity from Peru listed a total of 1018 species (Paredes et al. 1999, Ramírez et al. 2003). Despite this high number of species, research efforts in some groups such as marine benthic heterobranchs, including opisthobranchs, are very limited and the biodiversity of these groups requires further attention.

Recently, molecular studies have reconstructed the phylogeny of opisthobranchs (e. g. Dinapoli & Klussmann-Kolb 2010, Jörger et al. 2010), suggesting that the opisthobranch subgroups are distributed over several different clades instead of being a major single group. Jörger et al. (2010) and Schrödl et al. (2011) distinguished Acteonoidea separated from Euthyneura and the latter comprising Nudipleura (with Pleurobranchoidea and Nudibranchia, sea slugs in a strict sense) as sister to the so-called Tectipleura. These divide into two clades; Euopisthobranchia (with cephalaspideans, sea hares and pteropods, among others) and Panpulmonata, comprising the traditional opisthobranch orders Sacoglossa and Acochlidia, plus several pulmonate and formerly enigmatic groups. For review and discussion of this "new euthyneuran tree" and its consequences with regard to evolution of sea slugs and snails see Brenzinger et al. (2013) and Wägele et al. (in press). In this work we concentrate on "opisthobranchs" in a traditional sense (e. g. Behrens 1991, Schrödl 2003), excluding pyramidellids but including acteonoideans and nudibranchs together with all other sea slugs and snails with more or less reduced shells (Behrens 1991). The current state of the number of species and distributional ranges of these molluscs along the Peruvian coast is still uncertain (Gosliner 1991). In the past twelve years, prosobranch gastropods have received most research effort (Paredes et al. 2011 and references therein) together with bivalves (Paredes & Cardoso 2008 and references therein). Only recently, the diversity of opisthobranchs has received more attention in terms of species descriptions and distribution (e. g. Nakamura 2006, 2007; Martynov et al. 2011, Ornelas-Gatdula et al. 2012, Uribe & Pacheco 2012).

The last review of opisthobranchs from the Peruvian coast compiled a total of 42 species including four new records (Nakamura 2006). Nakamura (2006) focused in the northern part of the coast (3°94'–4°23'S), thus information coming from lower latitudes are probably underestimated. Since research effort on opisthobranchs was poor along the Peruvian coast, several authors have predicted that further records may be reported in the region in the future (Gosliner 1991, Schrödl 2003, Terán et al. 2004, Nakamura 2007). Accordingly, new species and distributional extensions have been recently published for nudibranchs (e. g. Martynov et al. 2011, Uribe & Pacheco 2012), and a first species of Acochlidia was reported from northern Peru by Jörger et al. (2012). On the other hand, numerous species of Anaspidea (Aplysiomorpha) or Thecosomata were described or reported from Peru, but have never been revised taxonomically. Furthermore, the presence of several opisthobranch species from Peru was based on predictions and extrapolations rather than original data. As an example, Álamo & Valdivieso (1987) published a list with Peruvian opisthobranchs, but including confirmed records together with hypothetic ones, i. e. assuming a continuous range for species that were previously reported from California and Chile, as is the case of *Rostanga pulchra* and *Cadlina sparsa*. Similarly, the conspicuous and common Chilean *Thecacera darwini* was mentioned to be present in Peru (e. g. Zagal & Hermosilla 2001). These assumptions on distribution are problematic because they may persist in the literature (e. g. Paredes et al. 1999), and are no longer marked as such. These reports were never substantiated by original data (Schrödl 2003, 2009), but Fischer et al. (2005) already emphasized the high probability that *T. darwini* also occurs in Peru. In this context, a critical revision on the previous records is needed in order to improve and update the list of the opisthobranch species from Peru. In this study, we present a revised taxonomic list and the geographical distribution of "opisthobranchs" (Acteonoidea, Nudipleura, Euopisthobranchia, Acochlidia and Sacoglossa) from rocky intertidal and shallow subtidal zones along the Peruvian coast. In addition, three species are reported for the first time from Peru.

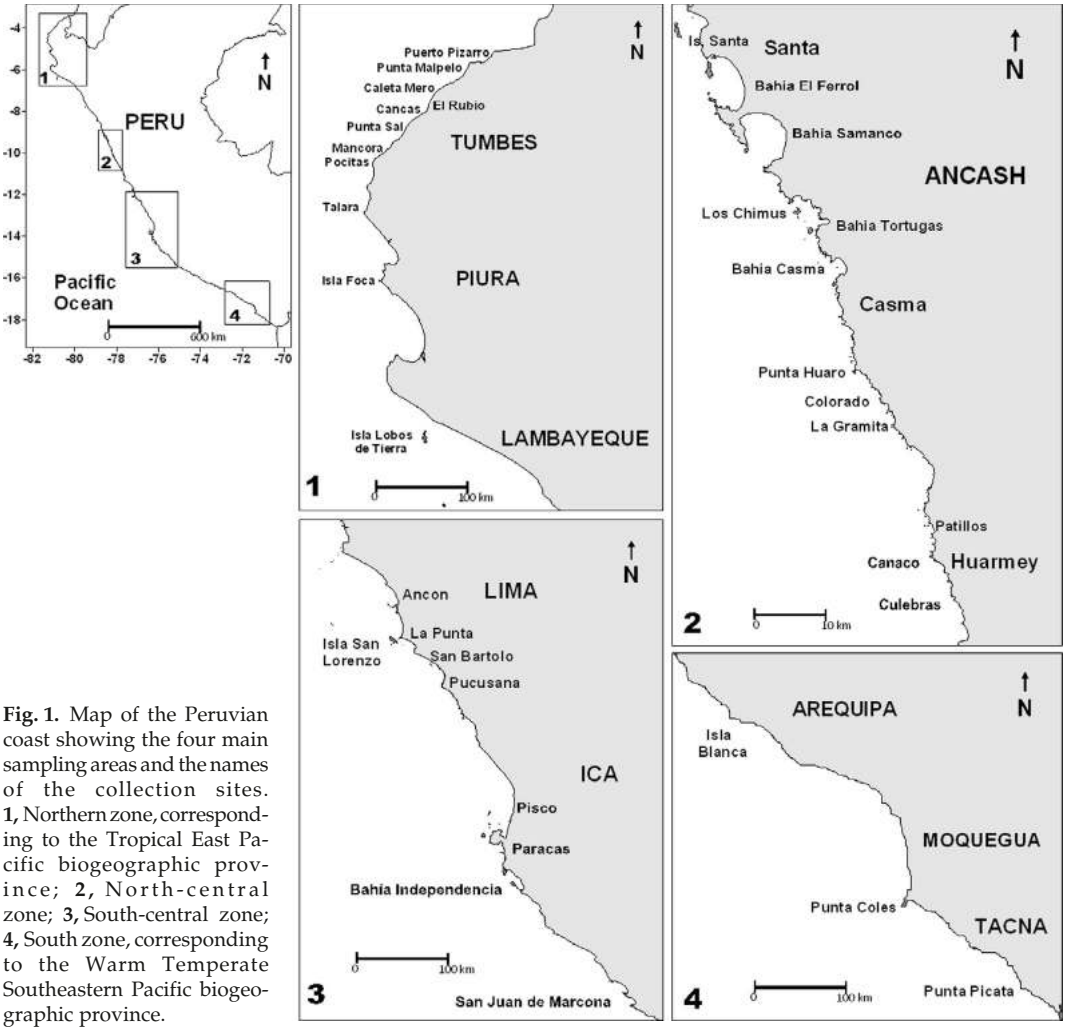

Fig. 1. Map of the Peruvian coast showing the four main sampling areas and the names of the collection sites. **1,** Northern zone, corresponding to the Tropical East Pacific biogeographic province; **2,** North-central zone; **3,** South-central zone; **4,** South zone, corresponding to the Warm Temperate Southeastern Pacific biogeographic province.

