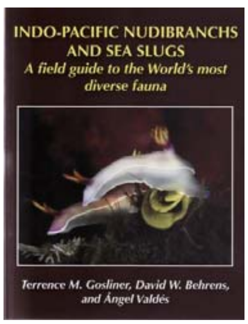
Opisthobranch Newsletter

Steven J. Long, editor
14541 Greenwood Lane, Tustin, CA 92780
http://www.seaslug.com
Volume 30, Number 1, pages 1-9 April 2009

Book Review of Indo-Pacific Nudibranchs and Sea Slugs (Gosliner, Behrens & Valdés, 2008), with Comparisons of Global and Indo-Pacific Opisthobranch Taxonomic Biodiversity and Biogeography

by Hans Bertsch
Departamento de Ingeniero en Pesquerías,
Universidad Autónoma de Baja California Sur, La Paz, B.C., México
Mailing address: 192 Imperial Beach Blvd. #A, Imperial Beach, CA 91932
hansmarvida@sbcglobal.net



Biology is not understandable without evolution. Change happens, and researchers look for patterns of change and differences. Discovery opens the way to other discoveries. The first photo-illustrated field guide to Indo-Pacific opisthobranchs (Bertsch & Johnson, 1981) emphasized *in situ* pictures of these marvelously colored marine invertebrates. Since this pioneering work, full-color, photo-illustrated guides to multiple areas within this region are now available, including, e.g., Australia (Marshall & Willan, 1999; Coleman, 2001; Cobb & Willan, 2006), Bali and Indonesia (Tonozuka, 2003), Japan (Nakano, 2004), and Korea (Koh, 2006). In the past decade, publication of nudibranch field guides has not been parsimonious!

In writing this review, I must clearly state that the authors of this book are my friends and colleagues, whom I have known for many years.

Gosliner, Terrence M., David W. Behrens, and Ángel Valdés. 2008. Indo-Pacific Nudibranchs and Sea Slugs. A field guide to the World's most diverse fauna. Sea Challengers Natural History Books and California Academy of Sciences. 426 pp.
ISBN 978-0-9700574-3-3
Available on the Internet from Sea Challengers Natural History Books: www.seachallengers.com ($79.95 US plus $10 S&H)

This truly magnificent book is the most comprehensive and scientifically accurate field guide to Indo-Pacific (IP) sea slugs. It is the best reference available for the opisthobranch fauna of that vast tropical zoogeographic region. It illustrates and describes 1387 species. The book probably covers about 60-70% of the known diversity, and about half of the total shallow water Opisthobranchia *s.l.* diversity of the IP. This latter percentage is similar to that found in the Sea of Cortez, eastern Pacific: with 4877 known macroinvertebrate species, Hendrickx, Brusca & Findley (2005) "estimate that less than half of its invertebrate fauna has been described." What Steinbeck & Ricketts (1941: 168) wrote about the Sea of Cortez, is still true for most of the oceans: "The shores of the Gulf, so rich for the collector, must still be fairly untouched."

Despite the plethora of IP research, there were inherent limitations in these authors' ability to include all the known species. The book is particularly short in Cephalaspidea *s.l.* There are many more species illustrated only from shells, but photographs of living animals are not available. There are 360 described species of Chromodorididae, but they only include 252. The other 108 are names of organisms that haven't been rediscovered since their original descriptions, many could be synonyms, or lack photos. Their decision not to include these species which require further research to properly identify is further testament to the scientific accuracy of this book.

This book is the culmination of an 11-year research project, involving numerous field trips by the authors and their colleagues. They are to be congratulated for their brilliant synthesis, which called upon the vast worldwide community of 'branchers in its writing. They incorporated the knowledge and experiences of many researchers, photographers, and authors of other sea slug guides.

The book consists of 2 parts: Introduction and Species Descriptions. The Introduction emphasizes biogeography, phylogeny and evolution, and coral reef conservation.

