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## Aggressive mimicry in *Aspidontus* and *Plagiotremus* (Pisces: Blenniidae): some mimetic phenotypes are not phylogenetically informative

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### Abstract

In the absence of sympatry, the delineation of species is essentially hypothesis open to refutation and mimicry can be a confounding factor. Two nominal species of Blenniidae, *Aspidontus tractus* and *Plagiotremus flavus*, previously recognized as subspecies but recently elevated to full species status, differ from their presumed allopatric sister species, *Aspidontus taeniatus* and *Plagiotremus laudandus*, only in having a different color pattern, which closely matches their mimetic models. We show that both taxa can exhibit differing and inconsistent color patterns over their biogeographic range, corresponding to variation in their local mimetic model. These mimetic phenotypes do not reflect genetic distances between independently evolving sibling species, but are local adaptations to the model, not necessarily linked to reproductive isolating mechanisms and not consistent with typical biogeographical boundaries for sibling species in the Indo-Pacific region. Indeed, both newly elevated taxa share their mitochondrial haplotypes with their original species, indicating that gene flow may not be interrupted. Thus, we consider *Aspidontus tractus* and *Plagiotremus flavus* to be junior synonyms of *A. taeniatus* and *P. laudandus*, respectively.

**Key words:** ichthyology, taxonomy, coral-reef fishes, mimic, species, subspecies, blennies, evolution.

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*We argue that the resolution of all taxa to absolutely distinct species or even completely diagnosable subspecies is incongruent with an acceptance of evolution as an active and ongoing process, regardless of which concepts are used.* Mundy et al. (2010)

## Introduction

Mimicry has been documented in a wide variety of organisms and has been the focus of interest since the first evolutionary analysis of butterflies by Bates in the first years after Darwin's "The Origin of Species" (Evans 1965). Coral reef fishes are no exception, and mimicry is relatively common among a number of prominent reef families, as reviewed by Randall (2005a). Among the many examples and different kinds of mimicry, one of the best known is the relationship between the Mimic Blenny *Aspidontus taeniatus* Quoy & Gaimard, 1834 and the Cleaner Wrasse *Labroides dimidiatus* (Valenciennes, 1839) (Randall & Randall 1960, Wickler 1968, Randall 2005a, Robertson 2013). In this case, the Mimic Blenny feeds, in part, on the fins and associated membranes of other fishes and it takes advantage of its superficial similarity to the harmless Cleaner Wrasse model to approach potential victims. The Cleaner Wrasse removes ectoparasites from reef fishes and has some immunity to predation, and the blenny is thus less recognizable as a danger and even shares in this immunity by its resemblance to the Cleaner Wrasse (aggressive mimicry). Another, more complex case, is between blenny species of the genera *Plagiotremus* and *Meiacanthus*, in which a species that targets larger fish mimics the color pattern of another one that does not (aggressive mimicry), but here the model has venomous fangs and the mimic shares in that protection—thereby adding Batesian mimicry (Springer & Smith-Vaniz 1972).

One overlooked aspect of mimicry is that it causes a strong local selective pressure on the phenotype of a mimic species to match the model, in addition to other phenotypic differences which develop as part of the reproductive isolation required for the origin and maintenance of speciation. The biogeographic distribution of the phenotype may or may not coincide with species boundaries and thus mimetic phenotypes should be used with caution as evidence of phylogeny. When the mimic phenotype is cited as evidence of speciation, it should be demonstrated that it is sufficiently consistent and also correlates with population-genetic boundaries. In another case, involving Cleaner Wrasses, the phenotype is not consistent and does not reflect population genetics and presents a difficult phylogenetic problem (Sims 2014). Indeed, a number of recent studies have shown discordance between phenotypes and genetic boundaries in a variety of taxa of reef fishes (Messmer et al. 2005, DiBattista et al. 2012, 2017). Since this discordance is frequent among reef fishes, it is even more important that the consistency and correlation of phenotypes be examined when used for phylogenetic or taxonomic purposes.

In this study, we examine two cases of mimicry in blennies in which the mimetic phenotype was used to justify the elevation of populations to species, without an evaluation of consistency or genetics. The two cases involve different evolutionary scenarios: in the case of *Aspidontus* a pan-Indo-Pacific species might be expected to split into different species in the two oceans, as is found in many other widespread IP reef fishes, while in *Plagiotremus*, local island populations within the western Pacific Ocean might be expected to become different species in the face of advantageous mimetic associations combined with some degree of isolation due to restricted pelagic dispersal. We examined these two cases in detail based on recent photographic and genetic evidence and show that the expected scenarios do not apply.

## Materials and Methods

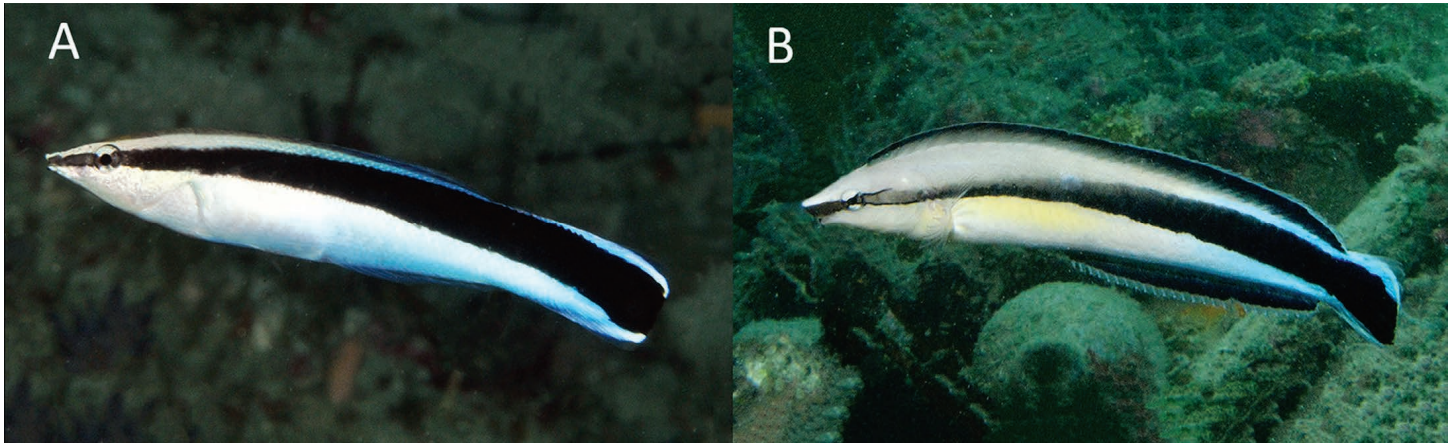
Institutional abbreviations are: BPBM, Bernice P. Bishop Museum, Honolulu, HI, USA; WAM, Western Australian Museum, Perth, Australia.

