

# First record and conservation value of *Periophthalmus malaccensis* Eggert from Borneo, with ecological notes on other mudskippers (Teleostei: Gobiidae) in Brunei

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## Abstract

The mudskipper *Periophthalmus malaccensis* is first reported from two mangrove areas of Brunei Darussalam, on the island of Borneo. This species has a relatively restricted geographic distribution and have been reported from Singapore, Philippines, Maluku Islands, western New Guinea, and northern Sulawesi. In Brunei, this species occurs at low population density in high intertidal habitats, which are highly impacted by anthropogenic destruction and fragmentation. For these reasons, the conservation status of this species should be evaluated. The distribution and habitat types of species belonging to *Periophthalmus* and *Periophthalmodon* in Brunei are also described.

*Index Terms:* mudskippers, Brunei Bay, mangrove destruction, extinction risk

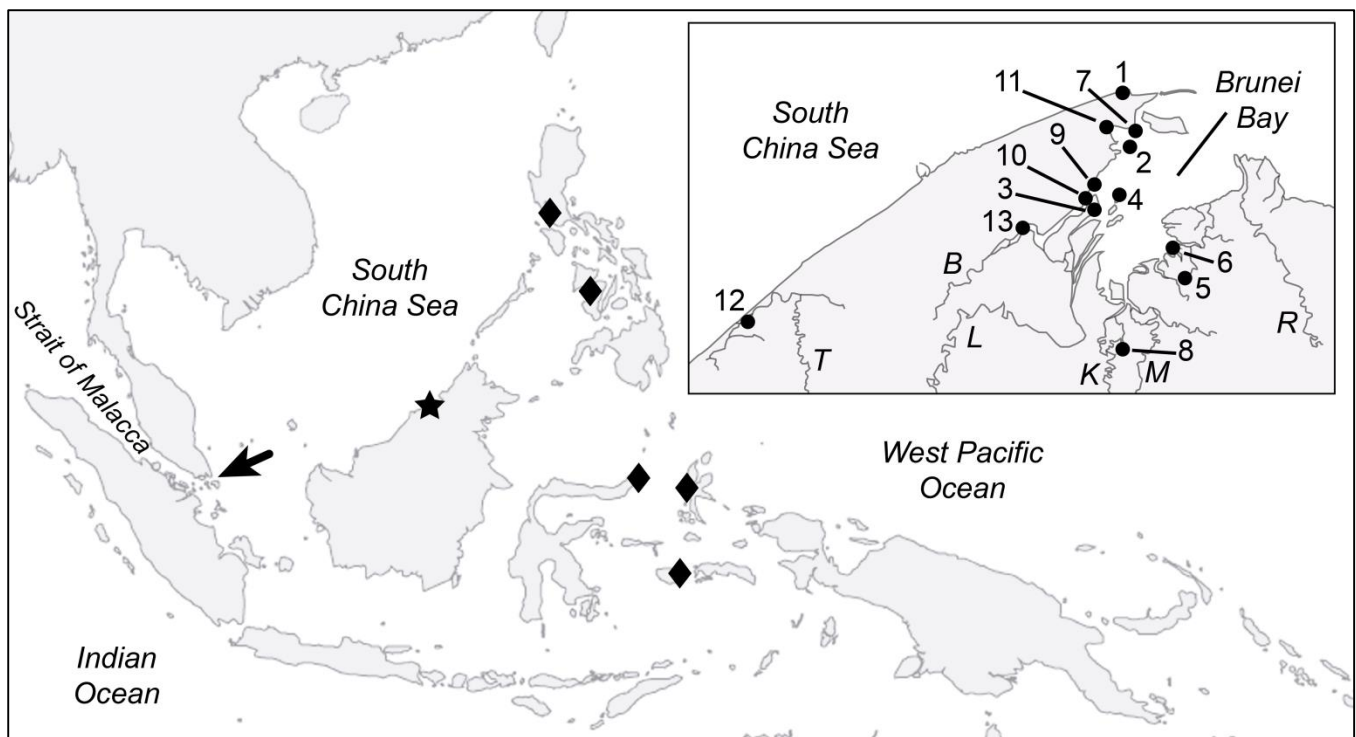
## 1. Introduction

The genus *Periophthalmus* (Perciformes: Gobioidae: Gobiidae; ‘*Periophthalmus* lineage’<sup>1</sup>) presently includes 18 species with amphibious lifestyles, known as mudskippers.<sup>2,3</sup> Four species were previously recorded from Borneo<sup>2</sup>: *P. argentilineatus* Valenciennes, 1837 (Malaysia: Sarawak); *P. gracilis* Eggert, 1935 (Sarawak); *P. chrysopilos* Bleeker, 1852 (Indonesia, Kalimantan: Sebatik Island = Pulau Sebatik), and *P. novemradiatus* (Hamilton, 1822) (= *P. variabilis* Eggert, 1935, sensu<sup>5</sup>; Malaysia: Sabah, Sarawak; Pulau Sebatik). *Periophthalmus argentilineatus* (USNM 356813-356814) and *P. gracilis* (USNM 366713) were collected in Brunei in 1997<sup>4</sup> (Sandra Raredon, pers. comm., **Appendix I**). However, I could not confirm the taxonomic status of USNM 366713.

Molecular data suggest that the morphospecies *P. argentilineatus* is a complex of three cryptic or pseudocryptic species.<sup>6</sup> These molecular clades are morphologically similar to three morphospecies revised by Eggert<sup>7</sup> (GP, unpublished data), that Murdy<sup>2</sup> synonymised as *P. argentilineatus*. Two of these species, *P.*

*vulgaris* Eggert (clade F in Polgar et al.<sup>6</sup>) and *P. argentilineatus* Valenciennes (clade K), occur sympatrically in Southeast Asia; *P. sobrinus* Eggert (clade I) occurs in Eastern Africa, Seychelles and Madagascar. A taxonomic revision of *P. argentilineatus* is beyond the scope of this contribution. Therefore, I will here record specimens of *P. argentilineatus* that are morphologically similar to those in clade F<sup>6</sup> as *Periophthalmus* cf. *vulgaris* Eggert, 1935. No specimens similar to clade K<sup>6</sup> were found during this study.

