Indo-Pacific opisthobranch gastropod biogeography: how do we know what we don't know?

Terrence M. Gosliner and **Robyn Draheim***

California Academy of Sciences, Golden Gate Park, San Francisco, California 94118 U. S. A.

Abstract: Recent studies on the biodiversity of Indo-Pacific opisthobranchs demonstrate that more than 3,400 species are known from the region, including more than 1,000 undescribed species. This estimate exceeds a recent estimate of worldwide opisthobranch diversity. Evidence from recent collections supports the contention that this figure represents a minimum diversity for the region and that many other undescribed species are presently undetected.

Distribution patterns of Indo-Pacific opisthobranchs remain poorly known. Recent rediscovery of previously described taxa from widely separated localities supports the idea that many fundamental distributional data are currently lacking. The apparent species composition of the Hawaiian opisthobranch fauna has increased by more than 75% in the last three years. This attests to the lack of baseline data even from localities that were believed to be well known.

Estimates of the percentage of the fauna endemic to a region range widely as is shown for the Hawaiian Islands. Despite this fact, it is apparent that the perceived level of endemism for Hawaiian opisthobranchs is decreasing with increasing taxonomic refinement and discovery of additional species. It is suggested that the disparity between levels of endemism of Hawaiian marine and terrestrial biotas is real rather than artifactual, as suggested by some previous workers.

Phylogenetic hypotheses, necessary for study of vicariant patterns in Indo-Pacific opisthobranchs, are limited in number. Of the phylogenies that do exist, none show vicariance of sister taxa within the Indo-Pacific, but exhibit marked sympatry between sister species. This suggests that subsequent to vicariance, dispersal has masked original allopatry of sister taxa. None of the opisthobranch taxa thus far studied have Pacific Plate endemics as described by Springer (1982) for shorefishes. However, it is clear that phylogenetic studies of opisthobranch taxa with more endemic representatives must be undertaken to further examine these patterns.

Studies of biodiversity of organisms are contingent upon reliable information regarding the species composition and distribution of taxa within and between different geographical regions. These distributional data are requisite for both classical and vicariant biogeographical studies. The tropical Indo-Pacific is unsurpassed in its species richness for most marine taxa and rivals tropical rainforests in its diversity. Owing to the vastness of the region, stretching from the eastern coast of Africa to the Hawaiian Islands, many localities remain poorly studied and and others imperfectly known. Winston (1988) estimated that 20-80% of the marine organisms inhabiting the region remain undescribed, depending upon the taxonomic group being considered. Few studies have focused upon acquiring more detailed estimates of the status of knowledge of marine taxa inhabiting the Indo-Pacific tropics or the potential impact of these data upon estimates of standing biodiversity. Ghiselin (1992) and Gosliner (1992) provided estimates of the status of knowledge regarding opisthobranch faunas at several localities within the Indo-Pacific tropics. Problems of comparability of data sets were noted.

Classical biogeographical studies have emphasized the composition of biotas from discrete geographic areas. The number of species known to occur in a particular area has been the primary focus of this approach. Determination of boundaries of biotic provinces has been another traditional concern of this descriptive approach. A third component has been the determination of biogeographic affinities to other geographical regions or provinces. The surrounding areas which share the largest number of species with the area of immediate concern are said to have the strongest biogeographic affinity to that area. Comparison of the percentage of species endemic to a region to those which are widespread provides an estimate of the isolation of that biota from other biotas either by means of strong barriers, limited dispersal, or both.

In contrast, vicariance biogeography is concerned with distributional comparisons of phylogenetically related taxa. In addition to taxonomic and distributional data, phylogenentic hypotheses are required to undertake comparisons of vicariant patterns of distribution. Vicariant patterns can only be recognized when there is geographical isolation of closely related taxa.

This paper critically evaluates the present status of knowledge of opisthobranch gastropods in the Indo-Pacific

*Present address: Virginia Institute of Marine Sciences, College of William and Mary, Gloucester Point, Virginia 23062 U. S. A.

tropics. Several aspects of biodiversity and biogeography are explored, especially within the context of the kind of data that are required for studies of phylogenetics and vicariance biogeography.