For the genetic analyses, a 652-bp segment (the "barcode" marker) was amplified from the 5' region of the mitochondrial cytochrome c oxidase (COI) gene using a variety of primers (Ivanova et al. 2007). DNA extractions were performed with the NucleoSpin96 (Machery-Nagel) kit according to manufacturer specifications under automation with a Biomek NX liquid-handling station (Beckman-Coulter) equipped with a filtration manifold. PCR amplifications were performed in 12.5  $\mu$ l volume including 6.25  $\mu$ l of 10% trehalose, 2  $\mu$ l of ultra pure water, 1.25  $\mu$ l of 10 $\times$  PCR buffer (10mM KCl, 10mM (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub>, 20mM Tris-HCl (pH8.8), 2mM MgSO<sub>4</sub>, 0.1% Triton X-100), 0.625  $\mu$ l of MgCl<sub>2</sub> (50mM), 0.125  $\mu$ l of each primer (0.01mM), 0.0625  $\mu$ l of each dNTP (10mM), 0.0625  $\mu$ l of *Taq* DNA polymerase (New England Biolabs), and 2  $\mu$ l of template DNA. The PCR conditions consisted of 94°C for 2 min., 35 cycles of 94°C for 30 sec., 52°C for 40 sec., and 72°C for 1 min., with a final extension at 72°C for 10 min. Specimen information and barcode sequence data from this study were compiled using the Barcode of Life Data Systems (Ratnasingham & Hebert 2007, Ward et al. 2009). The sequence data is publicly accessible

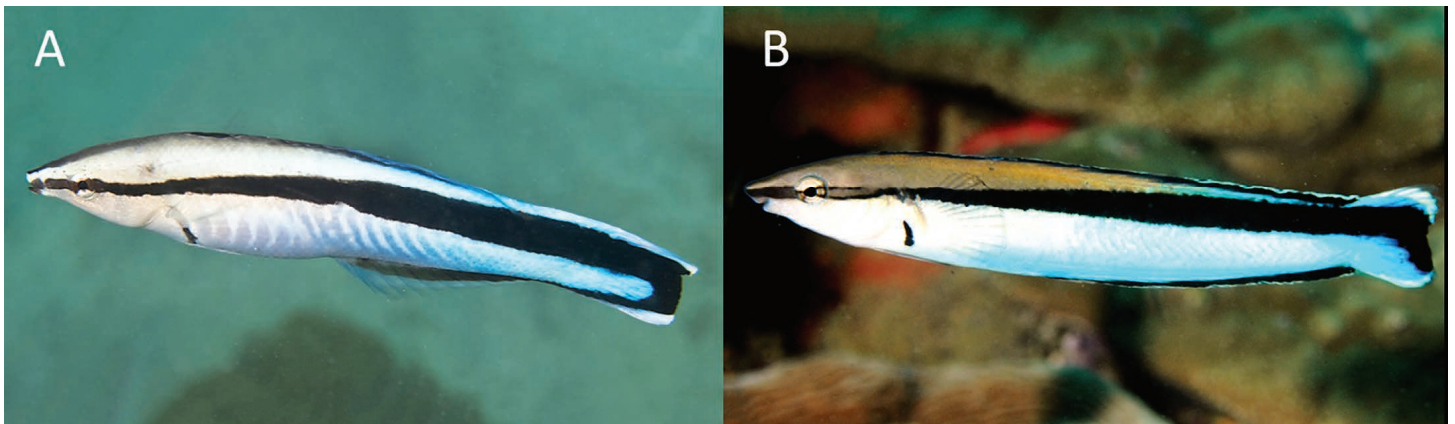
on BOLD and GenBank. Sequence divergences were calculated using BOLD with the Kimura 2-parameter (K2P) model generating a mid-point rooted neighbor-joining (NJ) phenogram to provide a graphic representation of the species' sequence divergences (for *Plagiotremus*). Different graphic methods were used to present the COI sequence data for the two species. Because we have a large number of *Aspidontus taeniatus* samples from a wide range of locations and most haplotypes are shared and there are very few nucleotide substitutions, a haplotype network captures the data better than a tree. In contrast, only a single *Plagiotremus* sequence was obtained from Fiji (despite strenuous efforts) and, since it is compared with a set of congeners with very deep divergences, a tree is used to capture the data.