*Periophthalmus malaccensis* is known from the Philippines, Maluku Islands, western New Guinea<sup>2,8</sup>, and northern Sulawesi<sup>6</sup>. In northern Sulawesi<sup>6</sup>, *P. malaccensis* occurs in riverine mangrove forests, up to 1.5 km from the coast (unpublished data). The type locality of this species is Singapore, and the species was named after the Strait of Malacca, between Sumatra and the Malay Peninsula<sup>7</sup> (**Figure 1**). However, this species has not been recorded in this area since its description, in spite of extensive sampling efforts.<sup>9,10,11,12</sup> In fact, both the coastal wetlands along the west coast of the Malay



**Figure 1.** Study sites in Brunei Darussalam (inset, numbered black dots; see **Table 1**; **Appendix 2**) and geographic distribution of *P. malaccensis*; some major river systems in the study area are illustrated: B = Brunei river; K = Kibi river; L = Limbang river; M = Temburong river; R = Batang Tarusan river; T = Tutong river; black arrow = type locality, black diamonds = previous records<sup>2,6,8</sup>; black star = new record and geographical position of the map in the inset.

Peninsula<sup>13</sup> and Singapore<sup>14</sup> underwent extensive deforestation, which severely impacted the higher intertidal and supratidal zone, and could have extirpated *P. malaccensis* in Singapore.<sup>15</sup>

The genus *Periophthalmodon* includes three species ecologically and systematically closely related to *Periophthalmus* species.<sup>2</sup> *Periophthalmodon schlosseri* (Pallas, 1770) was recorded in northern Borneo (Sarawak; Sebatic Island)<sup>2</sup>; *Periophthalmodon septemradius* (Hamilton, 1822) was also collected in Sarawak<sup>2</sup>. A first record of *P. malaccensis* from Borneo is here documented from two mangrove areas in Brunei Darussalam, with notes on the presence and habitat of the species of the genera *Periophthalmus* and *Periophthalmodon*. The potential conservation interest of *P. malaccensis* is also briefly discussed.

## 2. Experimental approach

### Study sites

Brunei Darussalam (**Figure 1**) is characterised by a tropical climate, with an average annual temperature of 27 °C, and an average annual rainfall of 2,880 mm (mean from 1966 to 2006), with two peaks in correspondence of Southwest monsoon (May), and the Northeast monsoon (December) (Brunei Meteorological Service, Department of Civil Aviation).