They define the IP as stretching latitudinally from the Indian Ocean coast of southern Africa to the central Pacific of the Hawai'ian, Easter and Marquesas Islands. The area is isolated from the coasts of west America by the Eastern Pacific barrier, although there is a "leak" (their word) of a few species that occur in both E–W extremes of the tropical Pacific. There is no sharp boundary for the IP, neither E–W nor N–S, and they describe a continuum of change between adjacent faunal provinces. This is similar to the ecotonal regions of faunal provinces along the Pacific coast of the Baja California peninsula (Bertsch, 1993).

Phylogenetic systematics (basing taxonomic names on evolutionary relationships) provides workable hypotheses for species' and higher taxa level nomenclature. GBV presents a clear explanation of this methodology and its consequences, using the synonymization of the "beloved" *Hopkinsia* with *Okenia*, and five similarly-patterned species of Hawai'ian *Hypselodoris* as examples.

I especially appreciate, respect and concur with their wake-up call for emergency action to save coral reefs, in the face of mass extinction: "Never in the history of our planet has any single species placed the fate of so many other species in such serious jeopardy....[W]e have the intellect, skills and resources to begin to change this....The future is in our hands, and we must act now" (GBV, p. 12). This extends, and forms part of a continuum to, the Conservation Ethic published 29 years ago, in which Bertsch & Johnson (1981: 108) wrote of the need to judiciously collect specimens necessary for scientific research, but pleaded that "A respectful appreciation of these living organisms will encourage one to look and admire, but to leave the animals in their natural environment so others can share their beauty. Besides, every nudibranch we have ever seen prefers the ocean to any other alternative." Now the entire ecosystem is endangered, and we must act.

Species' descriptions (pp. 13-409) are phylogenetically arranged within 8 major groups: Acteonoidea, Cephalaspidea (which two comprise Cephalaspidea *s.l.*), Acochlidiacea, Anaspidea, Sacoglossa, Umbraculoidea, Pleurobranchoidea (these latter two comprise Notaspidea *s.l.*), and Nudibranchia. The smallest group is the Acochlidiacea (4 spp.), whereas Nudibranchia (1077 spp.) comprise the majority of the 1387 species described. Some speciose genera are arranged by shared morphological features. For instance, the 94 *Chromodoris* species are grouped among the flat egg-mass clade, the *C. tinctoria* group, species that raise and lower the anterior portion of the head, mantle raising and lowering, etc.

Each description includes species name, authorship and year; comments on Identification, Natural History, Size and Distribution (with precise known occurrence sites); and at least one photograph of the living animal. The authors considered over 20,000 photos in making their selections for the book. Most are excellent portrait-style "tub shots," although there are a fair number of superb *in situ* photographs that illustrate aspects of the natural history. Marvelous examples of these "field shots" include *Gymnodoris nigricolor* and *G. ceylonica* by Mary Jane Adams; *Platydoris sanguinea, Glossodoris cincta* and *Phestilla melanbrachia* by Michael D. Miller; and the cover photo of *Hypselodoris bullocki* by Fred Bavendam. I personally would have included more of these types of photographs, because of the additional visual biological information they provide, but it's their book—and they chose their pictures very well! John and Ed would have been pleased: "We wished to take photographs of many of the animals....However, none of us was expert in photography and we had a very mediocre success (Steinbeck & Ricketts, 1941: 46-47). Over 65 years later, the photos in GBV are very successful.

The incredible wealth of information in GBV requires comparisons and contrasts with reports from other faunal regions.

Of great surprise was the record of the rare eastern Pacific *Aglaja regiscorona* from widespread IP locations (from Hawai'i to Japan, including intermediate island groups). For over 30 years, it had been known only from the type specimens collected at Las Cruces, Baja California Sur, México (Bertsch, 1972), until it was found in Costa Rica (Camacho-Garcia, Gosliner & Valdés, 2005). Discoveries still await nudibranch researchers; it will be interesting to see the changes, new records and new species in the 2nd edition of GBV ten years from now.