### *Aspidontus taeniatus* versus *A. tractus*

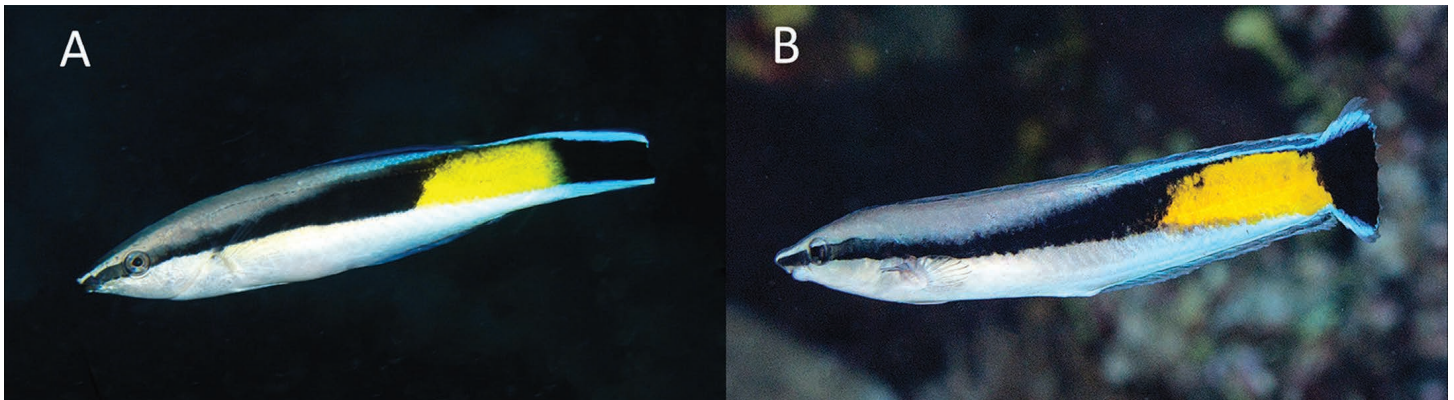
The blenny *Aspidontus taeniatus* (Fig. 1B) is a specialized aggressive mimic that feeds, in part, on the fins and associated membranes of other fishes. It is a close match in color to the widespread Cleaner Wrasse, *Labroides dimidiatus* (Valenciennes) (Fig. 1A), permitting the blenny to sneak up on prey unnoticed. It benefits further by sharing the immunity to predation that the Cleaner Wrasse has developed by its symbiotic association removing ectoparasites from larger fishes. When in the presence of fishes at a cleaning station, the blennies' deception is enhanced by adopting a labroid mode of swimming by primarily using its pectoral fins, and even mimicking the characteristic "dance" the cleaning wrasse employs to signal its readiness to clean at cleaning stations on the reef. Eibl-Eibesfeldt (1959), Randall & Randall (1960), and Robertson (2013) describe this mimetic association and behavior in detail. *Aspidontus taeniatus* is widespread in the Indo-Pacific, ranging from the Red Sea to French Polynesia, with the holotype from Guam in the Marianas Islands. The model Cleaner Wrasse occupies the same very wide range, with the type locality in the Red Sea. Early on, the Cleaner Wrasse was noted to have marked variation in markings from one location to another, mostly in the shape of the black markings, including the bar



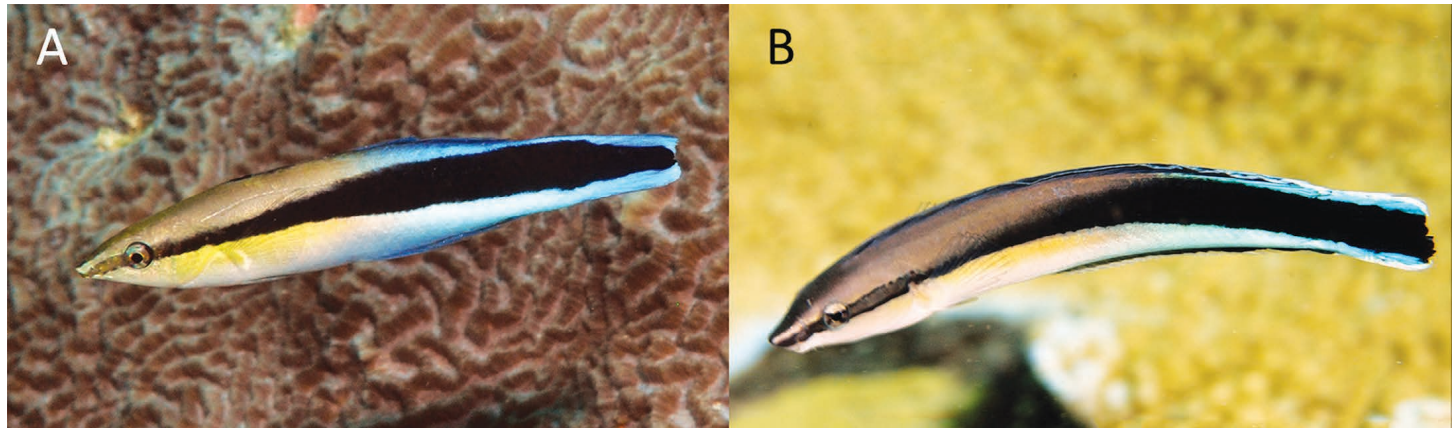
**Figure 1.** Mimetic pair, approx. 50 mm SL: A) *Labroides dimidiatus*, Raja Ampat Islands, Indonesia; B) *Aspidontus taeniatus*, Milne Bay, Papua New Guinea (G.R. Allen).



**Figure 2.** Mimetic pair, approx. 50–60 mm SL: A) *Labroides dimidiatus*, Lahami Bay, Egypt, Red Sea (S. Bogorodsky); B) *Aspidontus taeniatus*, southwestern Madagascar (G.R. Allen).



**Figure 3.** Mimetic pair, approx. 50–60 mm SL: A) *Labroides dimidiatus*, Fiji (G.R. Allen); B) *Aspidontus taeniatus*, Fiji (M. Rosenstein).



**Figure 4.** Mimetic pair, approx. 50–60 mm SL: A) *Labroides dimidiatus*, New Britain, Papua New Guinea); B) *Aspidontus taeniatus*, Fiji (G.R. Allen).

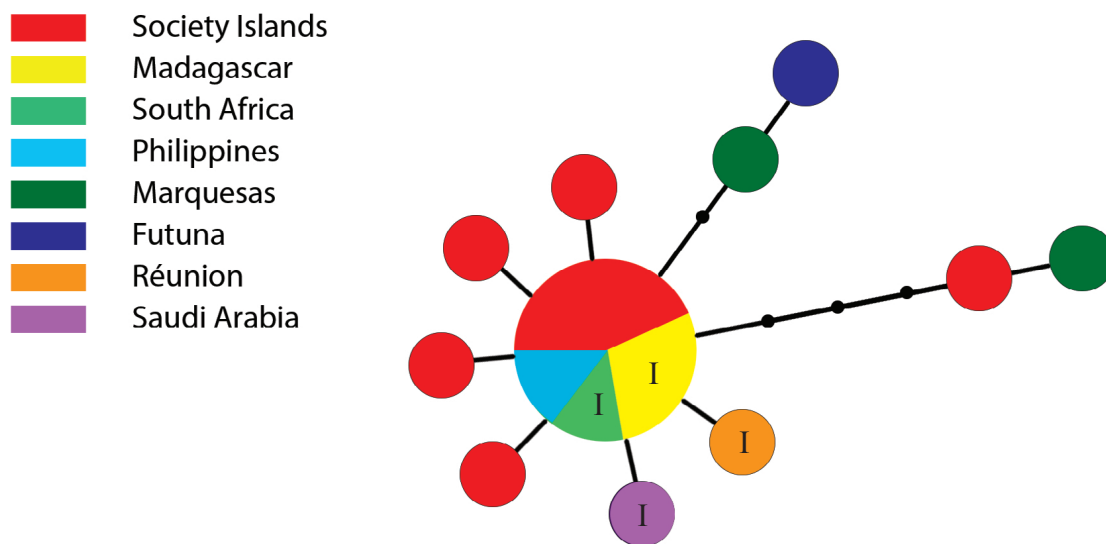
on the fleshy pectoral-fin base, the width of the lateral stripe, the shape on the tail, and the color on the flanks (e.g. Randall 1958, Sims et al. 2014).