Material and methods

A database was built using published information reporting the presence of species along the entire coast of Peru (c. 2500 km) (Fig. 1). In addition, our own collections and comments provided by expert taxonomists previously working in the region were used to supplement the database. We used the taxonomical classification into families according to Bouchet & Rocroi (2005). Higher classification follows Jörger et al. (2010), Wilson et al. (2010) and Schrödl et al. (2011). We include the Acteonidae family ("lower Heterobranchia") in this revision but exclude Pyramidelloidea (Panpulmonata, according to Jörger et al. 2010), which had been previously included within Opisthobranchia by D'Orbigny (1835–46), Dall (1909), Álamo & Valdivieso (1997), among others.

Our own samples were collected since the early 1990's in intertidal and subtidal areas of Pucusana and the Marine Reserve of Paracas in the central and southern coast respectively, using SCUBA diving. Sampling in Paracas was conducted until the beginning of 2000, and again from 2005 until 2006. Between 2006 and 2008 sampling was carried out in southern locations such as San Juan de Marcona and Bahía Independencia, Ica (Fig. 1). These expeditions also included explorations and direct collection in the rocky intertidal and shallow subtidal. Finally, sampling was conducted between 2008–2010 in Santa, Casma and Huarmey located in the north-central coast of Peru (Fig. 1). These samplings were also conducted in sublittoral areas using SCUBA diving. During all collections, sea slugs were carefully deposited in plastic bags filled with sea water and transported to the laboratory. Live animals were maintained in seawater aquarium, photographed and observed. Thereafter, animals were narcotized in magne-

Table 1. Biogeographic checklist of opisthobranchs from Peru. Confirmed faunal records and distributions are listed; thecosomes and *Aplysia* species still need critical revision. Regions are depicted following Spalding et al. (2007).

	Species	Eastern Pacific Coast						Western Atlantic Coast							
		Magellanic	Warm Temperate Southeastern Pacific	Tropical East Pacific	Warm Temperate Northeast Pacific	Cold Temperate Northeast Pacific	Galapagos	Caribbean	North Brazil Shelf	Tropical Southwestern Atlantic	Warm Temperate Southwestern Atlantic	Lusitanian	Mediterranean coast	Circumtropical	Cosmopolitan
ACTEONOIDEA															
Acteonidae	*Acteon traskii*			x	x										
	Crenilabium venustus			x											
NUDIBRANCHIA															
Doridoidea															
Chromodorididae	*Glossodoris baumanni*			x	x		x								
	Felimare agassizii			x	x		x								
	Tyrinna evelinae			x	x			x	x						
	Tyrinna nobilis	x	x												
Dendrodorididae	*Doriopsilla janaina*			x	x		x								
Discodorididae	*Baptodoris peruviana*		x				?								
	Diaulula variolata	x	x												
Dorididae	*Doris fontainei*	x	x								x				
Okeniidae	*Okenia luna*		x												
Onchidorididae	*Corambe mancorensis*			x											
Polyceridae	*Polycera alabe*		x	x	x										
Dendronotoidea															
Dendronotidae	*Dendronotus* cf. *venustus*		x		x	x									
Dotidae	*Doto uva*	x	x								x				
Tritoniidae	*Tritonia* sp.		x												
Aeolidioidea															
Aeolidiidae	*Spurilla* cf. *neapolitana*	x	x	x				?	?	?		?	?	?	
"Arminoidea"															
Arminidae	*Armina californica*		x	x	x	x									
Facelinidae	*Bajaeolis bertschi*			x	x										
	Phidiana lottini		x	?											
Fionidae	*Fiona pinnata*		x									x			x
Flabellinidae	*Flabellina cynara*		x	x	x										
	Flabellina cerverai		x												
Glaucidae	*Glaucus atlanticus*		x									x		x	
Tergipedidae	*Cuthona* sp.			x											
TYLODINOIDEA															
Umbraculidae	*Umbraculum umbraculum*		x	x	x							x		x	
CEPHALASPIDEA															
Aglajidae	*Navanax aenigmaticus*		x	x	x										
Bullidae	*Bulla punctulata*		x	x	x		x							x	
Cylichnidae	*Acteocina infrequens*			x	x		x								
Haminoeidae	*Haminoea peruviana*		x	x			x								
Scaphandridae	*Scaphander cylindrellus*		x	x	x										

sium chloride (7–10 %) and preserved in 70 % alcohol. For morphological descriptions of our new records we have followed the specific recommendations of Schrödl (2003, 2009) for species of the southeast Pacific coast. Samples were deposited in the marine species collection of the Laboratorio Costero de Chimbote (IMARPE-LCCH, Chimbote, Peru), Laboratorio de Biología Marina – Universidad Científica del Sur (UCSUR, Lima, Peru) and Laboratorio de Biología Marina – Universidad Peruana Cayetano Heredia (UPCH, Lima, Peru).

Results

56 species belonging to 30 different families (and seven traditional order-level taxa) were compiled into a distributional checklist (Table 1). Euopisthobranchia is best represented by the pelagic Cavoliniidae (Thecosomata) family with ten species, and Aplysiidae (sea hares) with eight species. However, identifications of Peruvian thecosomes with circumtropical distribution should be confirmed, and also *Aplysia* species need further taxonomic clarification. The cephalaspidean families were represented each

Table 1. (continued).

	Species	Eastern Pacific Coast						Western Atlantic Coast							
		Magellanic	Warm Temperate Southeastern Pacific	Tropical East Pacific	Warm Temperate Northeast Pacific	Cold Temperate Northeast Pacific	Galapagos	Caribbean	North Brazil Shelf	Tropical Southwestern Atlantic	Warm Temperate Southwestern Atlantic	Lusitanian	Mediterranean coast	Circumtropical	Cosmopolitan
ANASPIDEA															
Aplysiidae	*Aplysia juliana*		x	x	x			x	x			x		x	
	Aplysia lessoni			x											
	Aplysia chierchiana		x												
	Aplysia nigra		x	x											
	Aplysia parvula		x	x				x						x	
	Aplysia inca		x	x											
	Aplysia dactylomela		x	x				x				x		?	
	Aplysia keraudreni		x												x[1]
	Dolabrifera dolabrifera			x				x				x		x	
THECOSOMATA															
Cavoliniidae	*Cavolinia inflexa*													x	
	Cavolinia longirostris													x	
	Cavolinia tridentata													x	
	Cavolinia uncinata													x	
	Diacria quadridentata													x	
	Creseis acícula													x	
	Creseis virgula													x	
	Hyalocylis striata													x	
	Styliola subula													x	
Limacinidae	*Limacina bulimoides*													x	
	Limacina inflata													x	
	Limacina trochiformis													x	
SACOGLOSSA															
Elysiidae	*Elysia diomedea*			x	x										
	Elysia hedgpethi		x	x	x										
Juliidae	*Julia thecaphora*			x	x		x								
ACOCHLIDIA															
Microhedylidae	*Pontohedyle* sp.			x											