METHODS

Several lines of investigation were pursued in order to survey the diversity of opisthobranchs known from the Indo-Pacific tropics. Records of previously described species were gleaned from a wide variety of literature sources. Data on shelled opisthobranch species were primarily obtained by means of Pilsbry's (1896) review of taxa and examination of *Zoological Record* subsequent to publication of Pilsbry's work. Nudibranch taxa were reviewed by Russell (1971, 1986) and through *Zoological Record*. Names of other opisthobranch taxa were obtained through *Zoological Record* and through perusal of primary literature and systematic reviews. It is widely known that *Zoological Record* has historically missed at least 20% of the molluscan names published (Bouchet and Rocroi, 1992). Every effort was made to survey the literature as thoroughly as possible, although it is likely that some taxa have been overlooked.

Taxa found were entered into a database using FileMaker Pro 2.1 (Claris Corp.). Every attempt has been made to incorporate as complete distributional data as are available. Species have been placed in synonymy according to the most recent published systematic treatment of that taxon and distributional data for junior synonyms have been combined with the known range of the senior synonym. Unpublished distributional records, based upon collections made in recent years from Aldabra Atoll, Madagascar, Malaysia, Papua New Guinea, the Philippines, and the Hawaiian Islands, were also incorporated into the database. Also included are unpublished records from Guam based on material collected by Clay Carlson and Patty Jo Hoff and unpublished records of material collected from Okinawa by Robert Bolland. Unpublished records from the Hawaiian Islands based upon collections of Pauline Fiene-Severns and Cory Pittman are included.

In addition to the described taxa represented in the above published literature, all known, but presently undescribed, taxa have been added to the database, with as complete distributional data as are known.

RESULTS

STANDING BIODIVERSITY OF OPISTHOBRANCHS

Boss (1971), in his review of the biodiversity of mollusks, estimated a global diversity of about 3,000 known species of opisthobranchs. From the published and unpublished records cited above, we have documented more than 3,400 species of opisthobranchs from the Indo-Pacific tropics. Of these, 1,019 are undescribed species. From these data, several conclusions can be drawn. The standing biodiversity of opisthobranchs worldwide is much higher than that estimated by Boss. Indo-Pacific opisthobranch diversity alone exceeds what was estimated for the whole world. A large proportion (more than 30%) of the species known to occur in the Indo-Pacific tropics are presently undescribed. Probably many other undescribed opisthobranch species have yet to be discovered within the Indo-Pacific and the estimates presented above represent the minimum percentage of undescribed species. This suggestion is supported by recent collection data from several localities throughout the Indo-Pacific. On a recent collecting trip to Tanzania, 11 undescribed opisthobranchs that had not been recorded from any other locality were documented in 11 days of observation. More recently, 20 completely novel, undescribed species were collected from the shallow waters of Luzon and Mindoro Islands in the Philippines within a 14-day period. Most of these were collected at specific localities that had been well-sampled by the same investigators employing the same sampling techniques over a period of several years. Many of these were large, brightly colored species that would not have been easily overlooked if they had been present during previous trips. This notion is further supported by the fact that some of the undescribed species found on previous trips were not located on subsequent trips, despite repeated intensive searching of the specific localities and habitats where they were originally encountered. Such data suggest that many of these species are sporadically encountered and probably have normally small populations.

Based on data presented in Table 1, approximately 40-50% of the species that occur in the better-known portions of the Indo-Pacific are undescribed. Using methods of estimating diversity for the entire Indo-Pacific by extrapolation as suggested by Colwell and Codington (1994) for terrestrial systems, it is likely that 4,000-4,800 species of opisthobranchs occur in the Indo-Pacific tropics. Perhaps

Table 1. Opisthobranchs from different Indo-Pacific localities.

Locality	# of species	% undescribed
Tanzania	258	16%
Madagascar	168	19%
Philippines	563	37%
Papua New Guinea	646	52%
Guam	474	47%
Hawaii	430	41%

twice that number occur in the world's oceans.