The Mimic Blenny also shows variation in markings over its wide geographic range, notably, paralleling the markings of the local model Cleaner Wrasse. Without a comprehensive study of the range of variation, Fowler (1903) described the population of *A. taeniatus* from Zanzibar as a distinct species, *Aspidontus tractus* Fowler, 1903, based solely on the presence of a pectoral-fin bar. This bar is typically present on Red Sea and western Indian Ocean populations of both the blenny and *L. dimidiatus* (Fig. 2), and generally absent in the remainder of the range of both species (Figs. 1, 3 & 4). As noted by Springer & Smith-Vaniz (1972), in the blenny “the bar is on the fleshy base of the pectoral fin under the level of the posterior margin of the opercle. In the wrasse it is at the posteroventral corner where the fleshy pectoral base joins the body...”. Hastings & Springer (2009) followed Fowler and based the species status of *A. tractus* on the presence or absence of the bar. They mentioned that the only specimen then available from the Cocos-Keeling Islands, in the eastern Indian Ocean, has a faint bar. They were unaware that specimens from the eastern Indian Ocean, at Shark Bay, western Australia (WAM P.26671-011, 74–95 mm SL), have inconsistent bar markings: in 3 of 5 specimens the pectoral-fin bar is very short and shaped like an inverted tear, another one has a narrow elongate bar and one lacked a bar. Furthermore, two of 18 specimens from the Palau Islands have a small black bar on the pectoral-fin base (Springer & Smith-Vaniz 1972). Additional color variations occur within Pacific Ocean populations of *A. taeniatus*. Russell et al. (1976) noted that in Samoa there were typically colored *Aspidontus* mixing with individuals with a large orange patch on the posterior part of the flanks and an incomplete dark lateral stripe. The local form of Cleaner Wrasse has the same unusual color pattern. In the Fiji Islands to the Coral Sea, both typical *L. dimidiatus* and those with a yellow (instead of orange) flank are present (Fig. 4).

There is also considerable variation in both model and mimic species at any given locality. The color patterns of *A. taeniatus* and *L. dimidiatus* also match those at other locations: in the Society Islands and Tuamotu Archipelago, *A. taeniatus* has a pink area below the lateral stripe, matching some local *L. dimidiatus* which also have the pink

area, but there are also co-occurring *L. dimidiatus* that display a more typical coloration with no pink evident. In the Marquesas islands, some *A. taeniatus* match typical *L. dimidiatus* they associate with, but there are also mostly grey individuals of *A. taeniatus*, which mimic females of an endemic local wrasse *Coris hewetti* Randall, 1999 (Delrieu-Trottin et al. 2016, fig. 2). This confounding local variation and incomplete delineation of populations between the Indian and Pacific Oceans is reflected in the corresponding populations of Cleaner Wrasses, where the marking variation boundaries are also inconsistent (Sims et al. 2014): a curled round black edge on the tail is characteristic of the Indian Ocean population of *L. dimidiatus* (Fig. 2A), but also occurs to some degree in Japan, and the thin stripe in the Indian Ocean vs. wide stripe in the Pacific was found to be inconsistent. Subsequently, the genetic boundary between lineages of *L. dimidiatus* was found to be not between the two oceans, but between most of the Indo-Pacific vs. the southwestern corner of the Pacific, in eastern Australia, Coral Sea, and Fiji (with overlap in Papua New Guinea). Sims et al. (2014) discussed the phenomenon of phenotypic characters in mimetic or cleaning associations not paralleling population genetics. But the two main populations of *L. dimidiatus* were not elevated to species or subspecies pending additional study.

Historically, Smith-Vaniz (1976) recognized *A. tractus* only as a subspecies of *A. taeniatus*, but subsequently Smith-Vaniz (1987: 3) did not recognize *A. tractus* as even subspecifically distinct. Whether to formally recognize as subspecies geographically variable allopatric taxa that only differ by their color patterns is debatable (Randall (1998:263). Although subspecies recognition is often subjective, the specific epithet does make the presumed closest relatives obvious and makes clear that they are not considered sufficiently different to merit separate species rank. Heemstra & Heemstra (2004) appear to be the first authors to reinstate *A. tractus* to full species status (albeit without discussion), and this action has been followed by Patzner et al. (2009), Hastings & Springer (2009), Robertson (2013), and Fricke et al. (2020). Springer & Hastings (2009: 6) were the only authors who gave any reason for elevation of *A. tractus* to species rank, but they did not evaluate geographic or genetic variation in the two populations or consider that aggressive mimetic associations might devalue phenotypic variation as an indicator of genetic relatedness. There are no differences in the mitochondrial DNA COI sequences of nominal *A. taeniatus* throughout the Indo-West Pacific, from the Red Sea to French Polynesia (Fig. 5). Those populations even share the same haplotypes, indicating that gene flow is (or very recently was) occurring between all populations, as is characteristic of single species with local phenotypic variation. In view of the lack of any mitochondrial genetic differences among populations, the marked local variation in color patterns, the inconsistency of the putative pectoral-fin bar character, and the use of a single marking to justify taxonomic decisions, we believe taxonomic recognition of *A. tractus* is unjustified and only one pan Indo-West Pacific *A. taeniatus* should be recognized.

