FISHES OUT OF WATER: BIOLOGY AND ECOLOGY OF MUDSKIPPERS

CHAPTER TWO

THE NATURAL DISTRIBUTION OF MUDSKIPPERS

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2.1. INTRODUCTION

Oxudercine gobies, the 'mudskippers', are distributed broadly throughout tropical and subtropical coastal habitats of the Indo-West Pacific and the eastern Atlantic (Murdy 1989; Clayton 1993; Fig. 2.1). These fishes live in close association with, or in proximity to, mangrove forests and adjacent mudflats that distinguish global tropical and subtropical coastlines (Hogarth 2001). The distribution of oxudercine gobies is largely coincident with that of modern mangrove habitats except that mudskippers are absent from the western tropical Atlantic and eastern tropical Pacific (Fig. 2.1).

We first summarize the biogeographic regions proposed for mangroves (Duke 1992; Duke et al. 1998; Fig. 2.2) and mudskippers (Murdy 1989; Fig. 2.3). We then present a revised classification of mudskipper areas based on updated distributional and taxonomic data (Fig. 2.4). For example, Murdy (1989) had no scientific collections of mudskippers from Sulawesi; today we have ample data on species of mudskippers collected during the past two decades from that island complex (e.g., Polgar et al. 2014; Parenti et al. 2015), and elsewhere throughout their range.

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An understanding of the biogeography of the mudskippers requires a detailed description of species distributions and a preliminary proposal of their areas of endemism. One of our future goals is a comprehensive comparative biogeographic analysis of mudskippers, mangrove plants and the associated biota of the marine intertidal zone, such as gastropods (e.g., Ozawa et al. 2015). In that analysis we will use phylogenetic and distributional data of the mangrove biota to infer the historical, hierarchical relationships among areas of endemism; a general classification of those areas is expected to identify repeated phylogenetic patterns of the endemic taxa and, therefore, reflect the shared history of components of the mangrove biota (Parenti and Ebach 2009). We defer that analysis until completion of a comprehensive phylogenetic analysis of oxudercine gobies currently underway. Thus, the areas of endemism for mudskippers that we propose, below, are preliminary and await rigorous testing.

2.2. Biogeographic Regions of Mangroves and Mudskippers

Modern mangrove forests are distributed in the littoral zone of tropical and subtropical regions between 30° N and 30° S latitude and are restricted largely to climates with an average monthly minimum air temperature of 20° C (Duke 1992; Ellison et. al. 1999; Giri et al. 2010). Mangrove forests extend farther south in eastern South America, Australia and the North Island of New Zealand, likely as relict populations of once broader distributions (Duke 1992).

Modern mangrove floristic communities are classified in six biogeographic regions: 1) western America and eastern Pacific; 2) eastern America, including the Caribbean and parts of the Gulf of Mexico; 3) west Africa; 4) east Africa and Madagascar; 5) Indo-Malesia, including Asia; and 6) Australasia and the western Pacific (Duke 1992: fig. 1; Fig. 2.2). These divisions are based on presence/absence data for sixty-nine species of mangrove plants classified in twenty-

seven genera and twenty-one families (Duke 1992: table 3). Just one species, the widespread fern *Acrostichum aureum,* lives in all six biogeographic regions. There is otherwise no overlap of native species between what Duke (1992) recognized as two global biogeographic hemispheres: the Atlantic East Pacific (AEP) comprising the first three biogeographic regions including eleven native mangrove plant species in seven genera; and the Indo-West Pacific (IWP) comprising the latter three biogeographic regions with fifty-eight native mangrove plant species in twenty-three genera. Although Duke (1992) was not explicit about how he delimited the six regions, those numbered 1, 2, 5 and 6 have at least one endemic species each, whereas regions 3 and 4 have no endemics and share species with the other areas in their own global biogeographic hemisphere.

Mudskippers are distributed in seven, disjunct divisions: 1) West Africa; 2) East Africa; 3) Arabian Gulf; 4) Indo-Malaya; 5) Australia/New Guinea; 6) China Sea; and 7) Oceania, according to Murdy (1989: fig. 98; Fig. 2.3). These mudskipper divisions differ from those proposed for mangrove forests in several ways. First, of course, they do not include the modern mangrove regions of the western Americas and eastern Pacific or eastern Americas and the Caribbean in which there are no oxudercine gobies. Also the ‘East Africa’ and ‘Arabian Gulf’ divisions of Murdy (1989) together equal the ‘east Africa’ region of Duke (1992) and Duke et al. (1998). Although Duke (1992) and Duke et al. (1998) included much of Asia in their ‘Indo-Malesia’ region, Murdy (1989) treated these as two separate areas: ‘Indo-Malaya’ and ‘China Sea’.

Further, Duke (1992) and Duke et al. (1998) included the western Pacific, as well as the island of Maluku, in their ‘Australasia’. In contrast, Murdy (1989) considered these to be two separate areas ‘Australia/New Guinea’ and ‘Oceania’ — and included the Moluccas (presumably the islands of Maluku and northern Maluku) in the former. The Philippine Islands and the

Indonesian island of Timor are part of the ‘Indo-Malesia and Asia’ region of Duke et al. (1998) but in the ‘Australia/New Guinea’ division of Murdy (1989).

Many species of mudskippers and mangroves have restricted distributions and are endemic to the proposed biogeographic regions. Presence of at least one endemic taxon is needed to recognize an area as biogeographically distinct (Humphries and Parenti 1986) and at least two endemic taxa to make the area potentially informative in a comparative biogeographic analysis (see Harold and Mooi 1994; Parenti and Ebach 2009). Murdy (1989: 74) claimed that he recognized his “seven divisional associations…based on maximal endemism…” yet, as with the regions for mangroves, two of his mudskipper areas, ‘East Africa’ and ‘Oceania’ have no endemic species. We summarize the distribution of mudskippers to support our preliminary, revised proposal of areas of endemism in which each area has at least one endemic taxon and the areas are allopatric (Fig. 2.4).

2.3. Distribution of Oxudercine Goby Genera and Species

We currently recognize forty-three valid species of oxudercine gobies classified in ten genera (Jaafar et al. 2016; Polgar et al. 2013; Jaafar and Larson 2008; Murdy 1989; Table 2.1; Fig. 2.5). We reconfirmed identification of most of the specimens examined by Murdy (1989) and added data on oxudercine species described since 1989 (Jaafar et al. 2016; Polgar et al. 2014; Polgar et al. 2013; Jaafar et al. 2009; Jaafar and Larson 2008; Larson and Takita 2004; Darumas and Tantichodok 2002; Murdy and Takita 1999; Lee et al. 1995).

Periophthalmus is the most speciose genus, with nineteen species, and is also the most widely distributed, ranging from the Gulf of Guinea eastward to Samoa (Jaafar and Larson 2008). For clarity, we illustrate the distribution limits of the species of *Periophthalmus* in a series

of maps (Figs. 2.6–2.11). A single species, *Periophthalmus barbarus*, lives on the tropical west coast of Africa and volcanic islands in the Gulf of Guinea (Fig. 2.6). The remaining eighteen species in the genus live throughout the Indo-West Pacific from east Africa to the western margin of the Pacific Plate (Springer 1982; Figs. 2.6–2.11). Their distribution is coincident with that of *Ps. argentilineatus*, the most widely distributed species of mudskipper (Fig. 2.7). A second widespread species, *Ps. kalolo*, is distributed from eastern Africa to Tonga, but does not live in the Arabian or East China seas (Fig. 2.6). These are the only two species of mudskipper that live in the southwestern Indian Ocean.

Widespread species are uninformative for cladistic biogeographic analysis (Nelson and Platnick 1981). But Gill and Kemp (2002) noted that many presumed widespread species of fishes throughout the Indo-West Pacific may simply represent an artifact of poor taxonomic understanding or practice. To investigate the phylogeography of these two widespread species, Polgar et al. (2014) collected samples of *Ps. argentilineatus* and *Ps. kalolo* from twelve localities in the South China Sea, northern Sulawesi and the southwestern Indian Ocean. Based on an analysis of molecular sequence data from two mitochondrial genes (D-loop and 16*S* rDNA) and one nuclear gene (*rag1*), they recognized three distinct molecular lineages of *Ps. argentilineatus*, one from the southwestern Indian Ocean which was sister to a second from northern Sulawesi and a third from northern Sulawesi which was sister to samples of *Ps. kalolo* from the southwestern Indian Ocean and northern Sulawesi; also, they found only shallow genetic differentiation between samples of *Ps. kalolo* from the southwestern Indian Ocean and northern Sulawesi (Fig. 2.5). Although preliminary, this study is significant for our proposal of areas of endemism because it provides the only evidence for an endemic oxudercine lineage, which could be recognized at the species level, from the southwestern Indian Ocean.

A single species of *Periophthalmus*, *Ps. waltoni,* lives in "…mudflat areas from the Arabian Gulf to Pakistan" (Murdy 1989: 44; Fig. 2.9). The remaining fifteen species of *Periophthalmus* all live east of the southern tip of India. They have restricted, yet highly overlapping distributions (Figs. 2.6–2.11).

The nine remaining oxudercine genera each have fewer species and smaller ranges, yet exhibit a high degree of endemism and allopatry which makes them ideal for a cladistic biogeographic analysis (Figs 2.12–2.20). Two of these genera, *Scartelaos* (Fig. 2.12) and *Boleophthalmus* (Fig. 2.13), each have a single species ranging from the Arabian Gulf to Pakistan or India (Table 2.1), respectively. The remaining oxudercine species live east of the southern tip of India. Two genera, *Apocryptes* (Fig. 2.14) and *Zappa* (Fig. 2.15), are each monotypic. Three genera – *Oxuderces* (Fig. 2.16), *Parapocryptes* (Fig. 2.17) and *Pseudapocryptes* (Fig. 2.18) – comprise two species each. *Apocryptodon* (Fig. 2.19), and *Periophthalmodon* (Fig. 2.20) comprise three species each, whereas *Scartelaos* comprises four species (Fig. 2.12), and *Boleophthalmus* comprises six species (Fig. 2.13).