Ghiselin (1992) reported that the opisthobranch fauna of the Hawaiian Islands was one of the better-known ones in the Indo-Pacific and noted that 244 species were known. Recent intensive collections (largely through the efforts of Pauline Fiene-Severns and Cory Pittman) in the Hawaiian Islands raises the known fauna to 430 nominal species. This marked increase is reflective of the incomplete knowledge of species composition of opisthobranchs for any Indo-Pacific locality, including the more well-studied regions. In addition, it suggests that the Hawaiian opisthobranch fauna is not as impoverished or as attenuated as suggested by previous workers.

The percentage of the known fauna of specific localities in the Indo-Pacific which is undescribed is another measure of the completeness of knowledge of the biota of those particular localities. The total number of known species and the percentage of undescribed taxa from six Indo-Pacific localities is provided in Table 1. While these figures suggest that western Indian Ocean localities (Tanzania and Madagascar) have fewer species and a smaller percentage of undescribed species, it is likely that both are artifacts of less intensive collecting.

Another way in which the state of knowledge of the systematics of Indo-Pacific opisthobranchs can be assessed is by comparing proportions of undescribed versus described species of particular taxa. In several groups of opisthobranchs (Table 2), the proportion of undescribed species ranges from 22-58%. This closely resembles the range of geographic- rather than taxon-based comparisons, presented above.

Whatever the measure of biodiversity of Indo-Pacific opisthobranchs, the conclusion that many undescribed species are present throughout the region remains. Yet undiscovered taxa are likely to continue to be found by future exploration, thus increasing the estimated biodiversity of the region.

KNOWN DISTRIBUTIONS OF INDO-PACIFIC OPISTHOBRANCHS

Estimating the known distributions of Indo-Pacific opisthobranchs is an extremely difficult undertaking, as lack of data is usually reflected by apparently narrow distributions. For species that are large, conspicuous in their coloration, and fairly abundant, it is far more likely that presently known distributional data reflect biogeographical reality. In other cases, where information is far more scanty, widely disjunct distributions are known. For example, the aeolid nudibranch, *Flabellina macassarana* Bergh, 1905, was originally described from a single specimen from the Macassar Strait in Indonesia. There are no other published records of this species. Recently, single specimens were collected in the Philippines and Tanzania. All three known specimens have been found in about 30 m depth and the two recently discovered ones have been found in association with a single species of the hydroid genus, *Eudendrium*. *F. macassarana* is a highly specialized predator which occurs at considerable depth and appears to be uncommon even in its preferred habitat. All of these factors contribute to the lack of distributional data. Nevertheless, it is widespread, ranging from the western Indian Ocean to at least the western Pacific. Additional records may fill in the gaps and possibly extend the known range farther eastward. Known distributions at least permit making inferences regarding the minimum known range for a species.

Distributional data from specific localities can also provide evidence to infer the relative state of knowledge of that biota and of adjacent ones. On a recent collecting trip to the Philippines, 218 opisthobranch species were observed in two weeks of sampling. Of these, 61 had not been previously recorded from the Philippines. This is despite the fact that most of the areas where collecting took place had been repeatedly sampled over a several-year period. Similarly, of the 127 species collected from Tanzania in 11 days, more than half (67) had not been previously recorded from the coast of eastern Africa, including 35 species which had not been found previously in the Indian Ocean.

All of these measures of distributional pattern indicate that the distribution of opisthobranch species in the Indo-Pacific remains poorly known. Despite gaps in distributional data, present distributions can serve as estimates of geographical limits for species known from widely separated localities. The exploration of areas that are poorly known as well as continued observation of areas which are better known is fundamental to building a basic understanding of Indo-Pacific opisthobranch distributions.

Table 2. Percentage of undescribed species within five genera of Indo-Pacific opisthobranchs.