[1] South Pacific

by less than four species, and there is a single Tylodinoidea species recorded. Sacoglossa is represented by three species and Acochlidia by a single species. The best represented major clade is Nudibranchia with seventeen families and twenty three species. Three nudibranch species are recorded for the first time in Peru: *Tritonia* sp., *Tyrinna nobilis* and *Diaulula variolata* (see detailed description below). We add new local distribution records for 19 species: *Bulla punctulata*, *Navanax aenigmaticus*, *Flabellina cynara*, *Spurilla* cf. *neapolitana*, *Aplysia juliana*, *Haminoea peruviana*, *Dolabrifera dolabrifera*, *Elysia diomedea*, *Elysia hedgpethi*, *Doris fontainei*, *Baptodoris peruviana*, *Polycera alabe*, *Felimare agassizii*, *Doto uva*, *Dendronotus* cf. *venustus*, *Fiona pinnata*, *Phidiana lottini*, *Bajaeolis bertschi* and *Glaucus atlanticus*. Authority names and remarks on distribution and identity are provided in the commented list. Finally we present a commented list of further opisthobranchs with confirmed records from Peru (excluding thecosomes and several *Aplysia* species, which need more detailed revision).

New records from Peru

Nudipleura, Nudibranchia, Chromodorididae

Tyrinna nobilis Bergh, 1898
Fig. 2A

Material examined. 2 (17, 20 mm length), UCSUR-02-00023, San Juan de Marcona, Ica, lower intertidal (K. Nakamura, 9 March 2006). 2, CZA-121, Isla Blanca, Arequipa, 22 m depth (Y. Hooker, 28 November, 2008).

Diagnosis. Body long and oval. Body coloration translucent white. Opaque white line marking edges of mantle and foot. Mantle surface smooth, covering head, with microscopic protuberances, with two or three submarginal rows of subepidermal mantle glands, round large and visible through tissue. Three irregular submarginal dorsal rows of orange or red spots, outermost consisting of many smaller spots; middle line containing slightly larger spots, and innermost one with a few much larger spots. Central region of mantle, between gills and rhinophores, lacking orange spots. Between five or six, bi- or tripinnate gills deployed in semicircle in front of posteriodorsal anus. Oral tentacles longitudinally enrolled. Anterior part of foot bilabiate and thick. Posterior foot extending beyond mantle in crawling individuals. Jaw plates bifid or occasionally tricuspid.

Distribution. From the Magellanic province, reaching the Valdés Peninsula in the Atlantic, Magellan Strait, Juan Fernandez Islands toward Los Hornos, northern Chile (Schrödl 2003, Schrödl et al. 2005) and Iquique (Fischer et al. 2005a).

New localities in Peru. Ica: San Juan de Marcona; Arequipa: Isla Blanca (Fig. 1).

Remarks. Schrödl & Millen (2001) pointed out that *T. nobilis* in the Pacific was known from the Chilean coast only; however, our work extends its distribution northwards to central Peru (Ica). All specimens were found in the low intertidal on hard substratum.

Discodorididae

Diaulula variolata (D'Orbigny, 1837)
Fig. 2B

Material examined. 7 (50, 60, 23, 55, 40, 60, 40 mm length) UCSUR-02-000017, Bahía Independencia, Pisco, rocky intertidal (K. Nakamura, 23 January 2006); 8 (40, 30, 30, 40, 30, 35, 40, 73 mm length), UCSUR-02-000017, Bahía Independencia, Pisco, intertidal (K. Nakamura, 24 January 2006); 4 (10, 13, 15, 20 mm length), UCSUR-02-000018, San Juan de Marcona, Ica, rocky intertidal (K. Nakamura, 9 March 2006); 2, CZA-117, El Chaco, Ica (Y. Hooker, 28 November 2006); 1, CZA-119, Caleta Atenas, Ica (Y. Hooker, 13 December 2008).

Diagnosis. White coloration with brown-purple dots over the notum. Some specimens show different degrees of coloration of the notum and more white dots. Long and oval body shape, body relatively convex in cross section. Mantle with spicules covered with tubercles of several sizes, with slender ones showing typical shape of caryophyllidia. Sheaths of perfoliate rhinophores and gills slightly elevated. Six branches of tri- to quadripinnate gills in a circle around anal opening. Foot bilabiate, upper lip notched. Oral tentacles digitiform.

Distribution. Bay of San Vicente to Iquique (Fischer & Cervera 2005a) and Arica, Chile (Schrödl 2003).

New localities in Peru. Ica: El Chaco, Caleta Atenas and San Juan de Marcona (Fig. 1).

Remarks. All Peruvian specimens were found in the low intertidal and upper subtidal on rocky substratum. The record of a preserved whitish dorid specimen from the southern Chilean Parque Bernardo O'Higgins as *D. variolata* by Aldea et al. (2011) would extend the otherwise central Chilean southern geographic limit of *D. variolata* far into the southern part of the Chilean fjord region. In absence of information given on characteristic external features, such as coloration of living specimens or the presence of the special caryophyllidiid tubercles of *D. variolata*, the record by Aldea et al. (2011) is not reliable until confirmed by additional external or anatomical data.