2.3.1. Oxudercine Goby Areas of Endemism

We recognize eight oxudercine-goby areas of endemism, as defined below (see Fig. 2.4): 1) Tropical Eastern Atlantic Ocean; 2) Southwestern Indian Ocean; 3) Arabian Sea; 4) Bay of Bengal; 5) South China Sea; 6) East China Sea; 7) Banda Sea; and 8) Oceania. Thirty of forty-three species of oxudercines live in only one area (see maps above, and Table 2.1). We assign these areas names of oceans and seas, rather than land masses, because the distributions span oceans, not continents (see Parenti 1991, on sicydiine goby distribution). Equally important, the larvae of mudskippers, and many other gobies, are passively carried out to sea where they live as

plankton for some 50 days prior to their transformation and ultimate return to the mangrove/mudflat adult habitats (Maeda and Tachihara 2014; Kobayashi et al. 1972). Therefore, the natural range of each species comprises the distribution of larvae as well as adults although the larval distribution of most gobies is unknown. Names and ranks of areas will be reconciled with others broadly in use, following the protocols of the International Code of Area Nomenclature (ICAN) (Ebach et al., 2008) when we test the areas.

2.3.1.1. Tropical Eastern Atlantic Ocean

This area comprises the western African coast from Morocco to Angola and the volcanic islands of Cape Verdes, Sáo Tomé, Principe and Ascension. Just one species of mudskipper, the endemic *Ps. barbarus*, lives in this area.

The islands of St. Helena and Ascension form their own province in the Tropical Atlantic realm in the classification of marine ecoregions by Spalding et al. (2007). Seventy-one species of nearshore fishes were reported from Ascension Island, collected on SCUBA up to a depth of 60 m (Lubbock 1980) but *Ps. barbarus* is not on the list. We examined a single collection of *Ps. barbarus* from Ascension Island, fifteen specimens in the Museum of Comparative Zoology (MCZ 13307), collected by Waldren in the mid-1880s. We consider the locality information dubious because mangrove areas, and other suitable habitats for *Ps. barbarus*, have never been identified as a component of the littoral ecosystem of this isolated volcanic island (Price and John 1980).

The Tropical Eastern Atlantic Ocean is equivalent to the ‘West Africa’ division of Murdy (1989: 74) and ‘Western Africa’ of Duke et al. (1998). It comprises the West African Transition and Gulf of Guinea provinces in the classification of marine ecoregions by Spalding et al.

(2007).

2.3.1.2. Southwestern Indian Ocean

This area comprises the east coast of the African continent south of the Red Sea, coastal habitats at the mouth of the Gulf of Aden, the Mozambique Channel, and the coasts of Madagascar and nearby islands.

Two widespread species of mudskippers, *Periophthalmus argentilineatus* and *Periophthalmus kalolo,* live in this area. There is molecular evidence, as described above, that the populations of *Periophthalmus argentilineatus* in this area represent a distinct lineage.

This area falls within the larger 'Eastern Africa and Madagascar' region of Duke et al. (1998) and is similar to the 'East Africa' division (southern Red Sea to South Africa) of Murdy (1989: 74).

2.3.1.3. Arabian Sea

This area comprises the Arabian Sea, including the Gulf of Khambhat, the Gulf of Kutch, and coastal areas at the mouth of the Gulf of Oman. Six species of oxudercines in three genera live in this area: *B. boddarti*, *B. dussumieri*, *Ps. argentilineatus*, *Ps. waltoni*, *S. histophorus*, and *S. tenuis*. Three of the six species are endemic: *Ps. waltoni*, *B. dussumieri*, and *S. tenuis*. The gulfs of Khambhat and Kutch, along the western coast of the Indian subcontinent, may be the westernmost limit of the distributions of *B. boddarti* and *S. histophorus*, respectively. This area is included within the larger 'Eastern Africa and Madagascar' region of Duke et al. (1998) and mirrors the 'Arabian Gulf' division of (Murdy 1989: 74) which he defined as ranging from Iraq to Bombay (present day Mumbai).

2.3.1.4. Bay of Bengal

This area comprises the Bay of Bengal, Laccadive Sea, and Andaman Sea, and the islands within these water bodies. Fourteen species of oxudercines in nine genera live in this area: *As. bato, An. madurensis, B. boddarti, O. nexipinnis, Pa. rictuosus, Pn. schlosseri, Pn. septemradiatus, Ps. argentilineatus, Ps. kalolo, Ps. novemradiatus, Ps. walailakae, Pd. elongatus, S. cantoris,* and *S. histophorus*. Four of these species are endemic to the Bay of Bengal: *As. bato*, *Pa. rictuosus*, *Ps. novemradiatus*, and *S. cantoris*.

The Bay of Bengal area falls within both the larger 'Indo-Malesia and Asia' region of Duke et al. (1998) and the 'Indo-Malaya' division of Murdy (1989: 74), the latter defined as areas on the "west coast of India to Borneo, including Java and Vietnam". Murdy (1989) considered that the areas on the western coast of India south of Bombay likely lack suitable oxudercine habitats. Eggert (1935) named a subspecies *Periophthalmus vulgaris ceylonensis* based on specimens collected from Galle, Sri Lanka. Murdy (1989: 36) reported specimens of *Ps. chrysospilos* from Madras, on the east coast of India, but these were re-identified as *Ps. walailakae* by G. Polgar (*pers. comm.*). Murdy (1989) also reported *O. dentatus* from India; Jaafar and Parenti (2016) reclassified these specimens as *O. nexipinnis*.

2.3.1.5. South China Sea

This area comprises the Straits of Malacca, western South China Sea (including the gulfs of Thailand and Tonkin), Java Sea, and includes coastal areas of the islands of Sumatra, Java, and Borneo. Eighteen oxudercine species in eight genera live in this area: *An. madurensis, B. boddarti, B.* cf. *pectinirostris, O. nexipinnis, Pa. serperaster, Pn. schlosseri, Pn. septemradiatus,*

Ps. argentilineatus, *Ps. chrysospilos*, *Ps. gracilis*, *Ps. kalolo*, *Ps. minutus*, *Ps. spilotus*, *Ps. variabilis*, *Ps. walailakae*, *Pd. borneensis*, *Pd. elongatus*, and *S. histophorus*. Five of these species are endemic: *B.* cf. *pectinirostris*, *Ps. chrysospilos*, *Ps. spilotus*, *Ps. variabilis*, and *Pd. borneensis*.

The South China Sea area falls within the larger 'Indo-Malesia and Asia' region of Duke et al. (1998) and 'Indo-Malaya' division of Murdy (1989: 74). The specimens identified as *B. pectinirostris* by Polgar and Bartolino (2010) and Polgar et al. (2013) likely represent an undescribed species, and are here included as *B.* cf. *pectinirostris* (see Zhang et al. 2015). Murdy (1989) reported *O. dentatus*, which Jaafar and Parenti (2016) reclassified as *O. nexipinnis*.

2.3.1.6. East China Sea

This area spans the East China Sea north of the Gulf of Tonkin and includes the Yellow Sea, the Sea of Japan, and the Taiwan Strait. The East China Sea is also an area of relatively high endemism. Six of the nine species of oxudercines that live in this area are endemic: *An. punctatus*, *B. pectinirostris*, *O. dentatus*, *Ps. magnuspinnatus*, *Ps. modestus*, and *S. gigas*. The East China Sea also represents the northern limit of three widely distributed species: *Pa. serperaster*, *Ps. argentilineatus*, and *S. histophorus*. This area falls within the larger 'Indo-Malesia and Asia' region of Duke et al. (1998) and mirrors the 'China Sea' (China and Taiwan northward to Southern Korea and Japan) division of Murdy (1989:75).

2.3.1.7. Banda Sea

This area ranges comprises the Philippine Sea, Luzon Sea (eastern South China Sea), Sibuyan Sea, Sulu Sea, Visayan Sea, Bohol Sea, Celebes Sea, Banda Sea, Flores Sea, Molucca

Sea, western Ceram Sea, Halmahera Sea, and Savu Sea. Ten species of oxudercines in five genera live in the area: *An. madurensis, B. boddarti, Pn. freycineti, Ps. argentilineatus, Ps. gracilis, Ps. kalolo, Ps. malaccensis, Ps. minutus, Ps. pusing* and *S. histophorus*. Two species, *Ps. malaccensis* and *Ps. pusing*, are endemic.

The Banda Sea area falls within the larger 'Indo-Malesia and Asia' and 'Australasia' regions of Duke et al. (1998); the island of Maluku, but not North Maluku, was included in the Australasia region. In contrast, Murdy (1989: 74) considered the Banda Sea as part of the 'Australia/New Guinea' division. His decision to include the Philippines, Timor, and Moluccas, in the 'Australia/New Guinea' division stemmed from the distribution of *Ps. malaccensis* (Fig. 11) and *Pn. freycineti* (Fig. 20). Murdy (1989) further supported this hypothesis citing Vari (1978) who showed that the terapon perches, family Terapontidae, are distributed in the Philippines, Sulawesi, New Guinea, and Australia. In 1989, no scientific collections of mudskippers were known from Sulawesi, therefore, Murdy (1989: 74) did not assign that island complex to any biogeographic area. We examined the specimen that Murdy (1989) identified as *Ps. novemradiatus* from the Philippines, and re-identified it as *Ps. malaccensis*.

2.3.1.8. Oceania

This broad area comprises the Arafura Sea (including the Gulf of Carpentaria and the Torres Straits), Timor Sea, Gulf of Papua, Cendrawasih Bay, Philippine Sea, Bismarck Sea, Solomon Sea, and the Coral Sea east to 175° W from the western margin of the Pacific Plate to Samoa (Springer 1982; Murdy 1989). Sixteen oxudercine species in six genera live in this area: *An. madurensis, An. wirzi, B. birdsongi, B. caeruleomaculatus, B. poti, Pn. freycineti, Ps. argentilineatus, Ps. darwini, Ps. gracilis, Ps. kalolo, Ps. minutus, Ps. novaeguineaensis, Ps.*

takita, *Ps. weberi*, *S. histophorus*, and *Z. confluentus*. Nine of these species are endemic to this area, the highest number of endemic species of oxudercine gobies in any area. The endemic species are: *An. wirzi*, *B. birdsongi*, *B. caeruleomaculatus*, *B. poti*, *Ps. darwini*, *Ps. novaeguineaensis*, *Ps. takita*, *Ps. weberi*, and *Z. confluentus*.