The Brunei Bay occupies an area of ~ 2,500 km<sup>2</sup>; several rivers flow into the bay, such as the Brunei, Limbang, Temburong River, and Batang Trusan (Yau 1991; **Figure 1**). Twenty-eight sampling surveys of gobioid fishes were conducted in coastal areas and tidally-influenced rivers where *Periophthalmus* species were found, at 13 sites, from May 2013 to August 2015 (**Figure 1**; **Table 1**; **Appendix 2**). All surveys were conducted during the day and  $\pm 2$  hours around low tide (TideComp v. 7.04 © Mike Harris; tidal reference stations: Bandar Limbang 4°45'0.0" N 114°59'60.0" E; Dato Gandhi 4°54'0" N 114°58'60" E; Kuala Limbang 4°50'60.00" N 115°1'0" E).

**Table 1.** Study sites where *Periophthalmus* and *Periophthalmodon* mudskippers were found, number of surveys (n), and species occurrence (X). Pulau = island; Sungai = river. Abbreviations: a = *P. cf. vulgaris*; g = *P. gracilis*; m = *P. malaccensis*; s = *Pn. schlosseri*.

	Site	Coordinates	n	Species occur.			
				a	g	m	s
1	Pemburungan Creek	5°02'36.8"N 115°03'21.1"E	2	X			
2	Pulau Bedukang	4°58'45.7"N 115°03'40.4"E	5	X	X		X
3	Pulau Berambang	4°54'13.0"N 115°01'15.8"E	1		X		
4	Pulau Pepataan	4°59'40.5"N 115°03'59.2"E	1	X*	X		
5	Pulau Selirong site A	4°49'30.9"N 115°07'51.9"E	1			X	
6	Pulau Selirong site B	4°51'18.7"N 115°6'47.9"E	1	X	X		
7	Serasa jetty	4°59'40.5"N 115°03'59.2"E	1	X			
8	Sungai Belayang	4°44'22.9"N 115°2'59.2"E	1		X		
9	Sungai Besar	4°55'39.8"N 115°00'52.0"E	3	X			
10	Sungai Bunga	4°55'0.5"N 115°00'25.0"E	6	X	X	X	X
11	Sungai Salar	4°59'59.1"N 115°1'51.8"E	1	X	X		
12	Sungai Tutong	4°46'10.8"N 114°36'23.4"E	2	X	X		
13	Ujong Bukit	4°53'17.9"N 114°56'07.5"E	3				X

\*examined specimens were not deposited in the UBDM collection (*Appendix 2*)

**Table 2.** Morphometric measurements of *P. malaccensis* (n = 4) from Brunei. %SL = percentage of standard length.

Total length (mm)	71.5-113.9
Standard length (mm)	54.2-90.3
<b>In % SL</b>	
Head length	25.3-27.2
Head depth	16.8-19.5
Head width	15.5-17.6
Body depth	14.9-16.5
Body width	15.9-17.7
Length of D1 base	17.0-23.7
Length of D2 base	18.1-21.5
Length of anal-fin base	16.1-18.6
Least caudal-peduncle depth	8.8-9.4
Pectoral-fin length, base included/not included (left)	25.2-28.4 / 16.2-17.7
Pectoral-fin height, base included/not included (left)	10.3-11.7 / 6.9-9.0
Pelvic-fin length	13.0-14.6
Caudal-fin length	25.2-31.9

**Table 3.** Meristic measurements of *P. malaccensis* (n = 4) from Brunei.

<b>Fin-ray counts</b>	
First dorsal fin	10-12
Second dorsal fin	12
Anal fin	12
Pectoral fin (left/right)	13-14 / 13
Principal-caudal rays	16
<b>Scale counts</b>	
Number of lateral-scale rows	54-58
Transverse scales counted ventrally backward	16-21
Transverse scales counted dorsally backward	17-21
Transverse scales counted ventrally forward	17-23
Predorsal scales	25-27
Number of interdorsal-scale rows	3-8