Four allopatric species of Pleurobranchoidea are indistinguishable by external morphology; two are IP. *Berthellina citrina* is known only from the Red Sea, whereas *B. delicata* occurs widely elsewhere throughout the IP. The eastern Pacific *B. engeli* occurs from the northern Sea of Cortez to the Islas Galápagos (Behrens & Hermosillo, 2005), with seemingly El Niño-correlated records from southern California (Kerstitch & Bertsch, 2007). *Berthellina quadridens* occurs in the western Atlantic on the Caribbean Islands, and from the shores of México to Brazil (Valdés, Hamann, Behrens & DuPont, 2006); in the eastern Atlantic it ranges from southern Britain to the Atlantic and Mediterranean coasts of Spain and France (Thompson & Brown, 1976; García & Bertsch, 2009). One cannot simply judge nor identify by appearances (similar to a book by its cover). There can be extreme intra-specific color variation (*e.g.*, *Pectenodoris trilineata* and *Pteraeolidia ianthina*) or no infra-specific external variation.

Rampant speciation has evolved in a number of IP opisthobranch families and genera. Most notable are the Chromodorididae, a group in which I have had more than a passing interest for over 4 decades (*e.g.*, Bertsch, 1970, and Bertsch & Gosliner, 1989). The 252 species represent 18.2% of the total fauna that GBV describe. Paraphrasing J.B.S. Haldane's apocryphally-attributed quote, "Madam Pele must have had an inordinate fondness for chromodorids." The authors describe 94 species of IP *Chromodoris*, mentioning there are approximately 165 species total in this region (compare with 7 in the eastern Pacific, and 7 in the Caribbean), 4 of *Mexichromis* (4 in the eastern Pacific, 1 Caribbean species), 45 species of *Hypselodoris* (with 4 in the eastern Pacific and 12 in the Caribbean) and zero *Cadlina* (but 7 in the eastern Pacific and 1 in the Caribbean) (eastern Pacific and Caribbean species numbers from Behrens & Hermosillo, 2005, and Valdés *et al.*, 2006). The IP absence of *Cadlina* brings up the question of the geographic origins and timing of the initial chromodorid evolutionary radiation within the dorids. Nudibranchs lack a fossil record, hence hypotheses depend upon careful correlations of vicariant events with phylogenetic analyses. Current data only permits placing the chromodorid origins within the larger context of dorid evolution, "shortly" after communication between the tropical IP and the Atlantic and eastern Pacific was closed during the Oligocene/Miocene transition approximately 23-24 mya (Rosen, 1984). However, communication was not strongly closed until much later (Valdés, 2004), when the cold water Benguela current barrier became continuous in the late Pliocene (Shannon, 1985); the east Pacific barrier probably allowed periods of significant gene flow until late Miocene/early Pliocene, 6.4-4.7 mya (Lessios *et al.*, 1999).

Evolution of the Atlantic and eastern Pacific clades of the genus *Hypselodoris* (Gosliner & Johnson, 1999) can be precisely correlated with the rise of the Panama isthmus 3–3.5 mya (Knowlton *et. al.*, 2003). For the origins of the Chromodorididae, Valdés (2002 and 2004) estimated a broad time span of 22-5 mya, which begs for a more accurate resolution. Using the taxonomic basis in GBV, resolving the identities of the other 108 "known" species, and establishing phylogenetic trees correlated with molecular clock techniques form the research protocol necessary to accurately determine these evolutionary events. I am confident that Terry, Dave, Ángel and their colleagues and students are developing this strategy. This brilliant book shows once again that answers to questions beget more questions!

Among the aeolids (extra-IP records from Behrens & Hermosillo, 2005; Camacho-García *et al.*, 2005; and Valdés *et al.*, 2006), the primarily polar and temperate genus *Flabellina* is represented by 14 IP species in GBV (16 in the eastern Pacific, and 11 in the Caribbean). They illustrate 45 IP species of *Cuthona* (contrast 29 in the eastern Pacific, and 8 in the Caribbean), and 12 *Favorinus* species (2 eastern Pacific and 1 Caribbean species). The endemic IP *Phyllodesmium* accounts for 31 species. Endemism in such a large area, although informative, may not be completely unexpected; additional research is needed to determine levels of endemic genera or species within various regions or island chains of the IP.