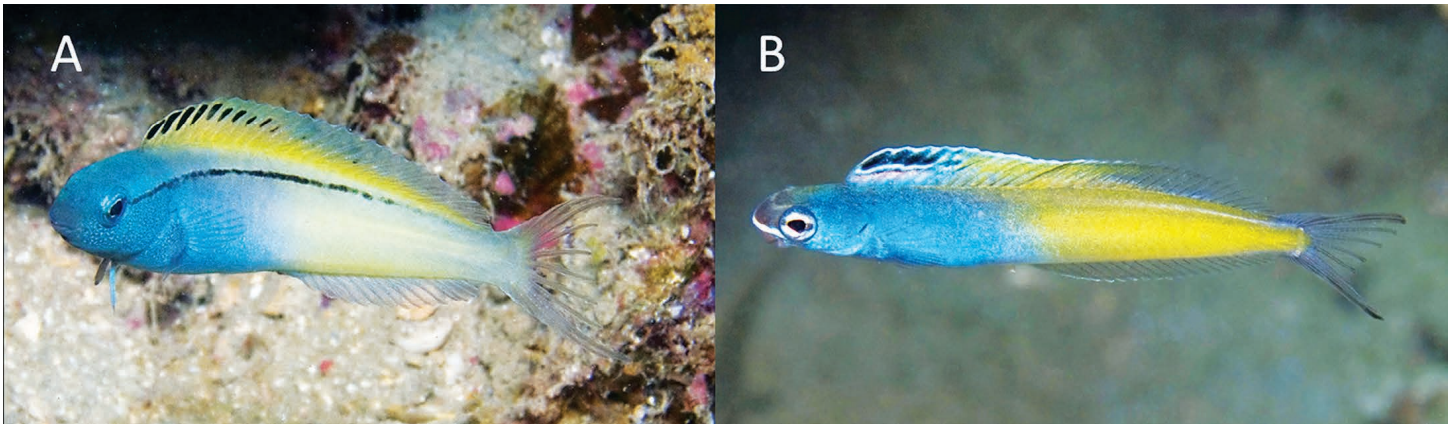


**Figure 5.** The haplotype network of COI mtDNA sequences of pan-Indo-Pacific *Aspidontus taeniatus* following the BOLD (Barcode of Life Database) algorithm. I=Indian Ocean, others are Pacific Ocean. Circle areas are proportional to number of individuals with that haplotype, small circles are n=1, black segments and nodes represent nucleotide substitutions. Collection data and GenBank accession numbers are in Appendix Table 1.

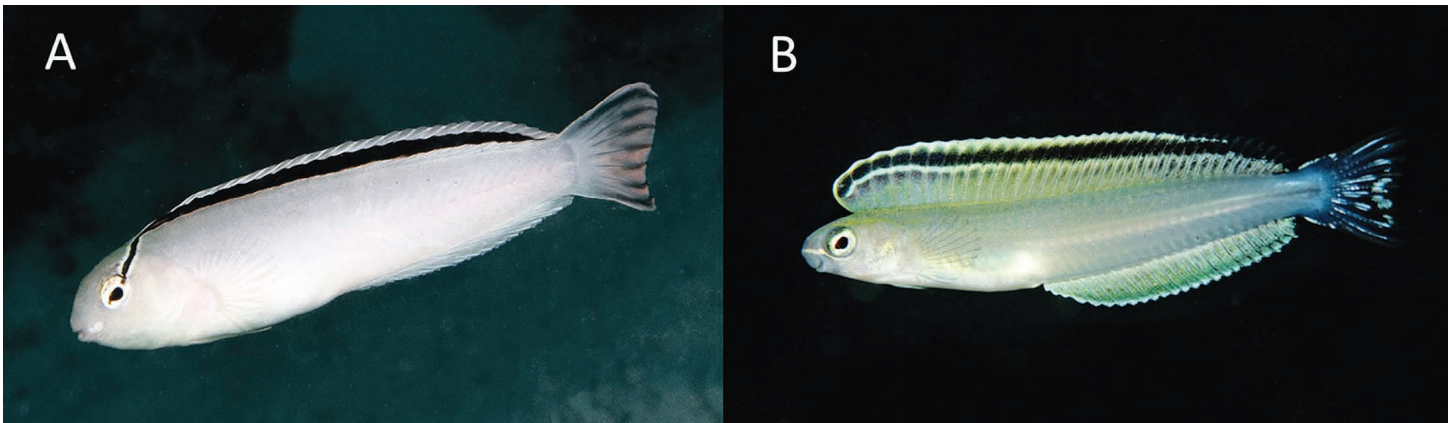
## *Plagiotremus laudandus* versus *Plagiotremus flavus*

All species of the fangblenny genus *Plagiotremus* are obligate feeders on mucus, epidermal tissue and scales of other fishes using specialized dentition ideally suited for that purpose (Smith-Vaniz 1976, figs. 72, 73). Several species (of the subgenus *Musgravius* Whitley) mimic the color pattern of sympatric members of another fangblenny species complex in *Meiacanthus* (Losey 1972, Smith-Vaniz 1987, Randall 2005a). The noxious mimic benefits to some degree from resembling a species that is not aggressive, especially if the model is more common, by being able to approach their victims unrecognized (aggressive mimicry). A more powerful advantage results from the venomous fangs of *Meiacanthus* blennies, which certainly discourage predation or any defensive attacks by victims of *Plagiotremus* (Casewell et al. 2017); see Springer & Smith-Vaniz (1972) for experimental evidence. Thus, the *Plagiotremus/Meiacanthus* mimicry is a textbook example of Batesian mimicry. The mimic/model pairs divide up the Indo-West Pacific region, with *Plagiotremus townsendi* (Regan, 1905) and *Meiacanthus nigrolineatus* Smith-Vaniz, 1976 (Fig. 6) in the Red Sea to Oman; *Plagiotremus phenax* Smith-Vaniz, 1976 and *Meiacanthus smithi* Klauswitz, 1962 (Fig. 7) in the eastern Indian Ocean; grey variants of *Plagiotremus laudandus* (Whitley, 1961) and *Meiacanthus atrodorsalis* (Günther, 1877) from West Papua, Indonesia to the Solomon Islands (Fig. 8) and typical *P. laudandus* and *M. atrodorsalis* (Fig. 9) in the western Pacific Ocean.