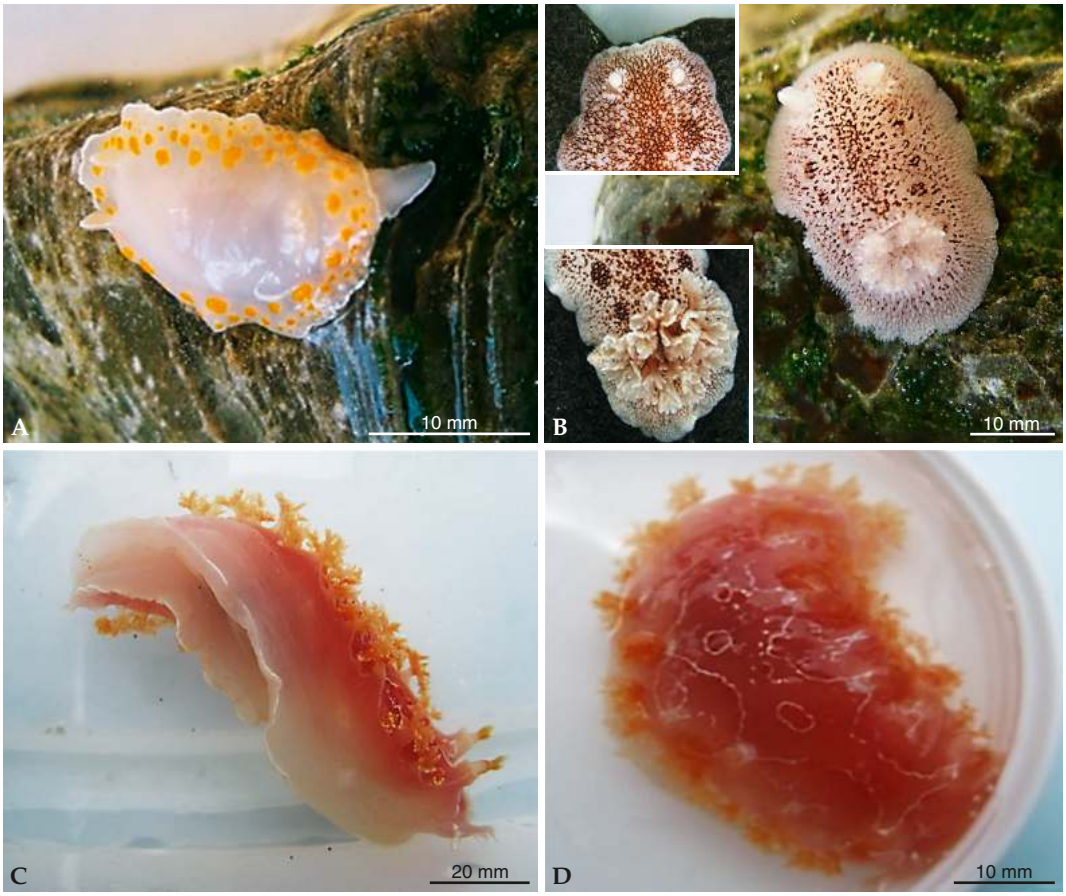

Fig. 2. New records for the Peruvian coast. **A.** *Tyrinna nobilis*, dorsal view; **B.** *Diaulula variolata*, detail of the anterior part (upper-left photo), detail of the posterior part (lower-left photo) and dorsal view of the whole animal (right photo); **C.** *Tritonia* sp. lateral view; **D.** *Tritonia* sp. dorsal view.

Tritoniidae

***Tritonia* sp.**
Fig. 2C

Material examined. 1 (50 mm length), Isla La Vieja, Bahía Independencia, Pisco, 15 m depth (A. Indacochea, 21 July 2008); 1, Punta Picata, Tacna (Y. Hooker); 1 (50 mm length), IMARPE-LCCH 2009.002, Punta Huaro, Casma, 5 m (R. Uribe, 22 October 2009); 2 (50 mm, 46 mm length), IMARPE-LCCH 2009.003, Colorado, Huarmey, 6 m (R. Uribe, 23 October 2009); 1 (46 mm length), IMARPE-LCCH 2009.004, La Gramita, Casma, 6 m (R. Uribe, 21 October 2009); 1 (48 mm length), IMARPE-LCCH 2009.005, Patillos, Huarmey, 7 m (R. Uribe, 21 October 2009); 1 (45 mm length), Isla Asia, Lima, 10 m (A. Indacochea, 18 December 2010); 4, CZA-124, Isla Foca, Piura (Y. Hooker, 14 June 2008).

Diagnosis. Long and translucent body, slightly angled laterally, pinkish or light orange coloration. Perpendicular white lines along mantle, foot, rhinophores folds and over back. White stripes forming a circular pattern of ornamentation on mantle. Upper part of gills similarly white. Oral tentacles bilobed with several digitiform processes in each lobe; lateral projections with external slit. Oral veil projections short. Rhinophores with lobulated folds and a squarish rhinophoral sheath; clavus (tip base) with branched processes. Abundant dorsolateral gills of different sizes and branch shape along each notal edge, light orange colour. No mandibular denticles present.

Distribution. Piura: Isla Foca, Ancash: Isla Santa, Bahia Ferrol, Punta Huaro, La Gramita, Casma, Colorado, Huarmey, Lima: Pucusana, Asia, Ica: Bahía Independencia; Tacna: Punta Picata. (Fig. 1).

Remarks. Currently only Peruvian locations are known. In Ancash and Ica, isolated specimens were observed on gorgonid corals *Leptogorgia peruviana* (which may serve as a food) on subtidal rocky areas with mix substrate of rocks and shell pieces with moderated current flow at depths between 6–15 meters. In Lima, *Tritonia* sp. also was observed on hard substrate. Egg masses are thin, spiral-shaped whitish bands. This species is somewhat similar to *T. odhneri* Marcus, 1959, which occurs in the Magellanic Province and north to Central Chile (Schrödl 2003, 2009) and lacks white ornamentation on the notum. *Tritonia* sp. externally resembles *T. festiva* (Stearns 1873), a species distributed in the north Pacific from Alaska to Baja California and Japan (Goddard 2000) due to the white line coloration pattern, and the shape of rhinophores and gills. However, *Tritonia* sp. has jaws with a smooth masticatory border and the oral veil presents six to seven short oral projections. In contrast, in *T. festiva* denticles on the jaw are conspicuous (MacFarland 1966) and the oral veil has four to five long projections. Comparative anatomical and molecular examinations will likely show that *Tritonia* sp. is an undescribed Peruvian species.

Reports of opisthobranchs from new localities in Peru

Euopisthobranchia, Cephalaspidea, Aglajidae

Navanax aenigmaticus (Bergh, 1893)

Distribution. Eastern Pacific (Ornelas-Gatdula et al. 2012). Baja California to Chile (Skoglund 2002, Valdés & Camacho-García 2004). Islas Galápagos, Ecuador (Camacho-García et al. 2005). Isla Malpelo, Colombia (Ardila et al. 2007).

Peru. Gosliner (1991), Paredes et al. (1999); Paita: Mancora, Bayóbar (Ornelas-Gatdula et al. 2012); Ica: Paracas (Ornelas-Gatdula et al. 2012).

New localities in Peru. Lima: Pucusana; Ica: Bahía Independencia, Pisco (Millen, pers. comm.) (Fig. 1).

Bullidae

Bulla punctulata A. Adams in Sowerby 1850
Fig. 3A

Distribution. From Bahía Magdalena, Baja California (Skoglund 2002), Costa Rica (Valdés & Camacho-García 2004) to Peru (Behrens & Hermosillo 2005), and IndoPacific (Camacho-García et al. 2005).

Peru. Paredes et al. (1999), Tumbes: Puerto Pizarro (Peña 1970; Álamo & Valdivieso 1997), Punta Malpelo (Álamo & Valdivieso 1997); Piura: Mancora (Álamo & Valdivieso 1987), Paita (Peña 1970, Dall 1909[1], Nakamura 2006[2]); Lambayeque: Isla Lobos (Dall 1909[3], Álamo & Valdivieso 1997); Ancash: Muelle Promar (Álamo & Valdivieso 1997).

[1 Reported as *Bullaria aspersa*; 2 reported as *Bulla aspersa*; 3 reported as *Bullaria punctulata*.]

New localities in Peru. Ancash: Bahía Samanco; Ica: Paracas (Millen, pers. comm.), Laguna Grande (Fig. 1).

Remarks. The record of the eastern Atlantic *Bulla striata* from Peru by D'Orbigny (1836–45) is considered unreliable in the light of a recent review of the genus by Malaquias (2008).

Haminoeidae

Haminoea peruviana (D'Orbigny, 1842)[1]

Distribution. From Archipiélago de Galápagos to Peru (Camacho-García et al. 2005).

Peru. Paredes et al. (1999); Callao (D'Orbigny 1835–46[2], Dall 1909[3], Álamo & Valdivieso 1997[2]).