Indo-Pacific and Nudibranchs and Sea Slugs is a very important work, and must be reviewed within a global context. The extensive faunal inventories and biogeographic comments and discussions in GBV allow and require comparisons with other oceanic basins.

As a consequence of plate tectonics, oceanic shallow water habitats worldwide are characterized by a great dissimilarity of area and geography. The IP extends across a majority of the tropical Indian and Pacific Oceans, covering more than 200º of longitude (approximately 120º W to 40º E), and more than 60º of latitude (approximately 30º N to 30º S); see maps in GBV, p. 2. Throughout the IP are numerous large and small islands and island chains, formed by either converging plates (*e.g.*, Papua New Guinea and the Philippines) or their lateral movements over hot spots (e.g., the Hawai'ian, Marquesas and Easter Islands); narrow continental margins not tectonically active occur only along southern Asia and eastern Africa. These multiple island groups provide vast expanses of opisthobranch habitats suitable for the inter- and subtidal research documented in GBV, *et al*.

By contrast the extent of these habitats is far less vast in the eastern Pacific and along both Atlantic coasts (excepting the minor longitudinally expansive Caribbean and Mediterranean Seas). Collecting in these regions is limited primarily to narrow coastal zones, where there is much less total area for both opisthobranch occurrence and research efforts. Sheer size of the IP faunal province is a contributing factor to its being "the world's most diverse fauna."

The highest IP marine species diversity is in the Coral Triangle (= Indo-Australian Archipelago) (map in GBV, p. 2, Fig. 1). This center of marine diversity is the third in a sequence of biodiversity hotspots (following the Eocene West Tethyan and Arabian hotspots) that have migrated eastward over the past approximately 50 my (Renema *et al.*, 2008: 655, maps Fig. 1 A-C). Each has been shaped by tectonic plate collisions, resulting in increased shallow water habitats. Island formation provides "new opportunities for isolation and disruption of genetic connectivity," with higher levels of biodiversity caused by speciation or accumulation of non-indigenous species. "Plate tectonic movements control the area and variability of suitable shallow marine habitat. Subject to global climate constraints, they will modulate ocean circulation, resulting in changes in surface water characteristics as well as altering connectivity between (meta)populations" (Renema *et al.*, 2008).

Because of the area size differences, the following biogeographic and biodiversity contrasts and comparisons are based on relative percentages of species of the total opisthobranch fauna within each region or province. Comparisons are based on species diversity, not the organisms' abundances. In contrast, Nybakken (1978), Bertsch, Miller & Grant (1998), Hermosillo González (2006) and Bertsch (2008) studied actual opisthobranch abundances at three eastern Pacific sites (Pacific Grove, California; Bahía de los Ángeles, Baja California; Bahía de Banderas, Jalisco–Nayarit). The provinces and regions from the eastern Pacific and both Atlantic coasts were chosen for these comparisons because they lie within the same approximate latitudes of the IP faunal province.

Among the opisthobranch orders, Anaspidea has the highest percentage of extra-provincial occurrences (herein, species shared with other longitudinal tropical provinces) throughout all regions examined: 35% of anaspideans in the IP occur in the eastern Pacific and/or the Atlantic/Caribbean coastlines; the percentages are 53.8% for species occurring in the eastern Pacific, 87% of Caribbean species, and 69% of eastern Atlantic species. Several testable hypotheses may account for the widespread multi-provincial distributions of numerous anaspidean species, *e.g.*, large size and catholic herbivorous diet (in contrast to the smaller-sized and more prey-specific diets of the herbivorous sacoglossans). They may have slower speciation rates than other taxa, or larval drifting and adult rafting on floating algae might maintain genetic interchange.

As shown in Table 1a, Anaspidea and Notaspidea (*s.l.*) have the fewest numbers of species in the faunal provinces and regions from the four ocean areas (IP, eastern and western Atlantic, and eastern Pacific), ranging from 1.2–6.3% (global average of 3.5–3.9%) of the total opisthobranch fauna. Sacoglossa represent 5.1–15.6% of regional fauna, with a global average of 8.4%. Most speciose are the Cephalaspidea *s.l.* (7.6–46.9% regionally, 23.8% globally) and Nudibranchia (38.5–77.6% regionally, 60.1% globally). Table 1b averages the percentages in each column of Table 1a, more clearly demonstrating taxonomic distributional patterns and differences. The IP fauna reported in GBV currently represents the lowest diversity of cephalaspideans (*s.l.*) and the highest diversity of nudibranchs in all these regions.