There is a different all-yellow morph of *Plagiotremus* endemic to Fiji, first named as the subspecies *Plagiotremus laudandus flavus* Smith-Vaniz, 1976, that matches the local endemic all-yellow *Meiacanthus oualanensis* (Günther, 1880) (Fig. 10) that replaces the widespread *M. atrodorsalis*. On nearby Tonga, there is another local representative of the model, *Meiacanthus tongaensis* Smith-Vaniz, 1987, which is bright yellow-green except for a conspicuous black stripe along the basal half of the dorsal fin (see Randall 2005b: 497 for color photograph). Hastings & Springer (2009), however, changed the taxonomic status of the all-yellow Fiji *Plagiotremus* subspecies and tersely stated “We elect to elevate them to species status following a similar conclusion made for the two

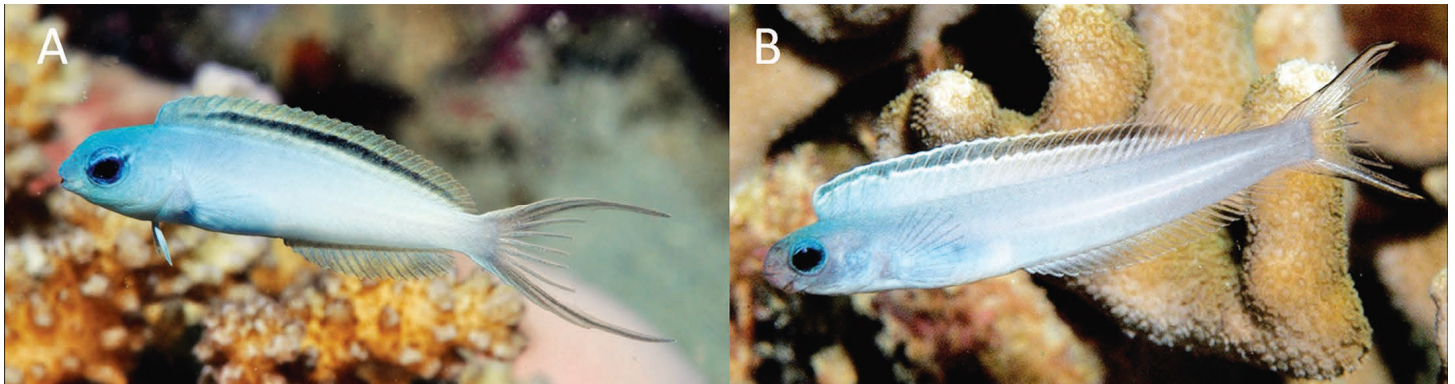


**Figure 6.** Mimetic pair, approx. 35–50 mm SL: A) *Meiacanthus nigrolineatus*; B) *Plagiotremus townsendi*, Shams Alam, southern Egypt, Red Sea (S. Bogorodsky).

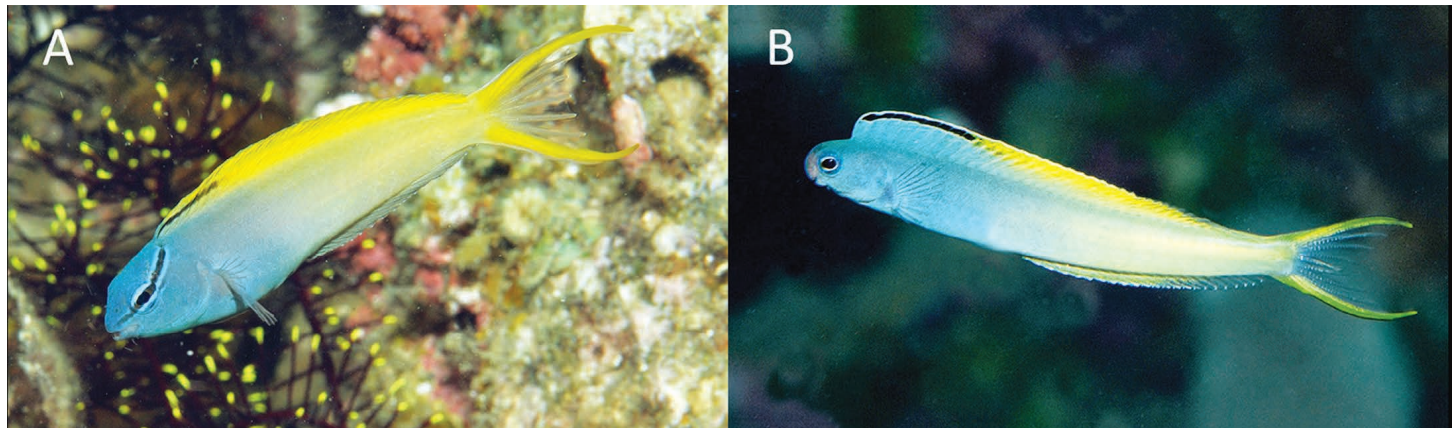


**Figure 7.** Mimetic pair, approx. 40–50 mm SL: A) *Meiacanthus smithi*, Laamu Atoll, Maldives; B) *Plagiotremus phenax*, Mergui Archipelago, Myanmar (G.R. Allen).

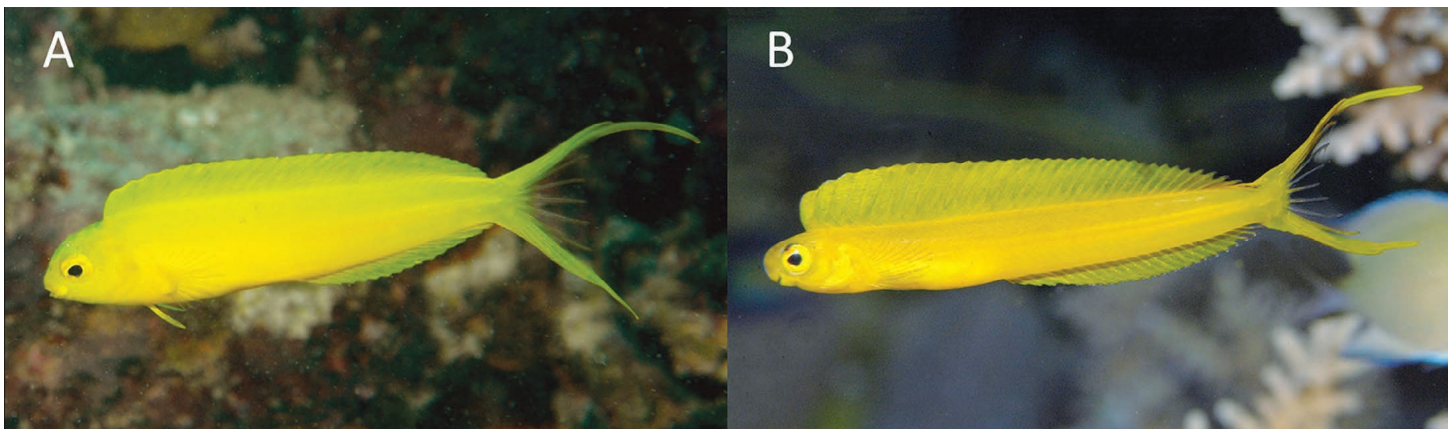
allopatric color morphs of their model *Meiacanthus* (*M. oualanensis* and *M. atrodorsalis*) by Smith-Vaniz (1987)". They furthermore overlooked Smith-Vaniz's (1987: 50) justification for assigning the yellow *Plagiotremus* morph to a subspecies: i.e. the inconsistency of local color patterns. Randall's collection of four Tongan *P. laudandus* (BPBM 30884) included one individual virtually identical to "*P. flavus*" and matching *M. oualanensis*, two others matching local *M. tongaensis*, and one with a narrow black stripe extending the length of the dorsal fin and similar to the color pattern of *M. atrodorsalis* from some other locations. This inconsistency argues that the color pattern-matching of the mimic is somewhat labile and may unevenly match local model color-pattern variations. The argument that because the morphs of the model are species, that it should be transitive for the mimic is untenable. In addition to color pattern differences, all of these *Plagiotremus* species can be distinguished from each other by morphology, except for the *P. laudandus*/*P. flavus* pair (Smith-Vaniz 1976).