[1 Reported with date 1837 as description year in Dall (1909) and year 1813 in Paredes et al. (1999); 2 reported as *Bulla peruviana*; 3 reported as *Haminea peruviana*.]

New localities in Peru. Ica: Pisco (Millen, pers. comm.) (Fig. 1).

Anaspidea, Aplysiidae

Aplysia juliana Quoy & Gaimard, 1832
Fig. 3B

Distribution. Circumtropical (Medina et al. 2005), in all temperate waters (Camacho-García et al. 2005, Behrens & Hermosillo 2005). Iberian Peninsula (Cervera et al. 2006). West Atlantic: Florida, Luisiana, Texas, Mexico, Belice, Costa Rica, Colombia, Venezuela, Bermudas, Curasao, Cuba, Jamaica, Puerto Rico, Santa Lucia, Barbados, Brazil (Zamora-Silva & Naranjo-García 2008). Pacific, Sonora, Mexico to Peru (Álamo & Valdivieso 1997).

Peru. Keen 1971; Piura: Paita (D'Orbigny 1835–46[1], Dall 1909[2], Álamo & Valdivieso 1997).

[1 Reported as *Aplysia rangiana*; 2 reported as *Thetys rangiana*.]

New localities in Peru. Mancora; Ancash: Bahía Samanco; Lima: Ancon (Millen, pers. comm.); Ica: Bahía Paracas (Fig. 1).

Remarks. Peruvian *Aplysia* species listed by Paredes (1999) need critical revision.

Dolabrifera dolabrifera (Rang, 1828)

Distribution. Tropical and subtropical waters (Camacho-García et al. 2005; Behrens & Hermosillo 2005). Canary and Selvagens Islands, Madeira (Cervera et al. 2006). Colombia (Ardila et al. 2007).

Peru. Tumbes: Punta Sal (Nakamura 2006).

New localities in Peru. Piura: Pocitas, Mancora (Fig. 1).

Remarks. Reported as *Dolabrifera nicaraguana* by Paredes et al. (1999).

Nudipleura, Nudibranchia, Doridoidea, Chromodorididae

Felimare agassizii (Bergh, 1894)
Fig. 3C

Distribution. From Gulf of California, Mexico to Panamá. Islas Galápagos, Ecuador and Isla de Malpelo, Colombia (Behrens & Hermosillo 2005).

Peru. Cancas (Nakamura 2006[1]).

[[1] Reported as *Hypselodoris agassizii;* chromodoridids were reclassified by Johnson & Gosliner (2012).]

New localities in Peru. Tumbes (Millen, pers. comm.); Lambayeque: Isla Lobos de Tierra (Fig. 1).

Discodorididae

Baptodoris peruviana (D'Orbigny, 1837)
Fig. 3D

Distribution. Valparaíso (?, see remarks), Isla Pájaros to North of Chile (Fischer et al. 2005b).

Peru. Paredes et al. (1999[1,2]), Schrödl (2003[3]), Lima: Pucusana (Schrödl 1996[2]); Callao (Dall 1909[4], Álamo & Valdivieso 1997[5]), Isla San Lorenzo (D'Orbigny 1835-46[1]).

[[1] Reported as *Doris peruviana*; [2] reported as *Platydoris punctatella*; [3] reported as *Platydoris peruviana*; [4] reported as *Doriopsis peruviana*; [5] reported as *Dendrodoris peruviana*.]

New localities in Peru. Ancash: Bahía Tortugas; Ica: Bahía Independencia and San Juan de Marcona (Fig. 1).

Remarks. The record from Galapagos by Pilsbry and Vanatta (1902) was considered doubtful by Schrödl (2003) and Fischer & Cervera (2005a). Schrödl (2003) also doubted Dall's (1909) record from Valparaíso, since externally *B. peruviana* (as *P. punctatella* Bergh, 1898) can be easily confused with premature specimens of common central Chilean *Diaulula* species such as *D. variolata*.

Dorididae

Doris fontainei (D'Orbigny, 1837)
Fig. 3E

Distribution. North of Argentina (Valdés & Muniaín 2002), Argentinean and Chilean Patagonica, Chonos archipelago (Schrödl & Grau 2006), Arica (Valdés & Muniaín 2002; Schrödl 2003[1]) to southern Peru (Schrödl 2000[2], Luque 2002).

[[1] Reported as *Archidoris fontaini*; [2] reported as *Anisodoris fontaini*.]

Peru. Ica: Bahía Independencia (Luque 2002, Schrödl & Grau 2006).

New localities in Peru. Ancash: Islote Ferrol; Ica: San Juan de Marcona (Fig. 1).

Remarks. For synonymy and some alternative taxonomic considerations see Schrödl (2003).

Polyceridae

Polycera alabe Collier & Farmer, 1964

Distribution. From California (Behrens 2004, Camacho-García et al. 2005), Puerto Vallarta, Mexico to Costa Rica (Behrens 2004); northern Chile (Schrödl 2003).

Peru. Paredes et al. (1999) (based on S. Millen, pers. comm.).

New localities in Peru. Tumbes: El Rubio (Millen, pers. comm.) (Fig. 1).

Dendronotoidea, Dendronotidae

***Dendronotus* cf. *venustus* MacFarland, 1966**
Fig. 3F

Distribution. Northeastern Pacific (Stout et al. 2010). Bahía de Coliumo, Central Chile (Schrödl 2003[1]).

[1] Reported as *Dendronotus* sp. 1.]

Peru. Paredes et al. 1999 (based on S. Millen, pers. comm.).

New localities in Peru. Lima: Pucusana (Fig. 1).

Remarks. Eastern Pacific specimens of *D. frondosus (*Ascanius, 1774) were assigned to the resurrected *D. venustus* by Stout et al. (2010). Whether or not Peruvian and central Chilean specimens are conspecific with each other and/or with Northeastern Pacific *D. venustus* needs confirmation by anatomical and molecular data.

Dotidae

***Doto uva* Marcus, 1955**
Fig. 3G

Distribution. Brazil (see Marcus 1959). Magellanic Province and Chilean coast (Schrödl 2003, 2009).

Peru. Paredes et al. 1999 (based on S. Millen, pers. comm.).

New localities in Peru. Ica: Bahía Independencia (Fig. 1).

Remarks. The disjoint amphi-South American distribution of *D. uva* needs reconfirmation with molecular data (see Schrödl 2003, 2009).

Aeolidoidea, Aeolidiidae

***Spurilla* cf. *neapolitana* (Delle Chiaje, 1823)**
Fig. 3H

Distribution. Mediterranean Sea, West Atlantic from Florida to Brazil. East Pacific (Baja California). Circumtropical (Camacho-García et al. 2005).

Peru. Ancash: Bahia Ferrol (Uribe & Pacheco 2012).

New localities in Peru. Lima: Pucusana (Fig. 1).

Remarks. Carmona et al. (2013) suggested the existence of cryptic species, with true *S. neapolitana* restricted to the eastern Atlantic, but no material from the East Pacific was included. Further molecular study will be necessary to see if the Atlantic and Pacific specimens are conspecific.

Facelinidae

***Bajaeolis bertschi* Gosliner & Behrens, 1986**
Fig. 3I

Distribution. From Bahía Los Angeles, Baja California, Panamá, northern Peru (Camacho-García et al. 2005).