### Sampling, preservation and measurements

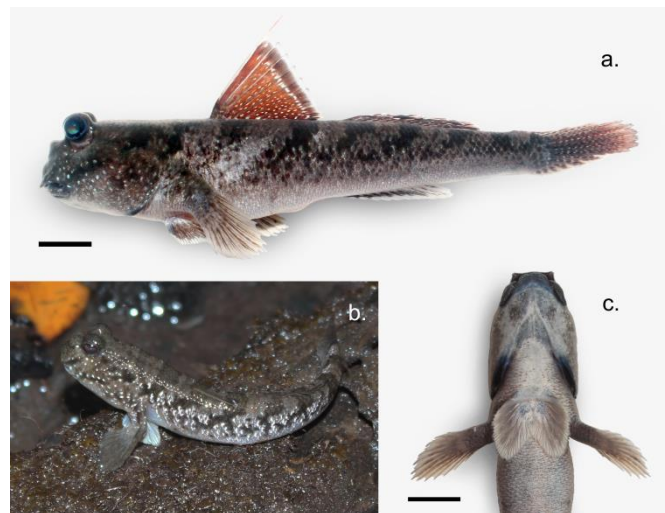
Specimens were sampled with hand nets, transported alive to the laboratory, anaesthetised placing them in a refrigerator at 4°C for 1 hour, euthanised by rapid cooling at -20°C, and then fixed and preserved in 70% undenatured ethanol. Measurements were taken with a digital calliper to the nearest 0.1 mm, and are reported as a percentage of the specimens' standard length (SL), unless stated. Counts were made under a dissecting microscope. All measurements followed Polgar et al.<sup>16</sup> Soft and spinous fin rays were counted together.

Several specimens were deposited in the zoological collection of the Universiti Brunei Darussalam Museum (UBDM; **Appendix 2**). Specimens from other museum collections were examined, to confirm taxonomic discrimination of species potentially present in the region, and verify previous records (**Appendix 1**). The heads of some specimens of *Pn. schlosseri* (UBDM MUb131013sch) and *P. malaccensis* (UBDM MBu111013mal) were fixed in Karnovsky fixative solution for histological preparations, and left pectoral fins were fixed in absolute ethanol for molecular analyses.

### 3. Results and Discussion

The specimens' morphology and colouration patterns corresponded to the available taxonomic descriptions<sup>2,7</sup> (**Tables 2, 3**). To my knowledge, there are no mudskippers' records from Brunei in the literature, therefore all the species recorded here are first records for Brunei. *P. malaccensis* is also a first record for the island of Borneo, near the western limit of the longitudinal range of this species (**Figure 1**).

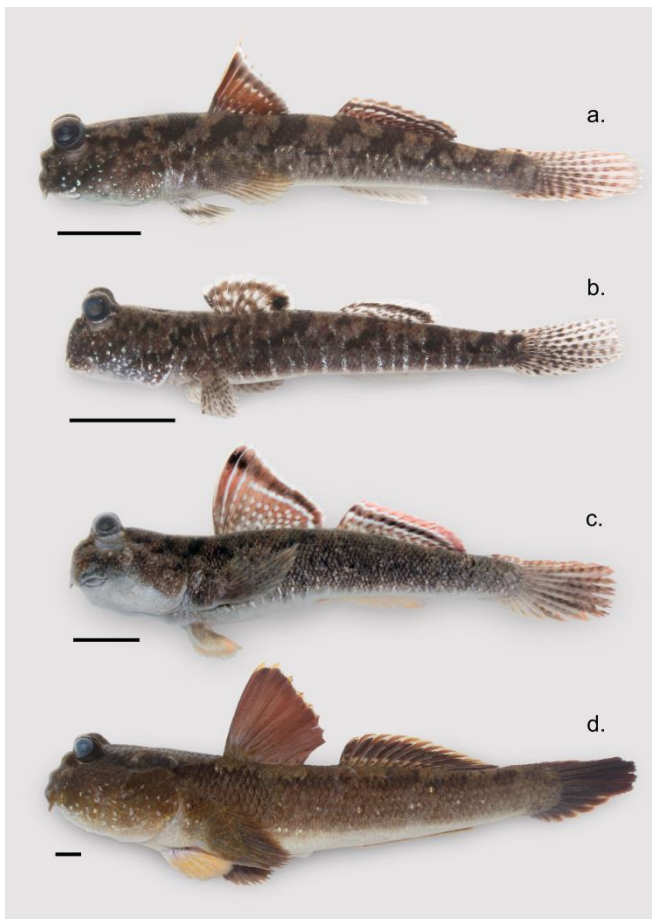
The examined specimens of *P. malaccensis* were characterised by (**Figure 1**): (i) squared-shaped pelvic fins, with prominent pelvic frenum, partially united by a basal membrane, both ventrally and dorsally pigmented, and with white margin; (ii) presence of dark pigmentation of anal interradiation membranes; (iii) sky blue speckles on cheeks and opercula; (iv) prominent transversal crease on snout; and (v) elongate first spine of D1 in both males and females (**Figures 2, 3**).