For mangrove forests, Duke et al. (1998) defined the 'Australasia' region as the area east of New Guinea and Australia that encompasses areas in the western Pacific Ocean, such as the island of Maluku. Murdy (1989) included the Philippine islands, the Moluccas islands, and the island of Timor in his 'Australia/New Guinea' division. The species Murdy (1989) reported as *O. wirzi* was reclassified in *Apocryptodon* by Jaafar and Parenti (2016). Murdy (1989) also recognized a separate Oceania, from the western margin of the Pacific Plate eastward to Samoa, but the two oxudercine species in this area, *Ps. argentilineatus* and *Ps. kalolo* are widespread and not endemic. We have no basis for recognizing this as a separate area of endemism for oxudercines and thus preliminarily combine two areas recognized by Murdy (1989), his Oceania and Australia/New Guinea, into one large area: Oceania.

2.3.2. Distributional Gradients

The broad scale patterns of species distribution of oxudercine gobies mirror those of mangrove plant communities, with species diversity higher in the Indo-West Pacific Ocean than in the Atlantic Ocean (Fig. 2.1). Collectively, mangrove plants display a unimodal distribution pattern as their diversity decreases to the east and to the west of Southeast Asia (Ellison et al. 1999). The number of species of mangrove plants is highest in Southeast Asia (Indo-Malesia and Asia region), in which there are thirty species and lowest in the Caribbean in which there are fewer than five species (Ellison et. al. 1999). In contrast, oxudercine gobies display a bimodal

species richness distribution pattern, with peaks in the South China Sea (eighteen species) and in the Oceania (sixteen species). The Banda Sea area lies between these two species rich areas, and is home to ten species of mudskippers. In contrast to the South China Sea and Oceania, the Banda Sea area is relatively poorly sampled and studied. Further exploration throughout the Philippines, East and West Nusa Tenggara, Sulawesi, Timor, and the Moluccas Islands, is expected to lead to discovery of more species in the Banda Sea area and, consequently, alter our understanding of the broad species distribution patterns of oxudercine gobies.

Longitudinal variation is observed in many tropical marine taxa; species richness is generally lower in the Atlantic and eastern Pacific oceans when compared to the Indo-West Pacific (Hoeksema 2007; Carpenter and Springer, 2005; Paulay 1997). The disjunct distribution of *Periophthalmus* – with one or more species in the Tropical Eastern Atlantic and congeners in the Indo-Pacific – is also observed in other tropical marine teleost genera: *Drepane* (Springer 1982: 40), *Grammoplites* (Springer 1982: 71), *Lethrinus* (Springer 1982: 40), *Monodactylus* (Springer 1982: 61) and *Psettodes* (Springer 1982: 81). The generality of this disjunct distribution will be explored in our larger study of the historical biogeography of mudskippers and the associated mangrove biota.

2.4. SUMMARY

Oxudercine gobies are distributed throughout tropical and subtropical coastal areas of the Indo-West Pacific and the eastern Atlantic. We recognize eight distinct oxudercine goby areas, each with at least one endemic species: Tropical Eastern Atlantic Ocean (one species), southwestern Indian Ocean (two species), Arabian Sea (six species), Bay of Bengal (fourteen species), South China Sea (eighteen species), East China Sea (nine species), Banda Sea (ten

species), and Oceania (sixteen species). Oxudercine gobies exhibit a bimodal distribution pattern with highest species diversity in the South China Sea and Oceania. Latitudinal variation is also observed; two subtropical communities, Arabian Sea and East China Sea, include fewer species than adjacent tropical communities.

Thirty of forty-three oxudercine species are endemic to a single area. The highest number of endemic species is in Oceania (nine species). *Periophthalmus argentilineatus* is the most widely distributed species; it is absent only from the Tropical Eastern Atlantic Ocean. Using molecular data, Polgar et al. (2014) recognized three distinct populations within the widespread *Periophthalmus argentilineatus*, which may be recognized at the species level. Thus, these areas will likely be revised further as more data become available. Oxudercine gobies are under-collected, hence under-represented in natural history museum collections globally. There is a paucity of data from many areas. Future investigations into poorly sampled areas and peripheral areas of biogeographic areas, along with fine-scale differentiation of populations, will further our understanding of the distribution patterns of oxudercine gobies and the extent of their endemism.

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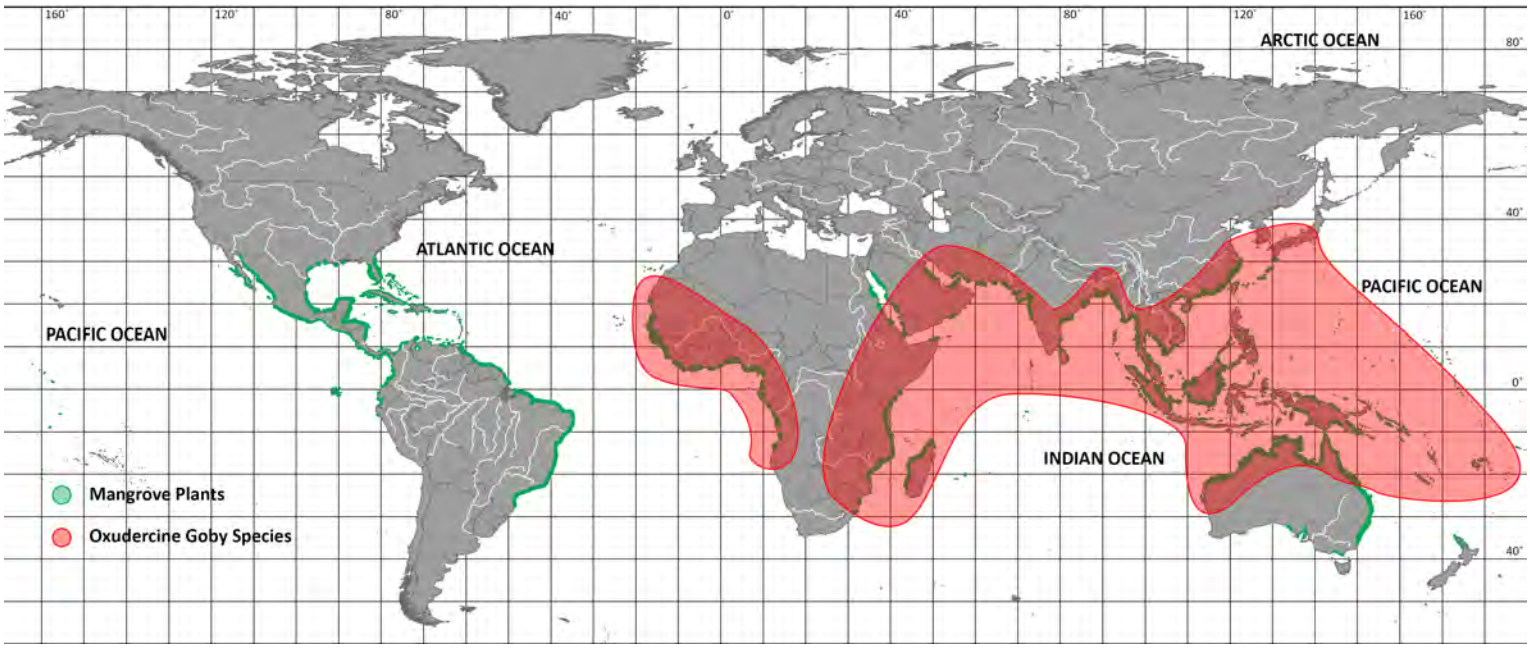
160°
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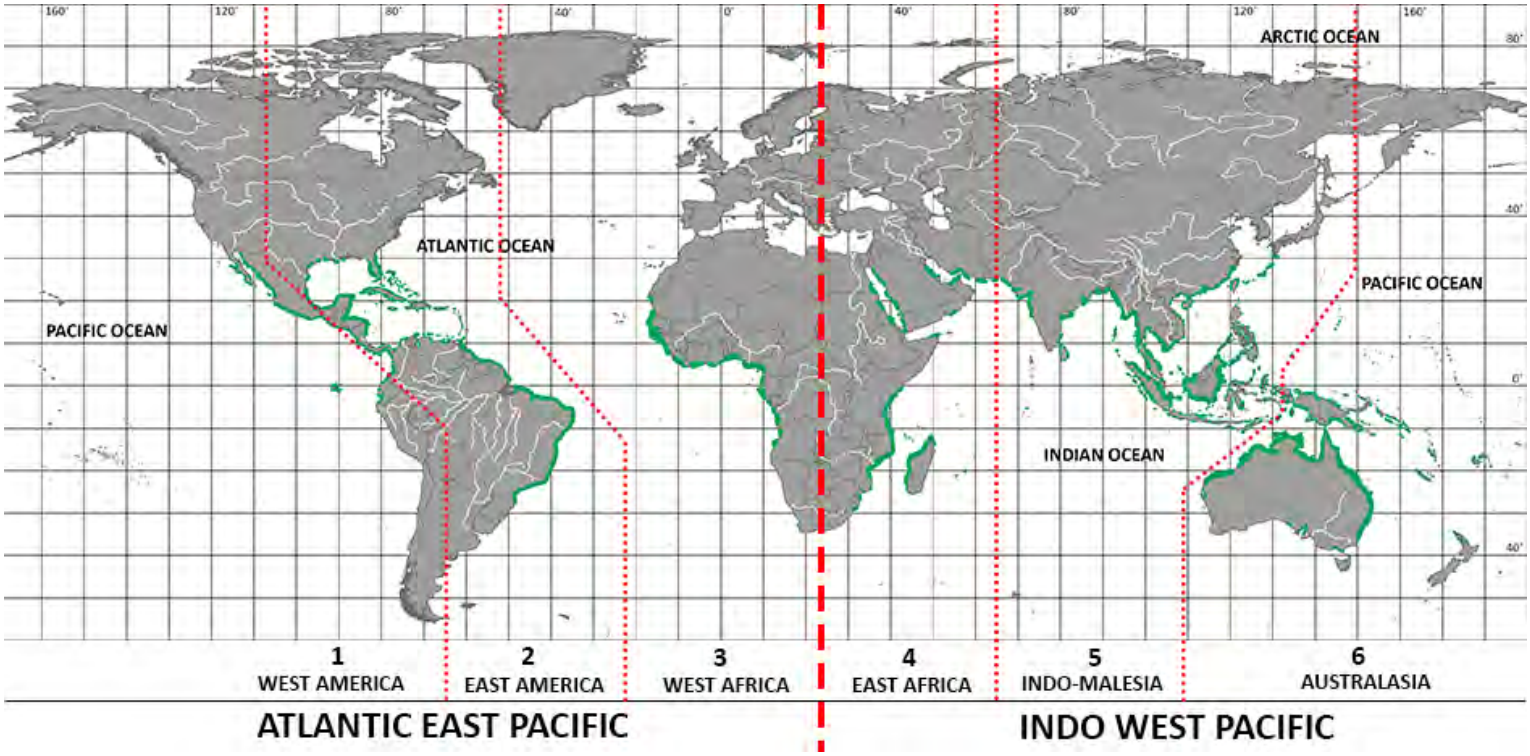
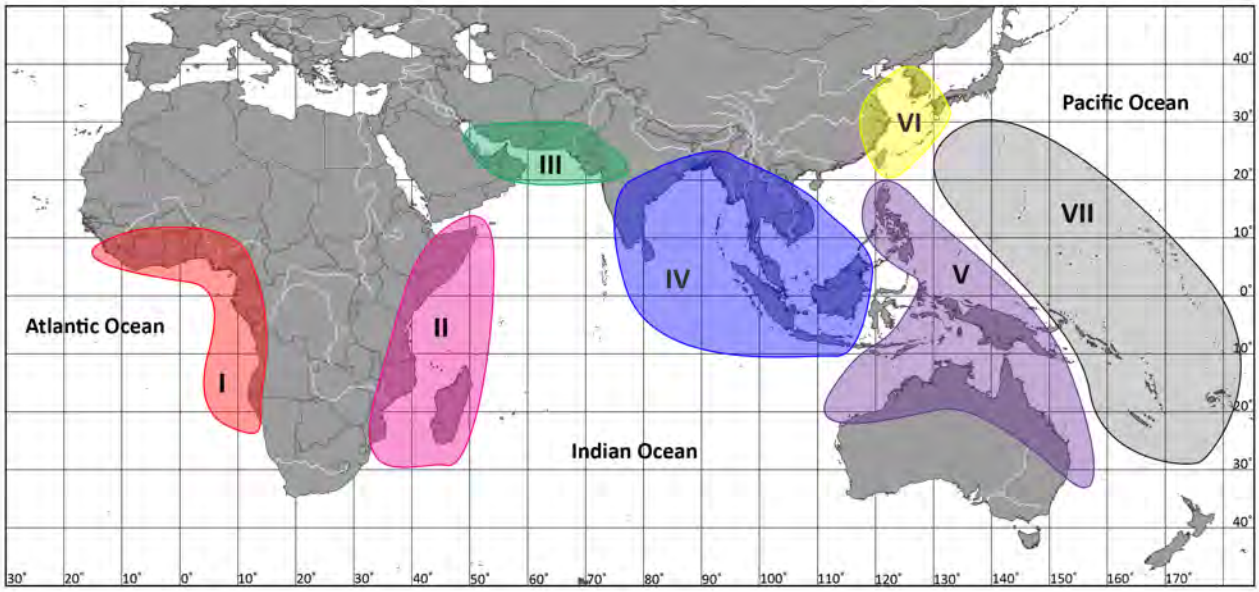
ARCTIC OCEAN
ATLANTIC OCEAN
PACIFIC OCEAN
PACIFIC OCEAN
INDIAN OCEAN
Mangrove Plants
Oxudercine Goby Species