Peru. Piura: Mancora, Pocitas (Nakamura 2006).

New localities in Peru. Tumbes: El Rubio (Millen, pers. comm.) (Fig. 1).

***Phidiana lottini* (Lesson, 1831)**
Fig. 3J

Distribution. West coast of South America (Schrödl 1997) to Chiloé Island (Schrödl 1999).

Peru. Peru (Paredes et al. 1999, Schrödl 2003); Callao (D'Orbigny 1835–46, Dall 1909[1], Álamo & Valdivieso 1997[1]).

[1] Reported as *Phidiana inca*.]

New localities in Peru. Ancash: Isla Santa; Lima: Ancon and San Bartolo (Millen, pers. comm.), Pucusana; Ica: San Juan de Marcona (Fig. 1).

Remarks. For synonymy and taxonomic review see Schrödl (2003). The tropical record of this otherwise temperate species needs confirmation.

Flabellinidae

***Flabellina cynara* (Marcus & Marcus, 1967)**
Fig. 3K

Distribution. From Gulf of California (Millen & Hermosillo 2007) to Panamá (Hermosillo-González 2003).

Peru. Tumbes: Punta Sal, Cancas, Piura: Mancora (Nakamura 2006).

New localities in Peru. Ancash: Santa, Casma, Huarmey (Fig. 1).

Fionidae

***Fiona pinnata* (Eschscholtz, 1831)**

Distribution. Cosmopolitan (Gosliner 1987). Isla Juan Fernández, Tumbes, Chile (Schrödl 2003).

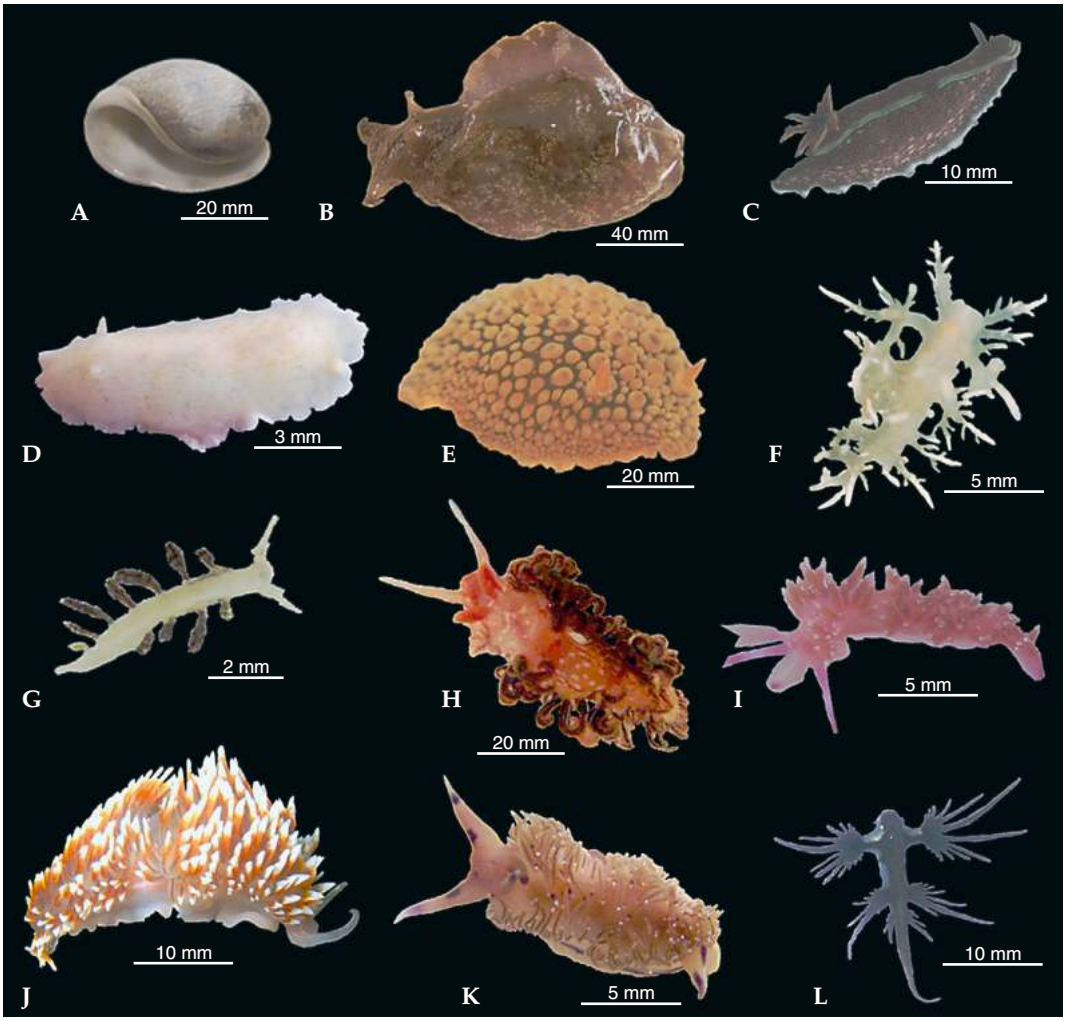

Fig. 3. Examples of species found in some of the new localities. **A.** *Bulla punctulata*; **B.** *Aplysia juliana*; **C.** *Felimare agassizii*; **D.** *Baptodoris peruviana*; **E.** *Doris fontainei*; **F.** *Dendronotus* cf. *venustus*; **G.** *Doto uva*; **H.** *Spurilla* cf. *neapolitana*, **I.** *Bajaeolis bertschi*; **J.** *Phidiana lottini*; **K.** *Flabellina cynara*; **L.** *Glaucus atlanticus*.

Peru. D'Orbigny 1835–46, Paredes et al. 1999 based on S. Millen, pers. comm., Lima (Dall 1909, Álamo & Valdivieso 1997[1]).

[1] Reported as *Phidiana natans*.]

New localities in Peru. Ancon (Millen, pers. comm.) (Fig. 1).

Remarks. Schrödl (2003) synonymized *Phidiana natans* with *Fiona pinnata*.

Glaucidae

***Glaucus atlanticus* Forster, 1777**
Fig. 3L

Distribution. Circumtropical (Thompson & McFarlane 1967). Off the northern Chilean coast (Schrödl 2003).

Peru. Paredes et al. (1999) (based on Millen, pers. comm.).

New localities in Peru. Ancash: Isla Santa (Fig. 1).

Remarks. Schrödl (2003) considered that *G. atlanticus* is a senior synonym of *G. distichoicus* D'Orbigny, 1837.

Panpulmonata, Sacoglossa, Elysiidae

***Elysia diomedea* (Bergh, 1894)**

Distribution. From Gulf of California to Panamá (Camacho-García et al. 2005, Behrens & Hermosillo 2005). Ecuador (Terán et al. 2004).

Peru. Paredes et al. (1999[1]); Tumbes: Punta Sal, Cancas; Piura: Mancora, Pocitas (Nakamura 2006).

[1 Reported as *Tridachiella diomedea*.]

New localities in Peru. Talara (Millen, pers. comm.) (Fig. 1).