**Figure 2.** *Periophthalmus malaccensis* collected in Sungai Bunga, Brunei (UBDM MBu081013mal); a. freshly dead specimen, lateral view; b. live specimen; c. freshly dead specimen, ventral view, detail (scale bars are 10 mm long).

In the field, *P. malaccensis* can be discriminated from other congeners in Brunei by the presence of an elongated first spine in the first dorsal fin, a prominent crease on the snout, and small sky blue speckles on cheeks and opercles. In this study, *P. malaccensis* reached 90 mm SL (**Table 2**). The collected *P. cf. vulgaris* were 32-61 mm SL, and *P. gracilis* were 25-40 mm SL (**Appendix 2**). Like *P. malaccensis*, *Pn. schlosseri* (109.8, 205.0 mm SL, **Appendix 2**) also possesses sky blue speckles on the head, but differs from *P. malaccensis* in the presence of a black stripe coursing posteriorly from behind the orbits to the caudal peduncle (not always visible), absence of white spots on the interspinous membranes of the first dorsal fin, and absence of series of dark brown speckles on the caudal interradiation membranes (**Figure 3**).

*P. variabilis* and *P. chrysopilos* were not found in Brunei during these surveys, but I found these species in Sarawak, in the Kuching area (unpubl. data). *Pn. septemradiatus* was also not found in Brunei. *P. cf. vulgaris* and *P. gracilis* are the most common mudskipper species in Brunei, and occurred at several sites, in a variety of habitats; *Pn. schlosseri* was only found in three sites (**Table 1, Appendix 3**).



**Figure 3.** Mudskippers of Brunei of the genera *Periophthalmus* and *Periophthalmodon*. a. *Periophthalmus malaccensis* (UBDM MSe170414mal); b. *Periophthalmus gracilis* (UBDM MBm050514gra); c. *Periophthalmus* cf. *vulgaris* Eggert (UBDM MBe070513arg, female); and d. *Periophthalmodon schlosseri* (UBDM MUb131013sch, female); lateral view of freshly dead specimens; scale bars are 10 mm long.

The highest recorded richness of mudskipper species was in Sungai Bunga (**Table 1**), a small mangrove forest adjacent to a mud bank 30-50 m wide during spring low tide, in front of Berambang Island (**Figure 1**; **Table 1**; **Appendix 3**). The mudskipper species *Boleophthalmus boddarti* (Pallas, 1770), *Boleophthalmus* cf. *pectinirostris* (Linnaeus, 1758), and *Scartelaos histophorus* (Valenciennes, 1837) were also observed in Sungai Bunga, on the exposed and unvegetated mud bank. However, these sightings were irregular, suggesting high seasonal variability of larval recruitment<sup>17</sup>. *Boleophthalmus* species were also always observed in very low numbers (< 3 individuals per

survey). In general, mudskippers appear to be less diverse and much less abundant in Brunei than in other neighbouring areas in the region, such as western Peninsular Malaysia<sup>9</sup>, and Sarawak (pers. obs.).

Among the surveyed sites, *P. malaccensis* was found only in Sungai Bunga and in Pulau Selirong (where only a single sighting was made), in the high intertidal zone<sup>10</sup>. The mangrove habitats of *P. malaccensis* were dominated by large trees of *Rhizophora apiculata* Blume; in the higher portion of this habitat, several *Thalassina* mounds occurred, up to several m wide and 0.5-1 m high, colonised by the sesarmid crabs *Episesarma chentongense* Serene and Soh, *E. mederi* A. Milne-Edwards, and *Acrostichum* ferns<sup>18</sup>. The *Acrostichum* zone was adjacent to a backforest supratidal swamp (sites 5 and 10, **Appendix 3**). The rather limited distribution of *P. malaccensis*, its probable recent extirpation from its type locality, its rarity in Brunei and its exclusive presence in the highly impacted high intertidal zone of mangrove forests<sup>15</sup> prompt for a conservation assessment of this species throughout its distributional range<sup>19</sup>.