In the Atlantic and eastern Pacific, each order shows varying N–S diversity trends, ranging from no change to a 20 percentage point decrease or increase of species (Table 1a). Slight N–S declines in species percentage points (~4-5) are seen in eastern Atlantic nudibranchs and eastern Pacific cephalaspideans. Significant changes (~20 points) are in the western Atlantic, with a N–S species percentage decline of Cephalaspidea, and a N–S increase of nudibranchs. Among nudibranchs (Table 2a) the only N–S trend occurs in western Atlantic dorids, increasing ~8 percentage points.

Diversity distribution (represented as total numbers of species) varies greatly throughout the IP. For instance, GBV (p. 3, Table 1) list 258 known species from Tanzania (with 16% undescribed), 717 from the Philippines (52% undescribed), and 430 from the Hawai'ian Islands (41% undescribed). These figures reflect the highest biodiversity levels occurring in the Coral Triangle. The species' distribution records in GBV need a highly ocmplex and extended analysis to determine either N–S or E–W biodiversity trends. It would be extremely enlightening to analyze the taxonomic biogeography and biodiversity within and between the various IP regions.

The new data of GBV show changes in species' percentages representation among the higher taxa from those presented nearly two decades ago by Gosliner (1992: 704, Table 2). His percentages of opisthobranch taxa were separately presented under four IP faunistic regions (W. Indian Ocean, Papua New Guinea, Guam and the Hawai'ian Islands); for this comparison, I use their averages.

The cephalaspideans show a decreased percent occurrence in the IP (17.9% to 10.7%), but an increased representation in the Caribbean (15.9% to 29%). As previously discussed, it should be noted that numerous cephalaspideans were not included in GBV.

Nudibranchs show an increased percentage in the IP (61.9% to 77.6%), but a decreased percentage in the Caribbean (55.6% to 45.7%). Among the four nudibranch orders (the polyphyletic Arminina *s.l.* is maintained as its traditional single order), percentages of species numbers in each and all regions (Table 2a) are highest for the dorids (ranging from 18.8–50.4%, globally 30.7%), followed by aeolids (ranging from 11.6–27.2%, globally 18.9%), dendronotids (ranging from 5.2–13.5%, globally 8.6%), and arminids (ranging from 1.3–4.4%, globally 2.0%). The highest percentages of dorids (>30%) are from the IP and the four eastern Pacific provinces and regions; aeolid maximum percentages (>20%) are in the eastern Atlantic Eastern Boreal and Mediterranean provinces, and in the eastern Pacific Mexican and Panamic regions. These numbers are reflected in the average percent of nudibranch suborders from each of the four contrasted temperate/tropical oceanic regions (Table 2b).

Comparing distributions in GBV (2008) again with Gosliner's 1992 data, dorids show an increase (42.3% to 50.4% of total opisthobranch fauna), but a slight decrease in the Caribbean (28% vs. 24.1%). The recent GBV data on aeolids show no percentage change in composition in the IP (15.2% vs. 15.9%), but a decrease in the Caribbean (18.1% vs. 11.6%).

This book provides an important, useful watershed of biodiversity and biogeographic data. It also reminds us that there is still much to be learned about opisthobranchs in the IP and elsewhere worldwide.

Literature Cited

Behrens, David W. & Alicia Hermosillo
2005. Eastern Pacific nudibranchs: A guide to the opisthobranchs from Alaska to Central America. Sea Challengers, Monterey, CA. vi + 137 pp.

Bertsch, Hans
1970. Opisthobranchs from Isla San Francisco, Gulf of California, with the description of a new species. Contributions in Science, Santa Barbara Museum of Natural History 2: 16 pp.

Bertsch, Hans
1972. Two additions to the opisthobranch fauna of the southern Gulf of California. The Veliger 15 (2): 103-106.