***Elysia hedgpethi* Er. Marcus, 1961**

Distribution. Vancouver, British Columbia to Bahía de Los Angeles, Gulf of California, and Bahia de Banderas, Mexico (Behrens & Hermosillo 2005). Fuerte Bulnes (Schrödl 1996) to central coast of Chile (Fischer 2006).

Peru. Paredes et al. (1999) (based on Millen, pers. comm.).

New localities in Peru. Lima: Pucusana; Ica: Paracas (Millen, pers. comm.) (Fig. 1).

Remarks. Further anatomical and molecular studies are necessary to clarify the taxonomy and distribution of Eastern Pacific *Elysia hedgpethi* and the relationships of tentatively identified, small-sized and green *Elysia* specimens from central and southern Chilean with Argentinian *E. patagonica* (see Schrödl 1996 versus Schrödl 2009).

Checklist of further confirmed Peruvian opisthobranch species

For full list, including poorly studied *Aplysia* species and Thecosomata, see Table 1.

"Lower Heterobranchia", Acteonidae

***Acteon traskii* Stearns, 1897**

Distribution. San Diego, California (Stearns 1898) to Panamic province (Bertsch 2010). Colombia (Valdés & Camacho-García 2004).

Peru. Piura: Paita, Islilla (Álamo & Valdivieso 1997) (Fig. 1).

***Crenilabium venustus* (D'Orbigny, 1840)**

Distribution. Costa Rica (Keen 1971, Valdés & Camacho-García 2004) to Peru (D'Orbigny 1840[1]).

Peru. Paredes et al. (1999[1]) (based on Millen, pers. comm.), Piura: Paita (Álamo & Valdivieso 1997[1]) (Fig. 1).

[1 Reported as *Acteon venustus*.]

Nudipleura, Nudibranchia, Doridoidea, Chromodorididae

***Glossodoris baumanni* (Bertsch, 1970)**

Distribution. Gulf of California to Panamá; Islas Galápagos, Ecuador; Isla de Malpelo, Colombia (Behrens & Hermosillo 2005).

Peru. Tumbes, Cancas (Nakamura 2006) (Fig. 1).

***Tyrinna evelinae* (Er. Marcus, 1958)**

Distribution. Gulf of California, Baja California, Mexico to northern Peru. Jamaica, Puerto Rico, Brazil, Ghana (Schrödl & Millen 2001).

Peru. Tumbes: El Rubio (Schrödl & Millen 2001) (Fig. 1).

Remarks. Molecular data are needed to confirm that the anatomically similar Atlantic and Pacific specimens are conspecific.

Dendrodorididae

***Doriopsilla janaina* Marcus & Marcus, 1967**

Distribution. From Baja California, Mexico, to Panamá and Islas Galápagos (Camacho-García et al. 2005).

Peru. Tumbes, Cancas (Nakamura 2006) (Fig. 1).

Okeniidae

***Okenia luna* Millen, Schrödl, Vargas & Indacochea, 1994**

Distribution. Peru (Millen et al. 1994) to Iquique (Fischer 2006) and Coliumo, Chile (Schrödl 2003).

Peru. Lima: Ancon (Millen et al. 1994) (Fig. 1).

Onchidorididae

***Corambe mancorensis* Martynov, Brenzinger, Hooker & Schrödl, 2011**

Distribution. North of Peru (Martynov et al. 2011).

Peru. Piura: Mancora (Martynov et al. 2011) (Fig. 1).

"Arminoidea", Arminidae

***Armina californica* (Cooper, 1862)**

Distribution. Aleutian Islands (Goddard & Foster 2002 in Behrens 2004). North Pacific Ocean, Panama, Peru (Báez et al. 2011).

Peru. Baez et al. (2011); Piura: Paita (Dall 1909[1], Nakamura 2006[2]) (Fig. 1).

[[1] Reported as *Pleurophyllidia cuvieri*; [2] reported as *Arminia cuvieri*.]

Remarks. Báez et al. (2011) reported that the specimen examined of *A. cuvieri* from Peru was erroneously identified. We think, however, in absence of central Chilean material available for anatomical examination, it is premature to synonymize *A. cuvieri* originally described from off Valparaíso (see Schrödl 2003) with *A. californica*.

Aeolidoidea, Flabellinidae

***Flabellina cerverai* Fischer et al. 2007**

Distribution. Coliumo, Chile (Schrödl 2003). Coquimbo, Chile (Fischer et al. 2007).

Peru. Lima: Ancon, Pucasana (Schrödl 2003[1]) (Fig. 1).

[[1] Reported as *Flabellina* sp. 2.]

Tergipedidae

***Cuthona* sp.**

Peru. Tumbes: Cancas (Nakamura 2006) (Fig. 1).

Euopisthobranchia, Tylodinoidea, Umbraculidae

***Umbraculum umbraculum* (Lightfoot, 1786)**

Distribution. Circumtropical (Camacho-García et al. 2005, Behrens & Hermosillo 2005). Cabo San Lucas, Baja California, Golfo de California, Panama to Peru Callao, Peru (Álamo & Valdivieso 1997).

Peru. Paredes et al. (1999[1]) (based on Millen, pers. comm.), Tumbes: Puerto Pizarro (Peña 1970[2], Álamo & Valdivieso 1997[3]) (Fig. 1).

[[1] Reported as *U. ovale* and *U. umbraculum*; [2] reported as *Umbraculum ovael*, which must be considered a typing error, the correct form being *ovale*; [3] reported as *Umbraculum ovale*.]

Remarks. *U. ovale* and *U. umbraculum* are regarded synonymous (Wägele et al. 2006).

Cephalaspidea, Cylichnidae

***Acteocina infrequens* (C. B. Adams, 1852)**

Distribution. Baja California (Valdés & Camacho-García 2004) to Peru (Keen 1971, Hardy 2006[1]). Galápagos (Finet 2001[1]).

Peru. Paredes et al. (1999[1]) (based on Millen, pers. comm.).

[[1] Reported as *Acteocina angustior*.]

Scaphandridae

***Scaphander cylindrellus* Dall, 1908**

Distribution. Bahía Magdalena, Baja California, Mexico (Hardy 2006) to Callao, Peru (Álamo & Valdivieso 1997).

Peru. Paredes et al. (1999) (based on Millen, pers. comm.); Tumbes: Caleta Mero (Álamo & Valdivieso 1997), Callao (Keen 1971) (Fig. 1).

Panpulmonata, Sacoglossa, Juliidae

***Julia thecaphora* (Carpenter, 1857)**

Distribution. Japan, Hawaii, Midway Atoll, Raratonga and Magaia (Cook Islands). From Baja California to Peru (Camacho-García et al. 2005). Galápagos (Finet 2001).

Peru. Keen 1971, Paredes et al. (1999) (based on S. Millen, pers. comm.); Tumbes (Álamo & Valdivieso 1987) (Fig. 1).

Acochlidia, Microhedylidae

***Pontohedyle* sp.**

Distribution. Punta Sal, Peru (Jörger et al. 2012) (Fig. 1).

Discussion

The diversity of Acteonoidea, Nudipleura, Euopisthobranchia and marine Panpulmonata is not yet well described along the Peruvian coast, particularly towards the north of the Warm Temperate Southeastern Pacific Province (WTSPP, 5°40'–18° S). In comparison with the numbers of other groups such as prosobranchs and bivalves, opisthobranchs might be considered of minor importance in terms of abundance and species richness. However, Ramírez et al. (2003) suggest that more attention to these groups would enhance our knowledge of the mollusc species richness on the Peruvian coast. Clearly, our study supports this notion. Three new records and range extensions of several species presented here suggest that the diversity of these molluscs can be higher than expected.