Taxon	# of species	# of species undescribed	% of species undescribed
Chelidonura	24	8	33%
Chromodoris	164	36	22%
Hypselodoris	39	19	48%
Nembrotha	29	7	24%
Cuthona	114	66	58%

LEVELS OF ENDEMISM IN INDO-PACIFIC OPISTHOBRANCHS

The percentage of species which are endemic to a particular region is a measure of its geographical isolation and is often reflective of isolating mechanisms that have permitted allopatric speciation, in the absence of gene flow. By definition, species are considered endemic to a region if they are known from nowhere else. Consideration of endemism is independent of the size of the region. Thus, a species can be considered endemic to a particular archipelago, while another more widespread species can be considered endemic to the Indo-Pacific. However, in the absence of sufficient distributional data, erroneous assumptions of endemism can be made. In the above example, *Flabellina macassarana* might have been considered endemic to Indonesia, prior to its discovery from other widespread localities. Given the present level of understanding of Indo-Pacific opisthobranch distributions, assumptions of endemism should be made with extreme caution. Species known only from their original description are especially suspect as being endemic.

Taxonomic considerations may also impact concepts of endemism. Within the Indo-Pacific tropics, the Hawaiian Islands represent one of the most isolated archipelagos. They are isolated from both continental sources and other island groups. In the early to mid-twentieth century, most species found in the Hawaiian Islands were considered to represent new species and were generally considered endemic to the archipelago. With taxonomic refinement and collection of additional taxa, the perceived percentage of endemic opisthobranchs has diminished over time (Table 3). However, taxonomic refinement can instead increase estimated levels of endemism as cryptic and sibling species are recognized.

Present estimates of levels of endemism of Hawaiian opisthobranchs vary widely (from 4-43%) depending on the manner in which endemism is calculated. If all species known only from the Hawaiian Islands are considered "endemic," then 43% of the taxa are apparently restricted to the Hawaiian Islands. Alternatively, one could take a far more conservative approach. Species that are fairly large, brightly colored, and commonly encountered are less likely to overlooked from other localities. When only conspicuous and common Hawaiian species are considered, the resulting level of endemism (4%) is an order of magnitude lower than literal assumptions of endemism. The more conservative estimate appears far more likely to represent biogeographical reality.

Endemism elsewhere in the Indo-Pacific tropics remains even more poorly known than it is in the Hawaiian Islands. Endemism in subtropical areas adjacent to strictly tropical regions such as southeastern and western Australia (Rudman, 1987; Wells and Bryce, 1993), Japan (Baba, 1949, 1955) and South Africa (Gosliner, 1987a) appears to be high. This perception is difficult to quantify, given the incomplete state of biogeographical knowledge of these regions.

Table 3. Percent endemism of Hawaiian opisthobranchs.

Publication	% endemism
Pease, 1860	90%
Pilsbry, 1921	88%
Ostergaard, 1955	89%
Kay, 1979	29%
Gosliner, unpublished	13%
Gosliner, present study	4.5% - 43%

It appears that some strictly tropical regions of the Indo-Pacific also exhibit some degree of endemism, as well. Present data suggest that the western Indian Ocean and the Red Sea contain species that are not found elsewhere in the Indo-Pacific. For example, Rudman (1987) discussed several species pairs of chromodorid nudibranchs, in which one sister species is restricted to the western Indian Ocean and its hypothesized sister species is found in the Pacific. These species generally have similar but divergent color patterns. The circumstantial evidence that these taxa are sister species is compelling, despite the fact that explicit phylogenies are not known for any of these taxa.

Apparent regional endemism within the Indo-Pacific is not restricted to marginal portions of this vast area. It appears that many species in the western Pacific are restricted to this area, in the region of highest diversity extending from the Philippines southward to Indonesia and Papua New Guinea. However, the systematics and distribution of taxa within this subregion remain poorly known. Consequently, levels of endemism of geographical restriction within the subregion remain largely unstudied.

While regional endemism within portions of the Indo-Pacific appears likely, there are even fewer examples of more restricted endemism to a single island or portions of archipelagos. Some Hawaiian endemics appear to be more restricted. Two undescribed chromodorids which are large and brightly colored are commonly encountered in the waters of leeward atolls such as Kure and Midway, but are apparently absent from the high islands of the chain. Other species are apparently restricted to certain islands of the western Indian Ocean, but absent from others. For example, *Siphopteron michaeli* (Gosliner and Williams, 1988), is known from Reunion Island, but is apparently absent from Mauritius, Madagascar, and the African mainland.