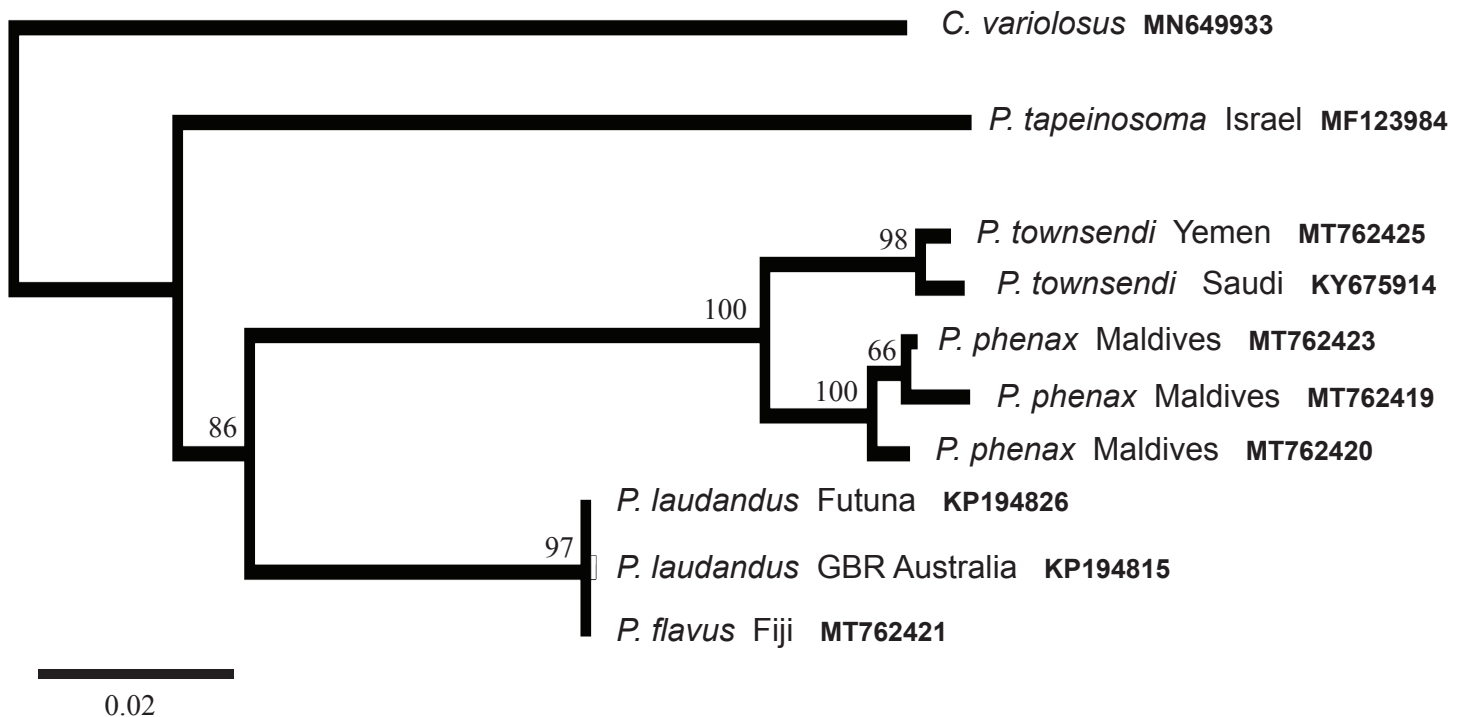
**Figure 8.** Mimetic pair, grey variant, approx. 40–50 mm SL, A) *Meiacanthus atrodorsalis*; B) *Plagiotremus laudandus*, Cenderawasih Bay, West Papua Providence, Indonesia (G.R. Allen).



**Figure 9.** Mimetic pair, approx. 40–50 mm SL, A) *Meiacanthus atrodorsalis*, Anilao Luzon, Philippines; B) *Plagiotremus laudandus*, Atauro Island, Timor Leste (G.R. Allen).



**Figure 10.** Mimetic pair, approx. 40–50 mm SL, A) *Meiacanthus oualanensis*; B) *Plagiotremus laudandus*, Fiji (G.R. Allen).