ARCTIC OCEAN
ATLANTIC OCEAN
PACIFIC OCEAN
PACIFIC OCEAN
INDIAN OCEAN
1
WEST AMERICA
2
EAST AMERICA
3
WEST AFRICA
4
EAST AFRICA
5
INDO-MALESIA
6
AUSTRALASIA
ATLANTIC EAST PACIFIC
INDO WEST PACIFIC


Pacific Ocean
Atlantic Ocean
Indian Ocean
I
II
III
IV
V
VI
VII
40°
30°
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10°
0°
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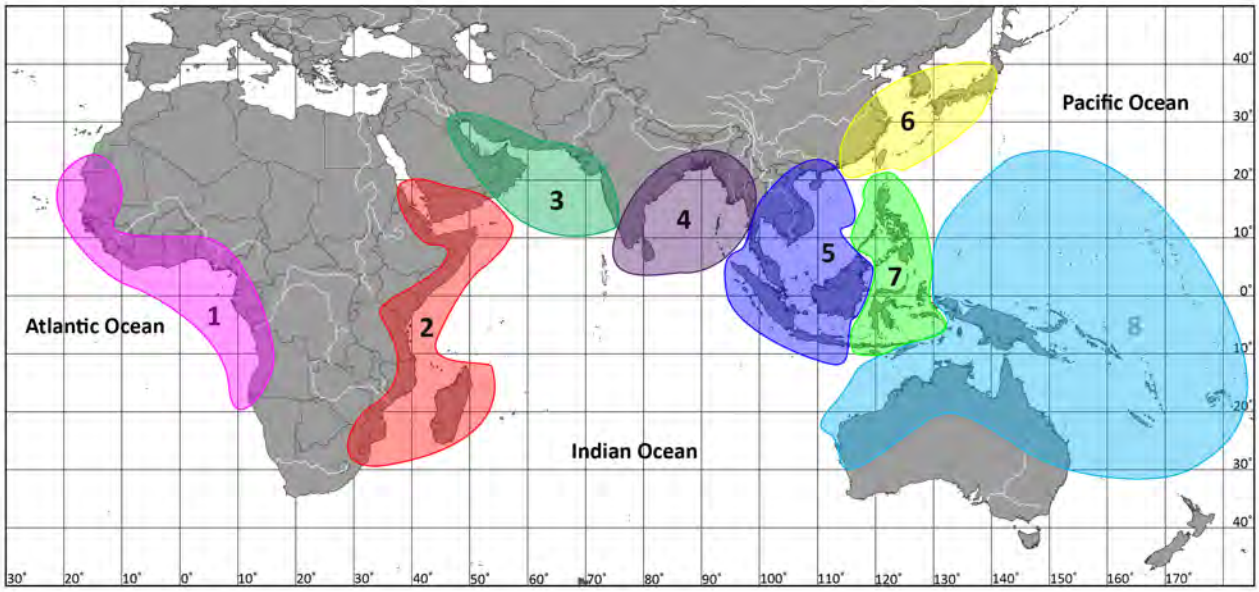
Pacific Ocean
Atlantic Ocean
Indian Ocean
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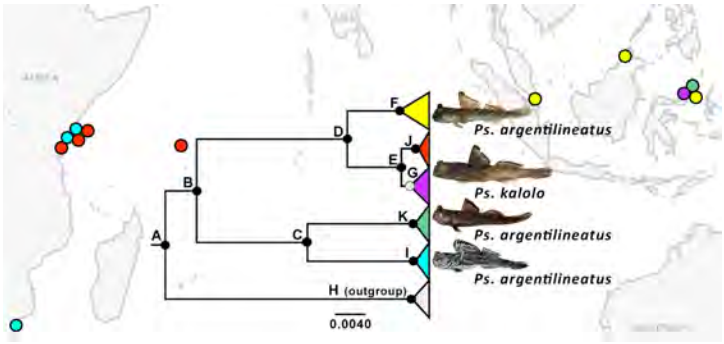
F
D
J
E
G
L
B
K
A
C
I
H (outgroup)
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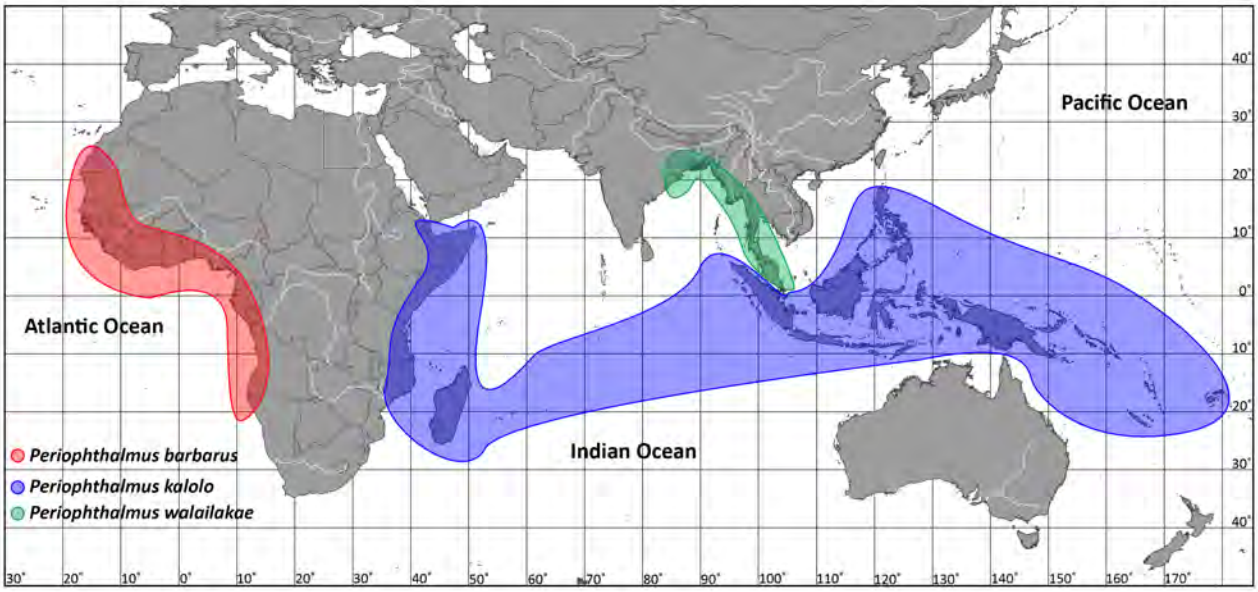
Ps. argentilineatus
Ps. kalolo
Ps. argentilineatus
Ps. argentilineatus