Bertsch, Hans
1993. Opistobranquios (Mollusca) de la costa occidental de México. In: Salazar Vallejo, S. I. & N. E.

Gonzalez (eds.), Biodiversidad Marina y costera de México. Comisión Nacional de Biodiversidad (CONABIO) y CIQRO, México. pp. 253-270.
Bertsch, Hans
2008. Opistobranquios. In: Gustavo D. Danemann & Exequiel Excurra (eds.). Bahía de los Ángeles: Recursos Naturales y Comunidad. Línea 2007. SEMARNAT, Pronatura Noreste, SDNHM and INE: Capítulo 11: 319-338.
Bertsch, Hans
2009. Biogeography of northeast Pacific opisthobranchs from Point Conception, California, USA, to the Galápagos Islands, Ecuador: Comparative faunal province studies of the Sea of Cortez. Biogeografía de Opisthobranchia del noreste Pacífico desde Point Conception, California, USA, hasta las Islas Galápagos, Ecuador: Estudios comparativos de la fauna provincial del Mar de Cortés. Western Society of Malacologists, Annual Report 40: 32-34.
Bertsch, Hans & Terrence M. Gosliner
1989. Chromodorid nudibranchs from the Hawaiian Islands. The Veliger 32 (3): 247-265.
Bertsch, Hans & Scott Johnson
1981. Hawaiian nudibranchs: A guide for SCUBA divers, snorkelers, tidepoolers, and aquarists. Oriental Publ. Co., Honolulu, Hawaii. 112 pp.
Bertsch, Hans, Michael D. Miller & Alan Grant
1998. Notes on opisthobranch community structures at Bahía de los Ángeles, Baja California, Mexico (June 1998). Opisthobranch Newsletter 24 (8): 35-36.
Camacho-García, Yolanda, Terrence M. Gosliner & Ángel Valdés
2005. Guía de campo de las babosas marinas del Pacífico este tropical. Field guide to the sea slugs of the tropical eastern Pacific. California Academy of Sciences, San Francisco, California. 129 pp.
Cobb, Gary & Richard C. Willan
2006. Undersea Jewels: A colour guide to nudibranchs. Australian Biological Resources Study, Canberra, ACT, Australia. 310 pp.
Coleman, Neville
2001. 1001 nudibranchs: Catalogue of Indo-Pacific sea slugs. Neville Coleman's Underwater Geographic Pty. Ltd., Springwood, Queensland, Australia. 144 pp.
García, Francisco J. & Hans Bertsch
2009. Diversity and distribution of the Gastropoda Opisthobranchia from the Atlantic Ocean: A global biogeographic approach. Scientia Marina 73 (1): 153-160.
García García, Francisco J., Marta Domínguez Álvarez & Jesús S. Troncoso
2008. Opistobranquios de Brasil: Descripción y distribución de opistobranquios del litoral de Brasil y del Archipiélago Fernando de Noronha. Feito, S.L., Vigo, Spain. 215 pp.
Gosliner, Terrence M.
1992. Biodiversity of tropical opisthobranch gastropod faunas. Proceedings Seventh International Coral Reef Symposium, Guam, 1992, vol. 2: 702-709.
Gosliner, Terrence M. & Rebecca F. Johnson
1999. Phylogeny of *Hypselodoris* (Nudibranchia: Chromodorididae) with a review of the monophyletic clade of Indo-Pacific species, including descriptions of twelve new species. Zoological Journal of the Linnean Society 125: 1-114.
Hendrickx, Michel E., Richard C. Brusca & Lloyd T. Findley
2005. Listado y distribución de la macrofauna del Golfo de California, México. Parte 1. Invertebrados. A distributional checklist of the macrofauna of the Gulf of California, Mexico. Part 1. Invertebrates. Arizona-Sonora Desert Museum, Tucson, Arizona. xi + 429 pp.
Hermosillo González, Alicia.
2006. Ecología de los opistobranquios (Mollusca) de Bahía de Banderas, Jalisco–Nayarit, México. Ph.D. Tesis. CUCBA, Universidad de Guadalajara, México. viii + 151 pp.
Kerstitch, Alex & Hans Bertsch
2007. Sea of Cortez Marine Invertebrates: A guide for the Pacific Coast, México to Perú, 2nd edition. Sea Challengers, Monterey, CA. ii + 124 pp.
Knowlton, N., L. E. Weigt, L. Al Solórzano, D. K. Mills & E. Bermingham
2003. Divergence in proteins, mitochondrial DNA, and reproductive compatibility across the Isthmus of Panama. Science 260 (5114): 1629-1632.
Koh, Dong Bum
2006. Sea slugs of Korea. Pungdeung Publ., Korea. 150 pp.