#### 4. Conclusion

The mudskipper *P. malaccensis* Eggert is recorded for the first time in Borneo. Three other mudskipper species (Teleostei, Gobiidae, ‘*Periophthalmus* lineage’<sup>1</sup>) were recorded in Brunei Darussalam in several sites, and three more species in a single site. Notes on the habitat of *P. malaccensis* are provided. It is suggested that this species is of high conservation interest.

#### Acknowledgements

Thanks to the Forestry Department of the Ministry of Industry and Primary Resources for permits to conduct research in the study sites. Thanks to Sandra Raredon, Smithsonian National Museum of Natural History, Division of Fishes Collections for providing high resolution images of USNM mudskipper lots from Brunei. Thanks also to Laura Ribero, Claas Damken and Rossana Bottone for their help in the field during the surveys, and to Zeehan Jaafar for her revision of the manuscript.



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## Appendix 1. List of examined museum specimens)

- Periophthalmodon freycineti* (Quoy and Gaimard, 1824): MCZR VP1018, VP1019, Papua New Guinea, Western Province, southern Fly river delta, Toro Pass. MSNG 54691, Papua New Guinea, Western Province, Fly river delta, Purutu Island, 2007. NTM S.15545-001, Australia, Northern Territory, Wildman river, Ten Inch Creek.
- Periophthalmodon schlosseri* (Pallas, 1770): MSNG 54125, Malaysia, Selangor, Kuala Selangor.
- Periophthalmodon septemradiatus* (Hamilton, 1822): BMNH 2009.4.23.29, Myanmar, Rakhine State, Mee Chaun, close to its mouth at Dalet Chaung. MSNG 54643, Malaysia, Selangor, Kampong Kuantan.
- Periophthalmus argenteolineatus* Valenciennes, 1837 (clade K, Polgar et al. 2014): MSNG 55637 (A,B), Indonesia, North Sulawesi, Bunaken island, 2005. MSNG 55638, Indonesia, North Sulawesi, Bunaken island, 2005.
- Periophthalmus chrysospilos* Bleeker, 1852: <sup>1</sup>FMNH 117467, 117468, Malaysia, Johor, mouth of Muar river, south side. MCZ 33228, Java Sea. MSNG 52024, Malaysia, Selangor, Pulau (= Island) Kelang. MSNG 54127, Malaysia Negeri Sembilan, Tanjung (= Cape) Tuan. MSNG 54128, Malaysia, Selangor, Morib. RMNH 4760 (syntypes), Indonesia, Banka Island (East of Sumatra). USNM 151130, Malaysia, Penang Island. USNM 244031, southeast Thailand, north of Chonburi Chachoengsao Province, Maenam Bang Pakong. USNM 278428, 278435, 279331, Malaysia, Johor, Muar, Southside Muar River. ZMUC P.781480, P.781481, Indonesia, Java, Soetji. <sup>2</sup>ZMUC P.781616, P.781617, P.781618, Thailand, Phuket Island.
- Periophthalmus darwini* Larson and Takita, 2004: MCZR VP1012, VP1013, Papua New Guinea, Western Province, Fly river delta, Purutu Island, 2007. MSNG 54692, Papua New Guinea, Western Province, Fly river delta, Purutu Island, 2007. NTM S.10554-004 (holotype), Australia, Northern Territory, Shoal Bay, Mickett Creek. NTM S.10694-

022 (paratype), Australia, Northern Territory, Gunn Point. NTM S.11360-015 (paratype), Australia, Northern Territory, Milingimbi, Darbilla Creek. NTM S.14400-006 (paratype), Australia, Northern Territory, Melville Island, beach south of Picker-Taramoor.

*Periophthalmus gracilis* Eggert, 1935: MSNG 54129, Malaysia, Selangor, Kuala Selangor. MSNG 54130, Malaysia, Selangor, Pulau (= Island) Kelang. MSNG 54131, Malaysia, Selangor, Morib. MSNG 54132, Malaysia, Negeri Sembilan, Tanjung (= Cape) Tuan. MSNG 55639, Indonesia, North Sulawesi, Bajo, Talawan River, 2005.