Pacific Ocean
Atlantic Ocean
Indian Ocean
Periophthalmus barbarus
Periophthalmus kalolo
Periophthalmus walailakae
40°
30°
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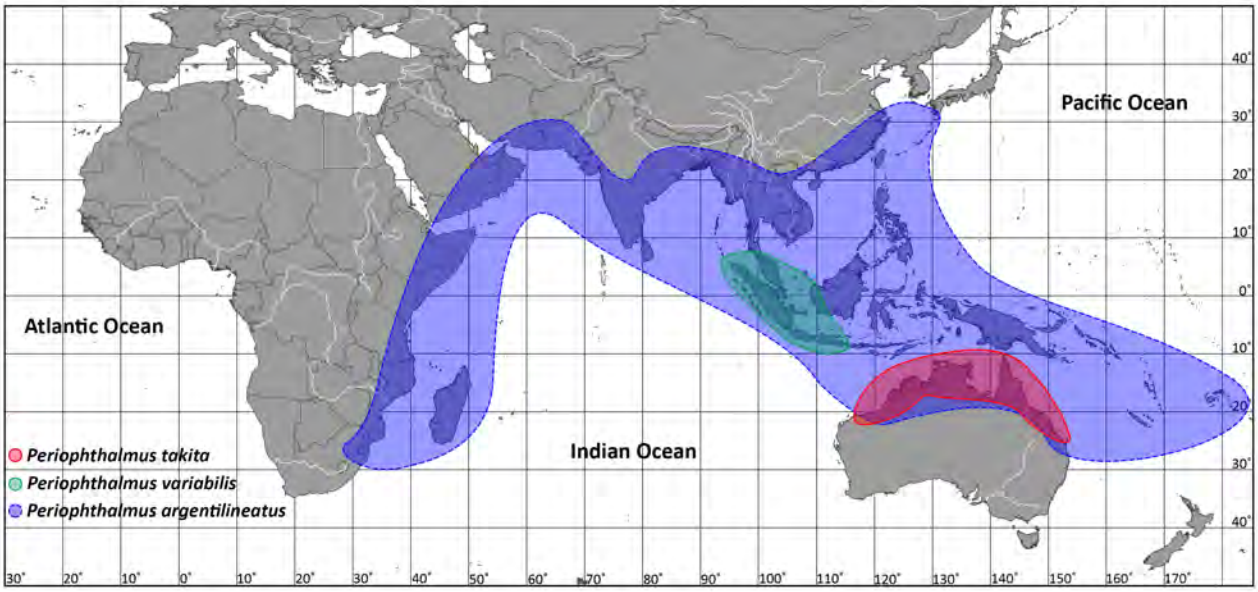
Pacific Ocean
Atlantic Ocean
Indian Ocean
Periophthalmus takita
Periophthalmus variabilis
Periophthalmus argentilineatus
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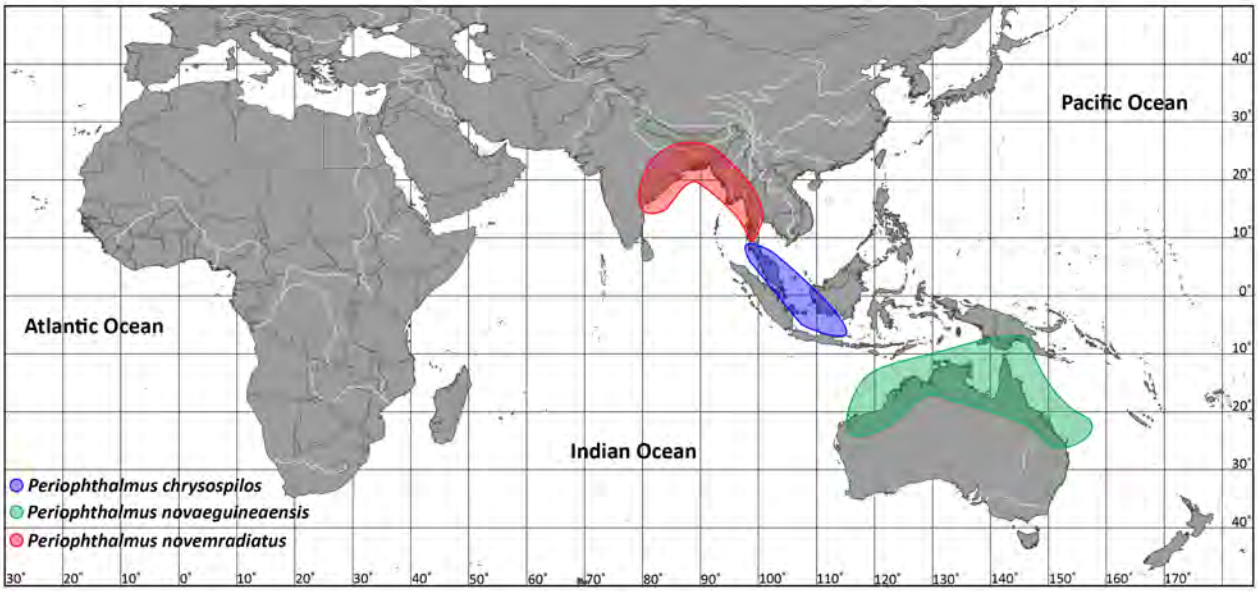
Pacific Ocean
Atlantic Ocean
Indian Ocean
Periophthalmus chrysospilos
Periophthalmus novaeguineaensis
Periophthalmus novemradiatus
40˚
30˚
20˚
10˚
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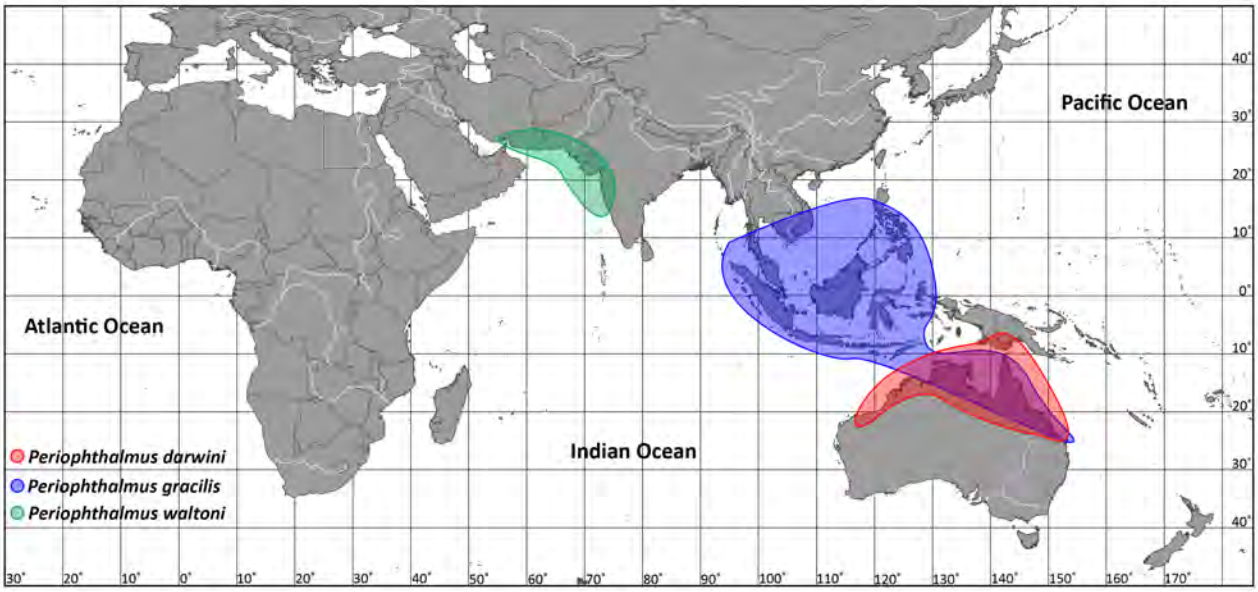
40˚
30˚ 20˚ 10˚ 0˚ 10˚ 20˚ 30˚ 40˚ 50˚ 60˚ 70˚ 80˚ 90˚ 100˚ 110˚ 120˚ 130˚ 140˚ 150˚ 160˚ 170˚