Of the 37 species presented in the commented lists, 28 species could be considered tropical, 9 are only common in temperate waters and 22 could be present in both tropical and temperate conditions. *Fiona pinnata* is considered cosmopolitan, *Aplysia keraudreni* is southern Pacific (if confirmed from Peru), and several other sea hares and all thecosomes listed in Table 1 appear to be circumtropical; all these cases remain to be assessed using comprehensive molecular data. Of the species reported in new locations, *Flabellina cynara, Bulla punctulata, Haminoea peruviana* and *Aplysia juliana* showed distribution in the Tropical East Pacific (TEP); here they are reported outside of this region, i. e. within the WTSPP, during no ENSO years (i. e. El Niño and the Southern Oscillation). However, paleo-climatic studies suggest that during El Niño year's *B. punctulata* extends their distributional range down to the coast of northern Chile (Ragaini et al. 2008). Similarly, *A. juliana* expands down to northern Chile during warm episodes (Castilla et al. 2005); *A. juliana* and *B. punctulata* are commonly found outside of their usual distributional range (within the TEP) in Bahía Samanco (9° S), during cold-normal years. This apparent disjoint distribution throughout the Peruvian coast and northern Chile is possibly the reflection that these species may have found refuge areas (e. g. protected bays) where the local conditions are adequate for extending their temporal permanence after El Niño years at some extent (Castilla et al. 2005, Ashton et al. 2008).

From the ~5000 species of opisthobranchs reported worldwide, 399 species known from the northeast Pacific are present between the south coast of California and northern Peru (Bertsch 2010). From these species, 254 are distributed in the Cold Temperate Northeast Pacific and Warm Temperate Northeast Pacific Province, from Alaska to Baja California in Mexico (Behrens 2004, Valdés & Bertsch 2010). In the TEP, there are 96 registered species (Camacho-García et al. 2005, Hermosillo & Valdés 2007). Along the South American coast, our list (Table 1) comprises 29 opisthobranch species for the warm temperate coast of Peru, and 29 further nudipleuran species are reported for northern and central Chile south to 41° S (Schrödl 2003). In total, Schrödl (2003, 2009) reported 67 nudipleuran species for Chile, with 34 species of Nudipleura conspicuously present in the Magellanic Province.

In contrast to the Chilean opisthobranch fauna, which has been partly revised and many synonyms have been revealed, our study is just a first step towards such critical work for the Peruvian fauna. Previous species compilations from the Peruvian coast include many unconfirmed or dubious records of opisthobranch sea slugs, which were just based on external identification of few or single individuals rather than on careful anatomical examination of several specimens covering the intraspecific range of morphological variation. In absence of comprehensive taxonomic revisions, herein we continue listing all Peruvian Thecosomata and *Aplysia* species in Table 1, but urge for future scrutiny. Several benthic sea slugs and snails were found and tentatively identified by Sandra Millen (University of British Columbia, Vancouver), who is an expert taxonomist, and these species were listed by Paredes et al. (1999). Even in absence of material available for re-examination, herein we trust the identifications of several charismatic species such as *Polycera alabe*. On the other hand, unsubstantiated Peruvian records, e. g. of the Magellanic cryptobranch dorid *Diaulula punctuolata* by Dall (1909), were doubted by Schrödl

(2003), and the Peruvian record of the southern Chilean and Subantarctic aeolid *Flabellina falklandica* listed by Paredes et al. (1999) also needs confirmation. Furthermore, previous Peruvian opisthobranch lists may have suffered from interpolations regarding the distribution of several species. For example, the disjunct northern and southern temperate *R. pulchra* and *C. sparsa* (see Álamo & Valdivieso 1997, Paredes et al. 1999, Ramírez et al. 2003) have not been found in Peru yet, and remain to be confirmed as "bipolar" species rather than allopatric complexes of distinct species by molecular data. Uncritical assumptions on geographic ranges of taxonomically problematic species may cause biases in current and future studies dealing with the biodiversity in this region, e. g. avoiding unnecessary overestimation of the regional species diversity. In this report we have critically revised previous reports and excluded dubious records from our checklist, but our Table 1 retains all sea hares, several originally described from Peru, and pteropods for now. Our commented lists just include reliable species coming from our own collections and those where the original data could be corroborated by us.

This study shows that *P. lottini*, *Tritonia* sp. and *D. variolata* are common species along most of the Peruvian coast and *B. peruviana* along the south coast Peruvian and north-central coast of Chile. The present review also shows that *B. punctulata* and *F. cynara* are common species of the northern area of the WTSPP within the Peruvian coast. Assuming conspecifity, species such as *D. dolabrifera* (Euopisthobranchia), *S.* cf. *neapolitana* and *T. evelinae* (Nudibranchia) also occur in the tropical western Atlantic. However, some caution should be applied to relying on such wide and disjoint distributions. For example, molecular data showed Peruvian and Northeastern Pacific cephalaspidean *N. aenigmaticus* to be conspecific, but distinct from a Western Atlantic and morphologically rather cryptic species that is separated by the Isthmus of Panama (Ornelas-Gatdula et al. 2012). Therefore, earlier Peruvian records of the Eastern Atlantic *Bulla striata* also must be doubted (see Malaquias 2008). Furthermore, from the extensive list of Cervera et al. (2006) in the eastern Atlantic, the benthic opisthobranchs *A. dactylomela*, *A. juliana*, *D. dolabrifera*, *U. umbraculum*, and the pelagic *F. pinnata* and *G. atlanticus* are also recorded on the Peruvian coast. While Caribbean *Aplysia dactylomela* genetically differ from Indo-Pacific ones (Alexander & Valdés 2013), the East Pacific remains unsampled; at least the latter five species still appear to be circumtropical, as well as all the thecosomes reported from Peru (Table 1). It is very likely that species occurring over great distances or even in different biogeographic provinces are organisms showing a wide adaptation capacity. At least in non-pelagic species colonization of remote habitats requires dispersal stages either using currents (e. g. pelagic larvae or rafting of eggs or adults) or anthropogenic sources of dispersal (e. g. ship traffic, floating debris). However, referring to Peruvian opisthobranchs, we are not aware of invasion cases aided by humans. An alternative explanation for wide geographic and/or ecological ranges is the presence of morphologically cryptic species complexes which eventually once diverged and further adapted to local conditions.

Outlook

There is much to discover along the Peruvian coast and we predict that many more species are likely to be reported and described as the research effort increases in this region. However, high phenotypic plasticity of several species (e. g. *Spurilla* spp., *Tritonia* spp.) or morphological stasis in others (e. g. *Pontohedyle*) often cause confusion; therefore, (micro) anatomical and especially molecular techniques should be added to the study of the biodiversity of these groups of molluscs. It is possible that more extensive collecting efforts will reveal that several species currently reported in north-central Chile are also distributed in Peruvian waters, at least sporadically. The presence of cryptic species is also a possibility, given the large number of disjoint species in temperate but not in tropical waters; but this is subject of research for future studies.

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