Lessios, Harilaos A., Bailey Kessing, D. Ross Robertson & Gustav Paulay
1999. Phylogeography of the pantropical sea urchin *Eucidaris* in relation to land barriers and ocean currents. Evolution 53 (3): 806-817.
Marshall, Julie G. & Richard C. Willan
1999. Nudibranchs of Heron Island, Great Barrier Reef: A survey of the Opisthobranchia (Sea Slugs) of Heron and Wistari Reefs. Backhuys Publishers, Leiden, The Netherlands. x + 257 pp.
Nakano, Rie
2004. Opisthobranchs of Japan Islands.
Rutles, Inc., Tokyo, Japan. 304 pp.
Nybakken, J.
1978. Abundance, diversity and temporal variability in a California intertidal nudibranch assemblage. Marine Biology 45 (2): 129-146.
Renema, W., D. R. Bellwood, J. C. Braga, K. Bromfield, R. Hall, K. G. Johnson, P. Lunt, C.P. Meyer, L. B. McMonagle, R. J. Morley, A. O'Dea, J. A. Todd, F. P. Wesselingh, M. E. J. Wilson & J. M. Pandolfi
2008. Hopping hotspots: Global shifts in marine biodiversity. Science 321 (5889): 654-657.
Rosen, B. R.
1984. Reef coral biogeography and climate through the Late Cainozoic: Just islands in the sun or a critical pattern of islands? In: Brenchley, P. (ed.), Fossils and climate. Wiley-Liss Inc., New York. pp. 201-262.
Shannon, L. V.
1985. The Benguela ecosystem. Part I. Evolution of the Benguela physical features and processes. Oceanography and Marine Biology Annual Review 23: 105-182.
Steinbeck, John & Edward F. Ricketts
1941. Sea of Cortez: A leisurely journal of travel and research. Viking Press, New York. 598 pp.
Thompson, T. E. & Gregory H. Brown
1976. British opisthobranch molluscs. Mollusca: Gastropoda. Keys and notes for the identification of the species. Synopses of the British Fauna (new series) No. 8. Linnean Society of London and Academic Press, London. 203 pp.
Tonozuka, Takamasa
2003. Opisthobranchs of Bali and Indonesia. Hankyu Communications Co., Ltd, Tokyo, Japan. 164 pp.
Valdés, Ángel
2002. A phylogenetic analysis and systematic revision of the cryptobranch dorids (Mollusca, Nudibranchia, Anthobranchia). Zoological Journal of the Linnean Society 136: 535-636.
Valdés, Ángel
2004. Phylogeography and phyloecology of dorid nudibranchs (Mollusca, Gastropoda). Biological Journal of the Linnean Society 83: 551-559.
Valdés, Ángel, Jeff Hamann, David W. Behrens & Anne DuPont
2006. Caribbean sea slugs: A field guide to the opisthobranch mollusks from the tropical northwestern Atlantic. Sea Challengers Natural History Books, Etc., Gig Harbor, Washington. vii + 289 pp.

TABLE 1a. Global comparisons of opisthobranch biodiversity and biogeography with the faunal inventory of Gosliner, Behrens & Valdés (2008): Percentages of opisthobranch groups *(s.l.)* in worldwide biogeographic regions at comparable latitudes. Indo-Pacific data calculated from GBV, 2008 (1387 total species); Atlantic data calculated from García, Domínguez & Troncoso, 2008 (205 spp. from Brazil), and García & Bertsch, 2009 (1066 total spp.); eastern Pacific data from Bertsch, 2009, in press, and in prep. ms. (399 total spp.).