Pacific Ocean
Atlantic Ocean
Indian Ocean
Periophthalmus darwini
Periophthalmus gracilis
Periophthalmus waltoni
40˚
30˚
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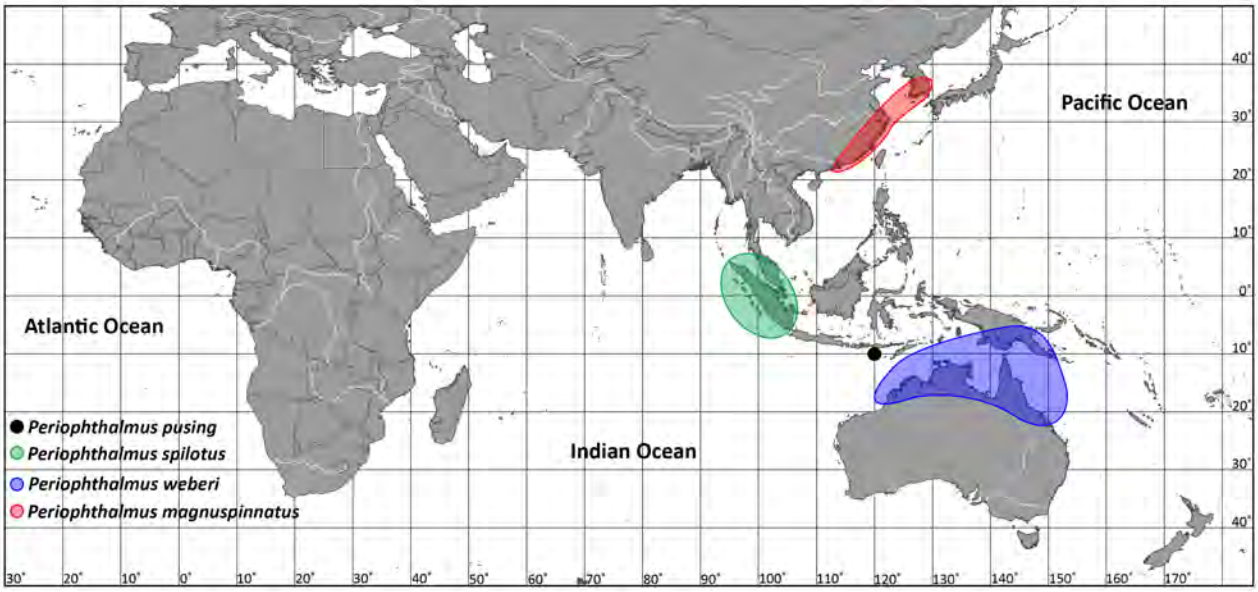
Pacific Ocean
Atlantic Ocean
Indian Ocean
Periophthalmus pusing
Periophthalmus spilotus
Periophthalmus weberi
Periophthalmus magnuspinnatus
40°
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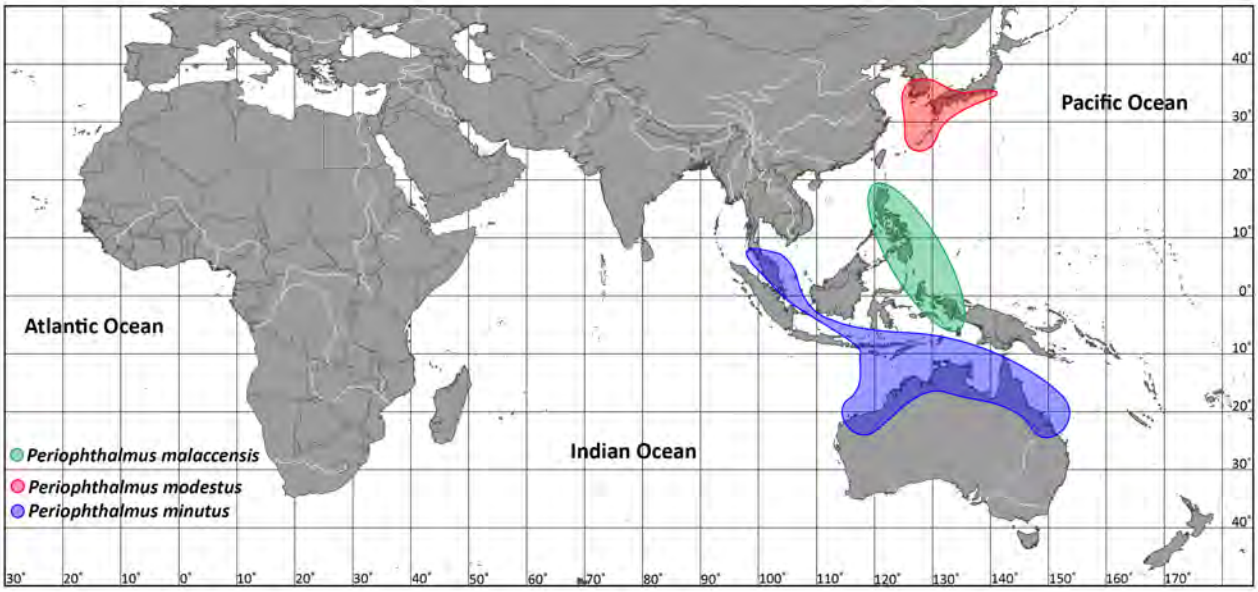
Pacific Ocean
Atlantic Ocean
Indian Ocean
Periophthalmus malaccensis
Periophthalmus modestus
Periophthalmus minutus
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30°
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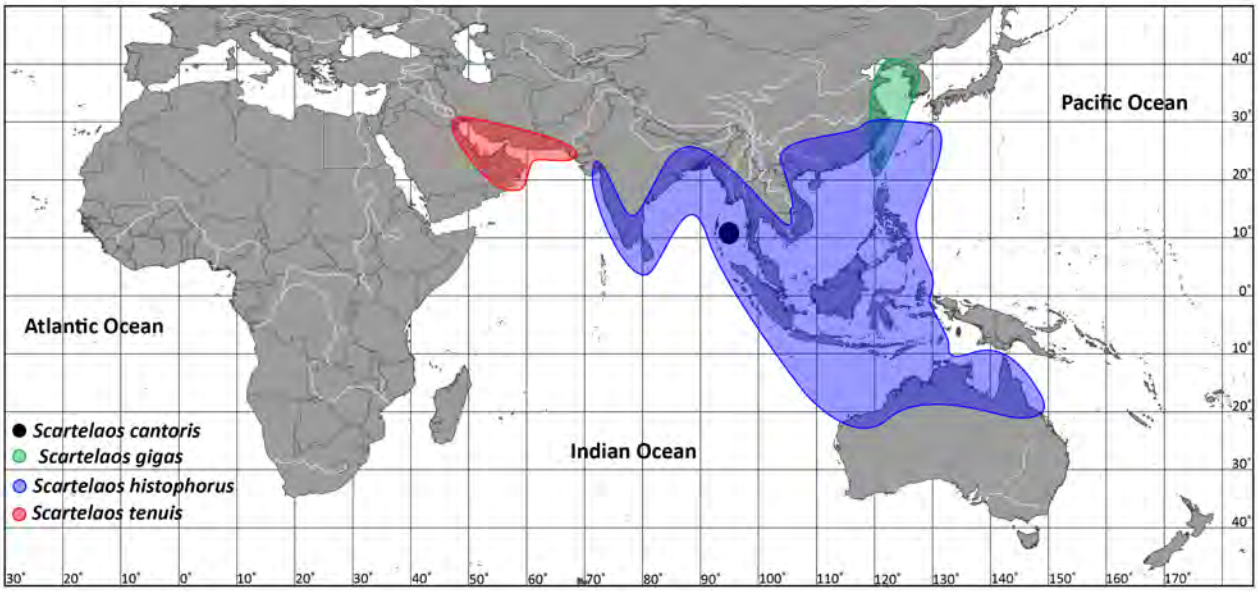
Pacific Ocean
Atlantic Ocean
Indian Ocean
Scartelaos cantoris
Scartelaos gigas
Scartelaos histophorus
Scartelaos tenuis
40°
30°
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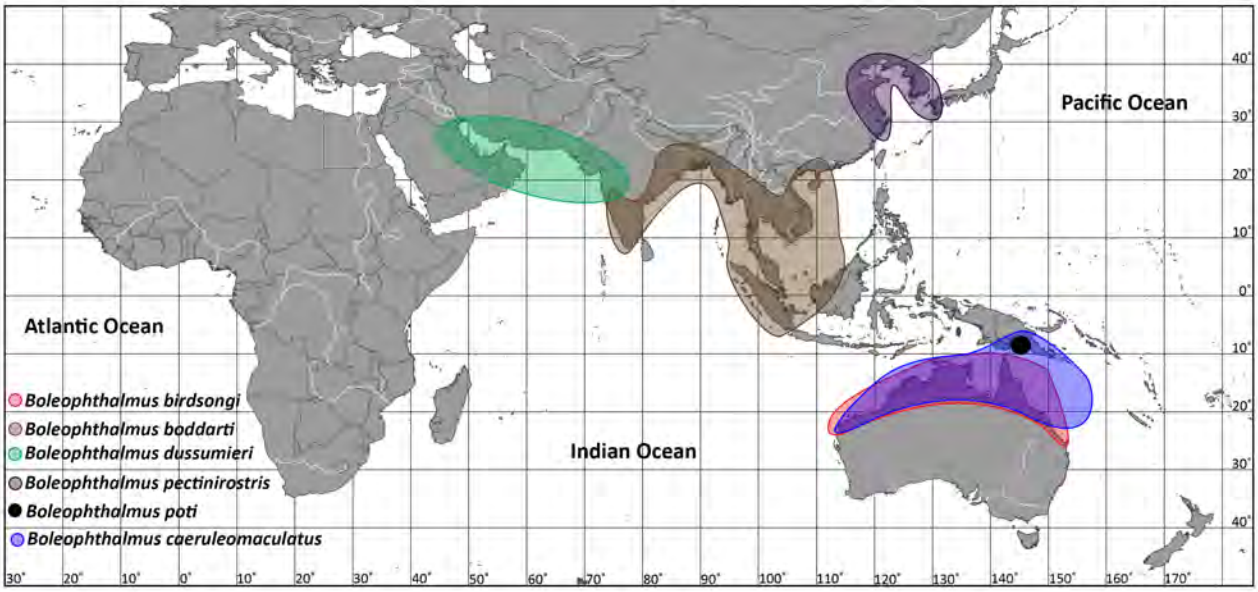
Pacific Ocean
Atlantic Ocean
Indian Ocean
Boleophthalmus birdsongi
Boleophthalmus boddarti
Boleophthalmus dussumieri
Boleophthalmus pectinirostris
Boleophthalmus poti
Boleophthalmus caeruleomaculatus
40°
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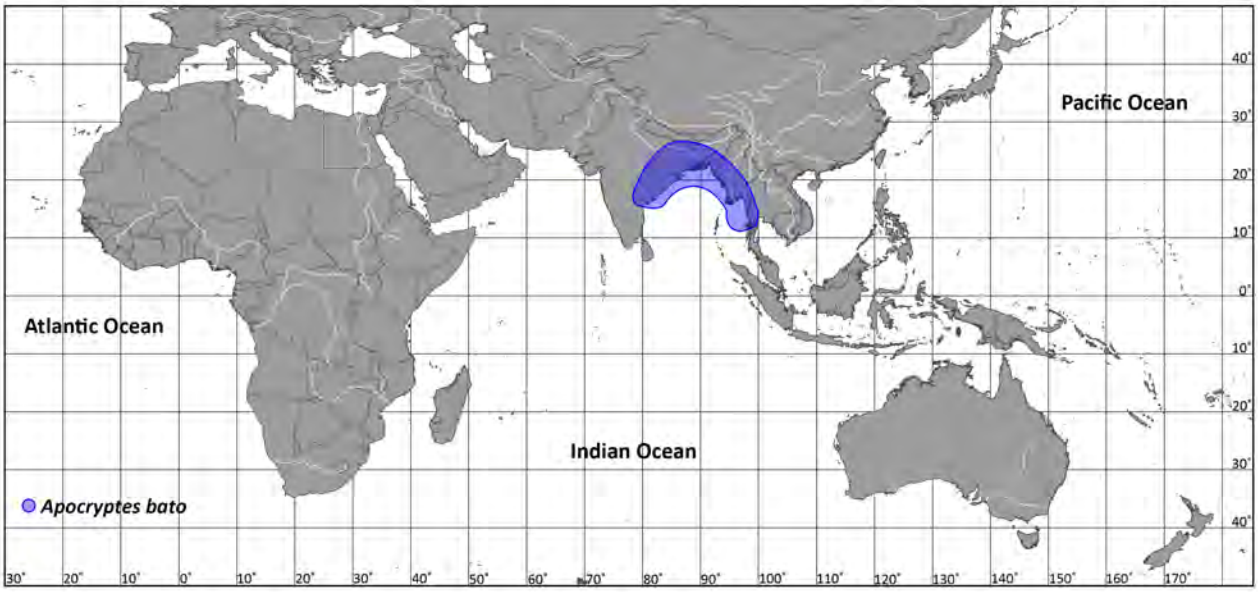
Pacific Ocean
Atlantic Ocean
Indian Ocean
Apocryptes bato
40°
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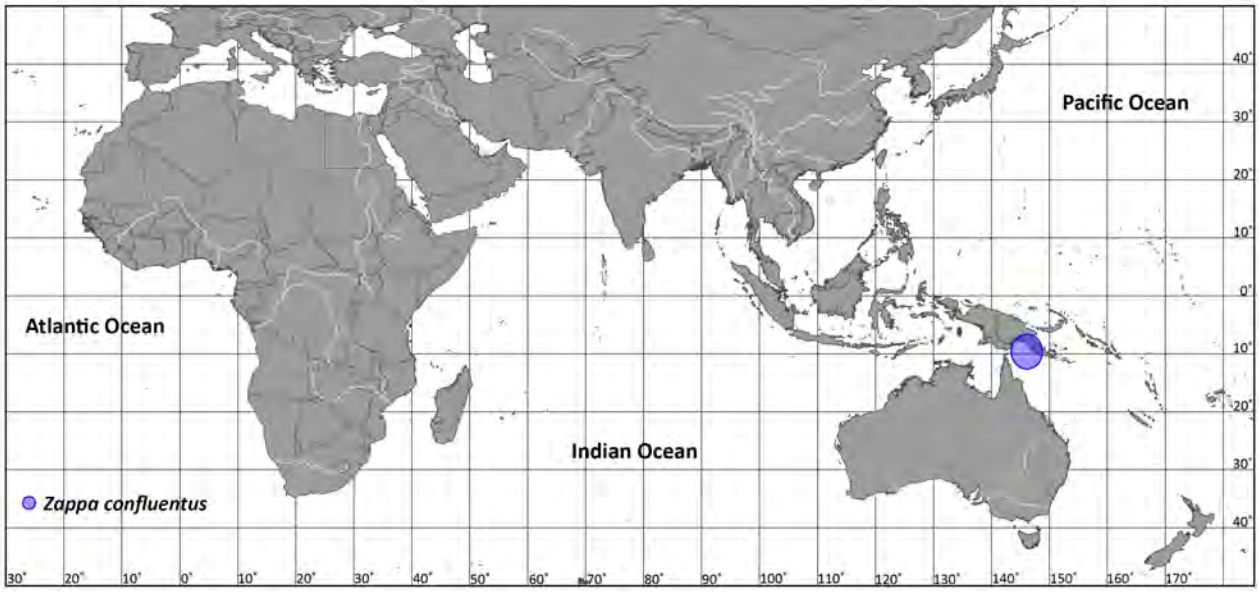
Pacific Ocean
Atlantic Ocean
Indian Ocean
Zappa confluentus
40°
30°
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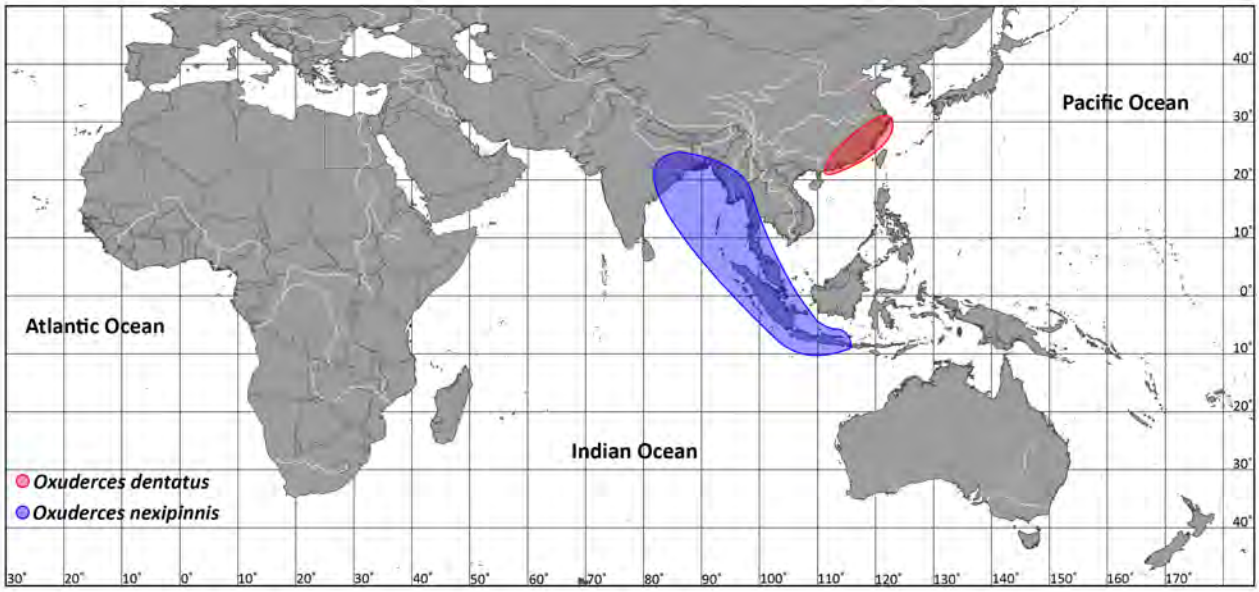
Pacific Ocean
Atlantic Ocean