Major gaps exist in the systematics and distribution of opisthobranch species inhabiting the Indo-Pacific tropics. Nevertheless, several conclusions can be drawn. Levels of endemism differ widely between terrestrial and marine environments of the same islands. Suggestions that these are taxonomic artifacts are not supported by increased disparity between Hawaiian land and marine environments with increased taxonomic refinement.

Other patterns of regional endemism appear to occur within Indo-Pacific opisthobranchs. Ascertaining levels of endemism for these regions or circumscribing the areas of endemism remain difficult owing to the absence of primary distributional and systematic data for most taxa and regions.

VICARIANCE BIOGEOGRAPHY IN INDO-PACIFIC OPISTHOBRANCHS

Vicariance biogeography focuses upon the study of phylogenetically related taxa, preferably sister taxa, which exhibit geographical separation from each other. The intent of these studies is to identify patterns of vicariance (or geographical separation) within and between clades, in order to recognize isolating mechanisms restricting gene flow and permitting speciation. As in the case of classical biogeography, taxonomy and distributional ranges of component taxa must be known. Additionally, vicariance biogeographical studies require hypotheses of phylogeny for the taxa being considered. In the case of Indo-Pacific opisthobranchs, this usually requires species-level phylogenies, because few higher taxa exhibit endemism within the regions (Gosliner, 1992). Few species-level phylogenies have been hypothesized for clades of opisthobranchs that inhabit the Indo-Pacific tropics. Phylogenetic studies of opisthobranchs which inhabit the region are restricted to those of the Gastropteridae (Gosliner, 1989), the Flabellinidae (Gosliner and Willan, 1991), *Hallaxa* (Gosliner and Johnson, 1994), and *Thuridilla* (Gosliner, 1995).

Another requisite element of vicariance biogeography is that sister taxa be geographically isolated from each other. This may mean classical geographical isolation such as construction of physical barriers (such as the Isthmus of Panama completely separating the Caribbean Sea from the eastern Pacific Ocean) or other barriers such as changes in oceanic current patterns or other factors which may significantly reduce gene flow between localities, thus permitting differentiation of isolated populations. When the above phylogenetic hypotheses are examined for geographical isolation of sister taxa, it is evident that there are few cases where sister taxa are allopatric. In the vast majority of cases, sister taxa have at least some area of geographical overlap and in many instances their entire ranges are almost completely sympatric (Gosliner and Willan, 1991; Gosliner, 1995). As vicariance biogeography assumes that speciation must be preceded by geographical separation, such sympatric distributions can be explained only by dispersal subsequent to speciation.

The relative failure of the above studies to demonstrate vicariance suggests that many taxa where subsequent dispersal has occurred are not informative for vicariance biogeographical studies. This is a common problem in the study of Indo-Pacific marine organisms, one which has led many investigators to suggest that it may be impossible to determine patterns of vicariance in Indo-Pacific taxa (see Kabat, this volume). However, it is apparent that some opisthobranch taxa do indeed exhibit endemism within the Indo-Pacific. Members of the genera *Halgerda*, *Chromodoris*, *Hypselodoris*, and *Nembrotha* appear especially fruitful for these studies, as they appear to contain species with distributions that are more restricted than many other taxa.

DISCUSSION AND CONCLUSIONS

The above data suggest several modifications of the conventional view concerning tropical opisthobranch diversity. Biodiversity of Indo-Pacific opisthobranchs is much higher than previously thought. Some of this is due to incomplete compilation of described taxa, but the bulk of increased diversity stems from the fact that at least 30% of the species are presently undescribed. Based on recent collections, many additional undescribed taxa likely remain to be discovered.

Primary distributional data are woefully lacking for both Indo-Pacific taxa and faunistic data for specific localities. The known opisthobranch fauna of the Hawaiian Islands has increased by more than 75% in the last three years. This, combined with the fact that the Hawaiian Islands are one of the better known portions of the Indo-Pacific, is indicative of the inadequate state of the knowledge of the entire region. Certainly, much additional data must be collected before a coherent picture of Indo-Pacific opisthobranch distributions can be presented.