	Cephalaspidea	Sacoglossa	Anaspidea	Notaspidea	Nudibranchia
Indo-Pacific	10.7%	8.7%	1.4%	1.2%	77.6%
East Atlantic					
E. Boreal	24.2%	5.1%	1.9%	2.8%	66%
Lusitanian	31.2%	6.0%	2.7%	3.0%	57.1%
Mediterranean	22.3%	9.3%	4.0%	2.8%	61.6%
West Atlantic					
W. Boreal	46.9%	7.3%	4.2%	3.1%	38.5%
Caribbean	29%	15.6%	5.2%	4.6%	45.7%
Brazilian	25.9%	10.0%	6.3%	5.4%	50.7%
Eastern Pacific					
Californian	25.7%	4.6%	2.8%	3.3%	63.6%
Sea of Cortez	18%	9.8%	4.4%	4.3%	63.4%
Mexican	7.6%	8.2%	5.7%	4.4%	74.0%
Panamic	20.6%	7.8%	4.6%	4.1%	63.1%
Global average of percentages:	23.8%	8.4%	3.9%	3.5%	60.1%

TABLE 1b. Global comparisons of opisthobranch biodiversity and biogeography with the faunal inventory of Gosliner, Behrens & Valdés, 2008: Average percentages of opisthobranch groups *(s.l.)* from the 4 temperate/tropical oceanic basins.

	Cephalaspidea	Sacoglossa	Anaspidea	Notaspidea	Nudibranchia
Indo-Pacific	10.7%	8.7%	1.4%	1.2%	77.6%
East Atlantic	25.9%	6.8%	2.9%	2.9%	61.6%
West Atlantic	33.9%	11.0%	5.2%	4.4%	45.0%
Eastern Pacific	18.0%	7.6%	4.4%	4.0%	66.0%

TABLE 2a. Global comparisons of opisthobranch biodiversity and biogeography with the faunal inventory of Gosliner, Behrens & Valdés, 2008: Nudibranch biodiversity of worldwide sites (data sources in Table 1). Percentages of nudibranch clades among all opisthobranchs.

	Doridina	Dendronotina	Arminina	Aeolidina
Indo-Pacific	50.4%	7.0%	4.4%	15.9%
East Atlantic				
E. Boreal	24.7%	13.5%	3.3%	24.7%
Lusitanian	26.4%	9.0%	2.1%	19.5%
Mediterranean	29.1%	9.6%	1.5%	21.4%
West Atlantic				
W. Boreal	18.8%	5.2%	—	14.6%
Caribbean	24.1%	8.6%	1.5%	11.6%
Brazilian	27.3%	6.8%	1.5%	15.1%
Eastern Pacific *				
Californian	35.0%	8.4%	2.3%	17.8%
Sea of Cortez	35.5%	7.1%	2.2%	18.6%
Mexican	34.8%	10.8%	1.3%	27.2%
Panamic	31.3%	8.8%	1.8%	21.2%
Global average of percentages:	30.7%	8.6%	2.0%	18.9%

* The three Panamic Province regions (Sea of Cortez, Mexican and Panamic) are N–S divisions with sufficiently distinct faunal components to warrant separate analyses, but not provincial-level designations.

TABLE 2b. Global comparisons of opisthobranch biodiversity and biogeography with the faunal inventory of Gosliner, Behrens & Valdes, 2008: Average percentages of nudibranchs (of total opisthobranch fauna) from the 4 temperate/tropical oceanic basins.

	Doridina	Dendronotina	Arminina	Aeolidina
Indo-Pacific	50.4% *	7.0%	4.4%	15.9%
East Atlantic	26.7%	10.7%	2.3%	21.9%
West Atlantic	23.4%	6.9%	1.5%	13.8%
Eastern Pacific	34.2%	8.8%	1.9%	21.2%

* Significant contribution by the high diversity of Chromodorididae, 18.2% of total opisthobranch fauna.