Indian Ocean
Oxuderces dentatus
Oxuderces nexipinnis
40°
30°
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0°
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30°
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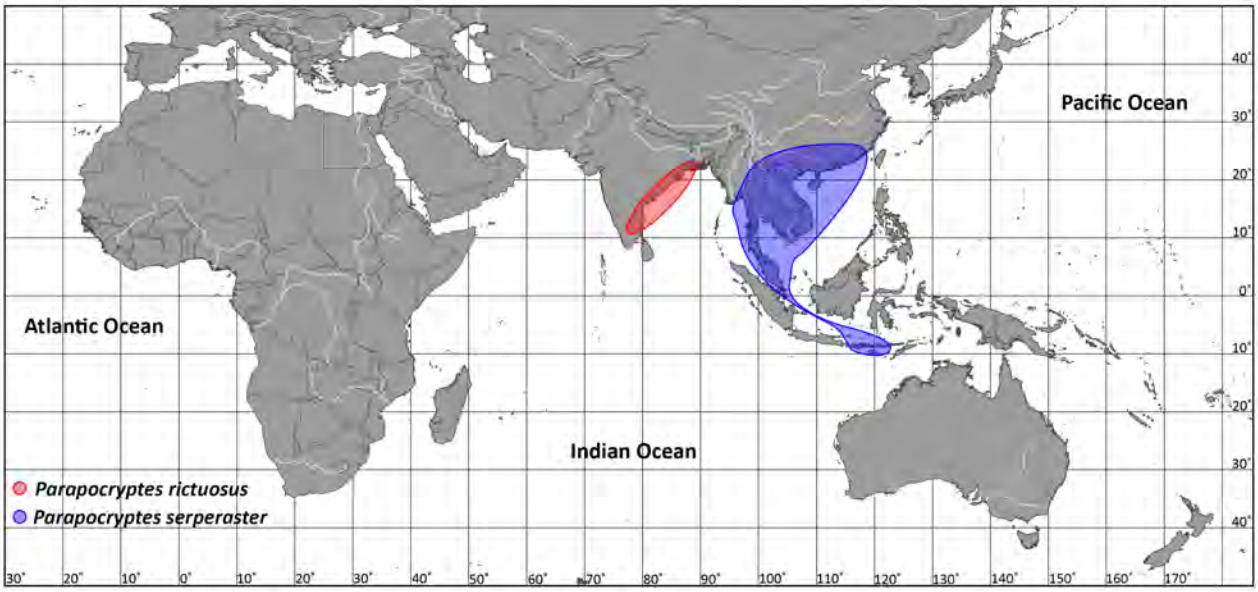
Pacific Ocean
Atlantic Ocean
Indian Ocean
Parapocryptes rictuosus
Parapocryptes serperaster
40°
30°
20°
10°
0°
10°
20°
30°
40°
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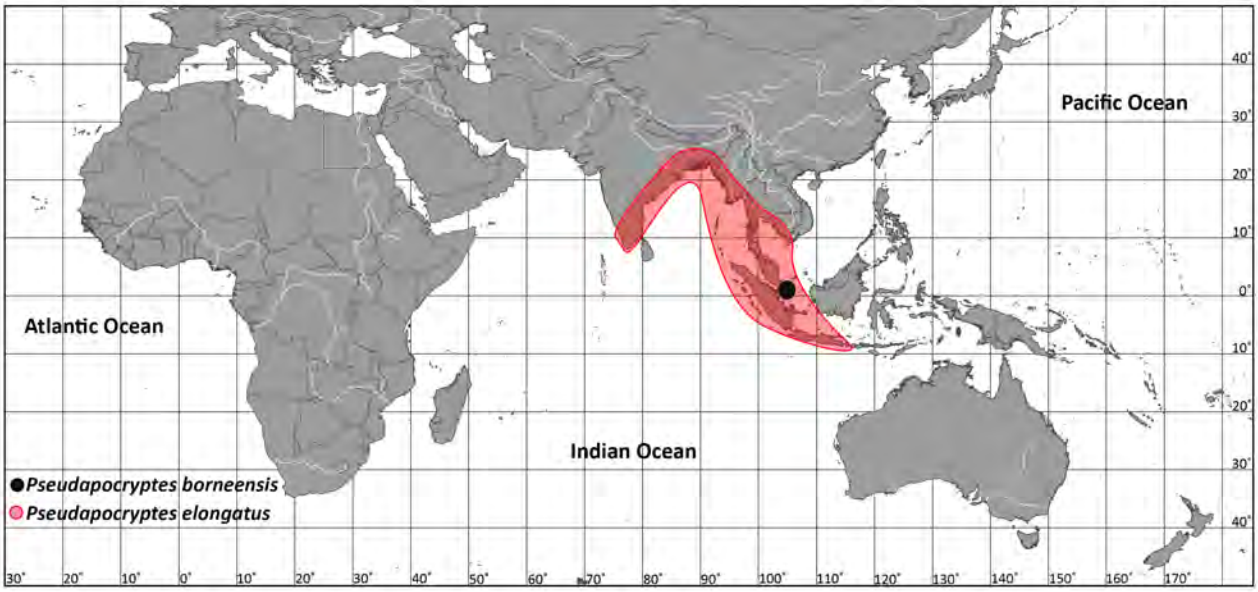
Pacific Ocean
Atlantic Ocean
Indian Ocean
Pseudapocryptes borneensis
Pseudapocryptes elongatus
40°
30°
20°
10°
0°
10°
20°
30°
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0°
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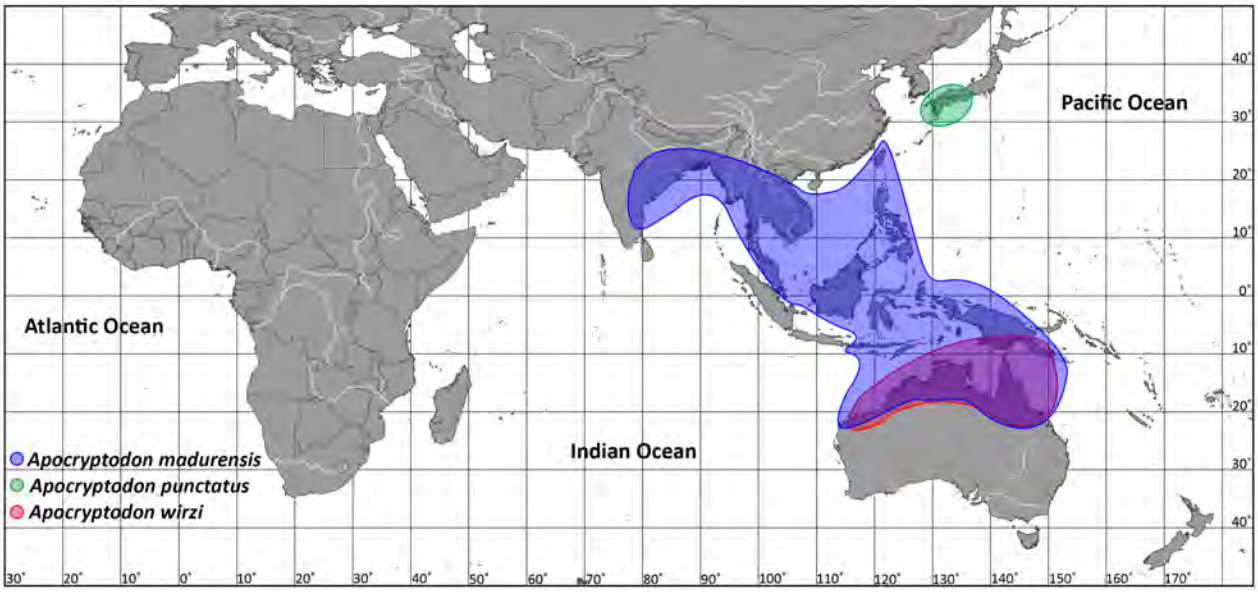
Pacific Ocean
Atlantic Ocean
Indian Ocean
Apocryptodon madurensis
Apocryptodon punctatus
Apocryptodon wirzi
40°
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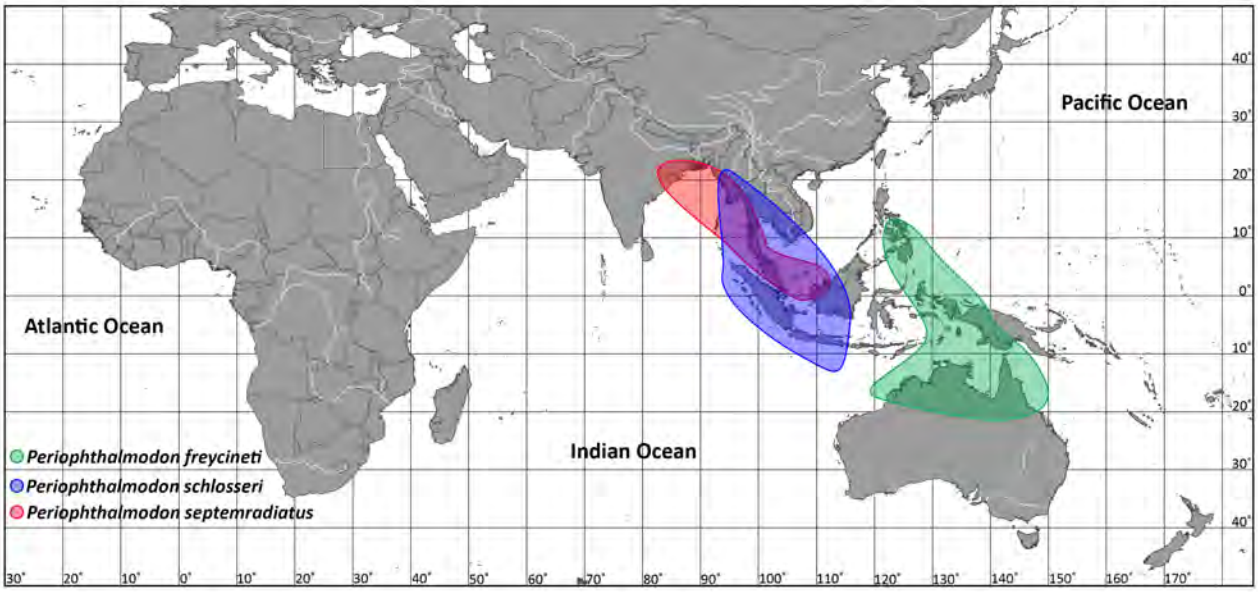
Pacific Ocean
Atlantic Ocean
Indian Ocean
Periophthalmodon freycineti
Periophthalmodon schlosseri
Periophthalmodon septemradiatus
40°
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GENUS	SPECIES	Tropical Eastern Atlantic Ocean	Southwestern Indian Ocean	Arabian Sea
Apocryptes (*As.*)	*bato*			
Apocryptodon (*An* .)	*madurensis*			
	punctatus			
	wirzi			
Boleophthalmus (*B* .)	*birdsongi*			
	boddarti			×
	caeruleomaculatus			
	dussumieri			×
	pectinirostris			
	poti			
	cf. *pectinirostris* (not included in analysis)			
Oxuderces (*O* .)	*dentatus*			
	nexipinnis			
Parapocryptes *Pa* .)	*rictuosus*			