Nelson and Platnick (1981) have suggested that the perceived level of marine endemism of the Hawaiian Islands would rise to approach the highly endemic terrestrial biota (± 90%) with greater taxonomic refinement. Gosliner (1987b) disputed this claim, stating that the consequences of larval dispersal of marine organisms differs fundamentally from the more limited dispersal of the terrestrial biota. Regardless of the variation in the currently perceived levels of endemism of the Hawaiian opisthobranch fauna, it is clear that the estimates are moving in the opposite direction with taxonomic and biogeographical refinement. These data strongly suggest that levels of endemism for marine taxa do differ from freshwater and terrestrial biotas and that differences in dispersal capabilities are responsible for these observed differences. Dispersal can affect endemism both prior to and following speciation. Initially, dispersal is essential in maintaining gene flow between separated populations of species, thus reducing the likelihood of speciation. Secondarily, if speciation has occurred as a result of geographical isolation, then subsequent dispersal may mask the original vicariance that permitted speciation.

Levels of endemism clearly differ between the terrestrial and freshwater and the marine environments. These differences do not appear to be taxonomic artifacts, but rather reflect different isolating mechanisms, different geographical barriers, and different dispersal capabilities. In other words, marine biotas appear to have evolutionary histories that are clearly separate from corresponding biotas associated with land masses. One exception to this general rule is the coastal strand vegetation of Indo-Pacific terrestrial environments. Plants inhabiting these regions have seeds that can float in sea water for extended periods and maintain their viability (Carlquist, 1974). The seeds of these plants are thus distributed by the same ocean surface currents that disperse marine larvae. Consequently, levels of endemism of strand vegetation are far lower than upland floras of the same islands. One difference between plant seeds and marine larvae is that most marine larvae are capable of undergoing vertical migration in and out of current and eddy systems, while seeds remain at the surface throughout their time in sea water. Nevertheless, the net effect of lower endemism in more readily dispersed taxa remains the same and is in sharp contrast to terrestrial biotas that are absent from the immediate shoreline.

There are few phylogenies of opisthobranch taxa with Indo-Pacific representatives. The available studies demonstrate little vicariance of sister taxa. Springer (1982) suggested the margin of the western Pacific Plate provided a historical geographical barrier for Indo-Pacific marine taxa and that sister species of taxa found on the Australasian Plate are likely restricted to the non-marginal portions of the Pacific Plate. None of the opisthobranchs for which there are hypothesized phylogenies exhibit this pattern, including the relatively few species that appear to have distributions that are vicariant with sister taxa.

Relatively few opisthobranchs have distributions which are widespread on the non-marginal portions of the Pacific Plate. One of the only examples of this pattern of distribution is an undescribed species of *Chelidonura*, which is thus far known from only the Hawaiian Islands and Easter Island. However, no hypothesis of phylogeny has been suggested the most likely sister species of this taxon. It is likely that other Indo-Pacific species could be found from more than one locality on the Pacific Plate, but it is premature to make that assessment for most taxa, owing to incomplete distributional data. It is also plausible to assume that some of the species endemic to particular islands of the Pacific Plate have sister taxa that are restricted to the Indian Ocean Plate. However, sufficient distributional and phylogenetic data are presently lacking to generalize whether this is a common pattern for Indo-Pacific opisthobranchs.

The systematics, biogeography, and phylogeny of Indo-Pacific opisthobranchs are all poorly understood. Recent evidence of previously undetected taxa and of distributions which are markedly more widespread than previously indicated, are strongly suggestive that many fundamental data are lacking. Additional intensive collections from many localities are essential to provide the necessary data for comprehensive biogeographical studies of Indo-Pacific opisthobranchs.

Although there is a paucity of biogeographical data for Indo-Pacific opisthobranchs, species level phylogenies of opisthobranchs, fundamental for vicariance biogeographical studies, are even less well-known. Despite the necessity for additional species descriptions and more detailed distributional data, the lack of phylogenetic hypotheses is the weakest link in building an understanding of vicariant patterns for Indo-Pacific opisthobranchs. While documenting the diversity and its distribution within the Indo-Pacific is certainly necessary, increasing knowledge of phylogeny is of paramount importance to understanding vicariant distributional patterns within the region.

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