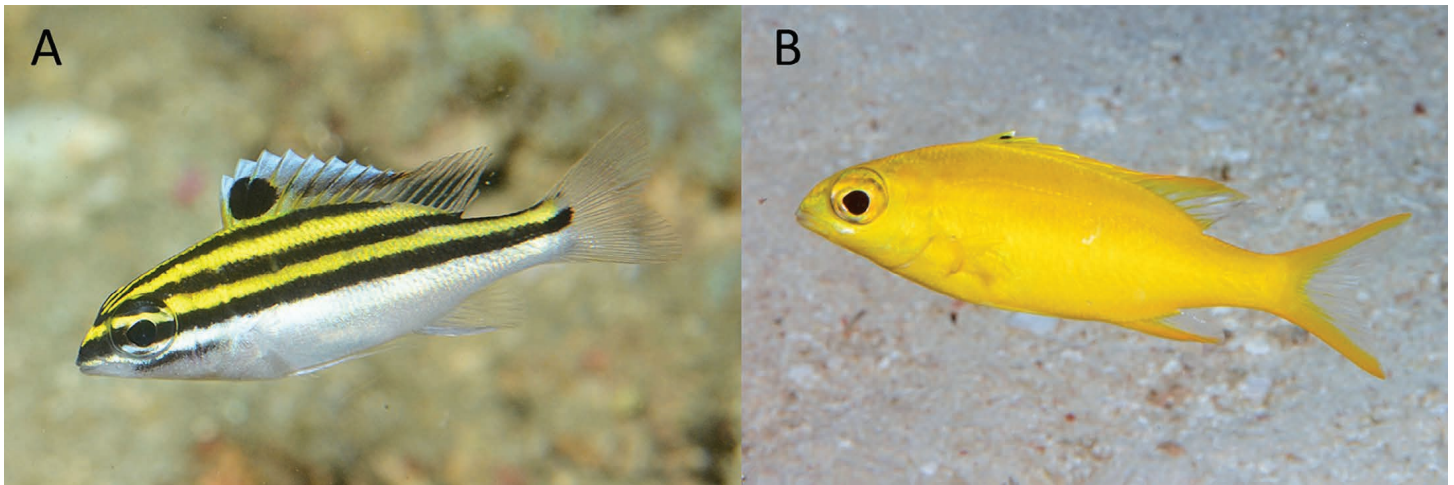


**Figure 11.** The neighbor-joining phenetic tree of COI mtDNA sequences of *Plagiotremus* species following the Kimura two-parameter model (K2P) generated by BOLD (Barcode of Life Database, <http://www.boldsystems.org>). The scale bar at left represents a 2% sequence difference. Collection locations and GenBank accession numbers for specimens are indicated, and *Cirripectes variolosus* is used as an outgroup. Values above branches are bootstrap values generated from a NJ optimal tree with 1000 replicates in MEGA X.

In addition to the basic idea that taxonomic decisions for a species should not depend on unrelated taxa, there is another argument in that mimic species are under strong selection to match a local model, but the model is not. The greater pressure to match a local phenotype would select for flexibility in color-pattern matching and is separate and independent of typical divergent selective forces to ensure reproductive isolation between sibling species. As noted by Moland et al. (2005: 455), “Preliminary data suggest a high degree of phenotypic plasticity in mimetic coloration and little genetic differentiation among different mimics of the same species.” Any apparent flexibility and unclear delineation of particular phenotypes, such as that found in *P. laudandus* in Tonga, suggest that the phenotype does not reflect phylogenetic boundaries. Additional evidence for this phenomenon in *Plagiotremus* is the experimental finding that juvenile *Plagiotremus rhinorhynchos* (Bleeker, 1852) can lose their model coloration when their juvenile models (*L. dimidiatus*) are removed from their vicinity (Moland & Jones 2004).

In the case of *P. laudandus flavus*, there is no difference in the mtDNA COI sequence we obtained for the yellow population, which shares COI haplotypes with two distant populations (100% similarity percentage in the BOLD algorithm with GBR and Australia and Futuna *P. laudandus*; Fig. 11), indicating that gene flow is (or very recently was) occurring between populations. However, analysis of faster-changing markers or microsatellites might reveal finer genetic structuring, if it exists. Shared haplotypes are characteristic of populations making up a single species but are not proof two populations are the same species. The exception would be when phenotypes are consistently different and the boundaries well-defined; in that case two populations sharing haplotypes may represent recently split species and/or established species with some low degree of hybridization. In this case, however, there are many versions of local color patterns matching local models, some overlapping, and inconsistency of the yellow morph. These findings, in combination with shared haplotypes, makes splitting off the Fijian population as a species distinct from the widespread *P. laudandus* unwarranted.





**Figure 12.** *Scolopsis bilineatus* juveniles, approx. 50 mm SL: A) normal variant, Lembah Strait, North Sulawesi, Indonesia; B) yellow variant, Fiji (G.R. Allen).

Another species complex of Batesian mimics of *Meiacanthus* are the monocle breams of *Scolopsis* (Allen et al. 1975, Russell 1975, Russell et al. 1976, Smith-Vaniz et al. 2001, Randall 2005a, 2005b). An all-yellow juvenile variation of *Scolopsis bilineatus* (Bloch, 1793) in Fiji, and the absence of this color morph in juveniles at other locations, is another example of local flexibility in phenotype (Fig. 12). This is especially apparent because the Fijian juveniles lose their yellow coloration when they outgrow the size of their much smaller *Meiacanthus* model.

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## Appendix

Table 1

GenBank accession numbers for specimens in haplotype network for *Aspidontus taeniatus* in Fig. 8

location	source	GenBank COI
Moorea, Society Islands, French Polynesia	Jeff Williams, Smithsonian Institution	KJ967915
Moorea, Society Islands, French Polynesia	Jeff Williams, Smithsonian Institution	KJ967916
Moorea, Society Islands, French Polynesia	Jeff Williams, Smithsonian Institution	KJ967917
Moorea, Society Islands, French Polynesia	Jeff Williams, Smithsonian Institution	KJ967918
Moorea, Society Islands, French Polynesia	Jeff Williams, Smithsonian Institution	KJ967919
Moorea, Society Islands, French Polynesia	Jeff Williams, Smithsonian Institution	KJ967920
Moorea, Society Islands, French Polynesia	Jeff Williams, Smithsonian Institution	KJ967921
Moorea, Society Islands, French Polynesia	Jeff Williams, Smithsonian Institution	KJ967922
Nosy Be, Antananarivo, Madagascar	Nicolas Hubert, Universite de La Réunion	JQ349782
Nosy Be, Antananarivo, Madagascar	Nicolas Hubert, Universite de La Réunion	JQ349783
KwaZulu-Natal, South Africa	Allan Connell, SA Institute for Aquatic Biodiversity	JF492902
Philippines	Dirk Steinke, Centre for Biodiversity Genomics	FJ582891
Eiao, Marquesas Islands, French Polynesia	Jeff Williams, Smithsonian Institution	MK566803
Eiao, Marquesas Islands, French Polynesia	Jeff Williams, Smithsonian Institution	MK566804
Alofi, Futuna, Wallis and Futuna, France	Jeff Williams, Smithsonian Institution	MT762424
St. Gilles, Réunion, France	Nicolas Hubert, Universite de La Réunion	JQ349784
Al Wajh, Saudi Arabia, Red Sea	Joseph DiBattista, Red Sea Research Center	MH331672