	serperaster			
Periophthalmodon (*Pn* .)	*freycineti*			
	schlosseri			
	septemradiatus			
Periophthalmus (*Ps* .)	*argentilineatus*		×	×
	barbarus	×		
	chrysospilos			
	darwini			
	gracilis			
	kalolo		×	
	magnuspinnatus			
	malaccensis			
	minutus			
	modestus			
	novaeguineaensis			
	novemradiatus			
	pusing			
	spilotus			
	takita			

	variabilis			
	walailakae			
	waltoni			×
	weberi			
Pseudapocryptes (*Pd*.)	*borneensis*			
	elongatus			
Scartelaos (*S*.)	*cantoris*			
	gigas			
	histophorus			×
	tenuis			×
Zappa (*Z*.)	*confluentus*			
Total number of species		1	2	6
Number of endemic species		1	possibly 1	3

AREAS OF ENDEMISM					
Bay of Bengal	South China Sea	East China Sea	Banda Sea	Oceania	No. of Areas
×					1
×	×		×	×	4
		×			1
				×	1
				×	1
×	×		×		4
				×	1
					1
		×			1
				×	1
	×				1
		×			1
×	×				2
×					1

	×	×			2
			×	×	2
×	×				2
×	×				2
×	×	×	×	×	7
					1
	×				1
				×	1
	×		×	×	3
×	×		×	×	5
		×			1
			×		1
	×		×	×	3
		×			1
				×	1
×					1
			×		1
	×				1
				×	1

	×				**1**
×	×				**2**
					1
				×	**1**
	×				**1**
×	×				**2**
×					**1**
		×			**1**
×	×	×	×	×	**6**
					1
				×	**1**
14	18	9	10	16	__
3	5	6	2	9	__