*Periophthalmus kalolo* Lesson, 1831: RMNH 4593 (in part), Indonesia, west Sumatra, Padang; east Flores, Lantaka. RMNH 4754 (in part), Indonesia, Ambon. MSNG 55640 (A-C), Indonesia, North Sulawesi, Bajo, Talawan River, 2005. MSNG 55641 (A,B), Indonesia, North Sulawesi, Bunaken Island, 2005. MSNG 55642, Indonesia, North Sulawesi, Mantehage, Buhias, 2005. MSNG 55643, Indonesia, North Sulawesi, Likupang, 2005.

*Periophthalmus malaccensis* Eggert, 1935: USNM 112908, Philippines, Luzon, Manila Bay. USNM 148591, Philippines, Iloilo. USNM 268451, Indonesia, Halmahera Island, Jailolo District, Kampong (= village) Pasir Putih. <sup>3</sup>USNM 278471, Philippines, Luzon, Bataan, Mariveles. MSNG 55644, Indonesia, North Sulawesi, Likupang, 2005. MSNG 55645 (A,B), Indonesia, North Sulawesi, Likupang, Marawuwung River, 2005. MSNG 55646 (A,B), 55647, 55648, Indonesia, North Sulawesi, Wawontulap, Talonka River, 2005.

<sup>4</sup>*Periophthalmus minutus* Eggert, 1935: AMS I.24684-001, Australia, Northern Territory, Melville Island. ZMUC P.781609, Thailand, Phang Nga, North East of Phuket Island. ZRC 52261, Thailand, Phuket Island, Rassada harbor.

*Periophthalmus novaeguineensis* Eggert, 1935: MCZR VP1003, VP1004, VP1005, Papua New Guinea, Western Province, Fly river delta, Purutu Island. AUM 47699, Papua New Guinea, Western Province, 40.7 km NE

of Daru. MSNG 54693, 54694, Papua New Guinea, Western Province, Fly river delta, Purutu Island. NTM S.10426-002 (paratype of *Periophthalmus murdyi*, Larson and Takita 2004), Australia, Northern Territory, Shoal Bay, Buffalo Creek. NTM S.11193-004 (5 paratypes of *P. murdyi*), Australia, Northern Territory, Adelaide river, bend northeast of Harrison Dam, Boustead's Barramundi farm. NTM S.14024-013 (paratype of *P. murdyi*), Australia, Northern Territory, Roper river. NTM S.14467-006 (paratype of *P. murdyi*), Australia, Northern Territory, East Alligator river, Smith's landing. NTM S.15800-001 (paratype of *P. murdyi*), Australia, Western Australia, Derby jetty.

*Periophthalmus pilotus* Murdy and Takita, 1999: AMS I.39049-001 (paratypes), Indonesia, Sumatra, Tebing Tinggi Island. NSMT-P 56864, NTM S.14699-001 (paratypes), Indonesia, Sumatra, Tebing Tinggi Island. USNM 352414 (paratypes), Indonesia, Sumatra, Tebing Tinggi Island. MSNG 54644, Malaysia, Selangor, Sementa.

*Periophthalmus takita* Jaafar and Larson, 2008: AMS I.34341-028, Australia, Queensland, Mangrove channel, Port Clinton. MCZR VP1002, Papua New Guinea, Western Province, Fly river delta, Purutu Island, 2007. MSNG 54695, Papua New Guinea, Western Province, Fly river delta, Sisikura Island. MSNG 54696, Papua New Guinea, Western Province, Fly river delta, Purutu Island. NTM S.10798-011, Australia, Northern Territory, Bathurst Island, Buchanan Island. NTM S.14637-032 (paratypes), Australia, Northern Territory, south end of Field Island, mouth of South Alligator river.

*Periophthalmus variabilis* Eggert, 1935: MCZ 54404, Malaysia, Sarawak, Kuala Samunsam (= mouth of the Samunsam river). MSNG 54133, 54134, Malaysia, Selangor, Kuala Selangor. MSNG 54135, Malaysia, Pulau (= Island) Kelang. MSNG 54136, Malaysia, Negeri Sembilan, Tanjung (= Cape) Tuan. NSMT-P 54453, Malaysia, Selangor, Kuala Selangor. NSMT-P 54464, Indonesia, Sumatra, Tebing Tinggi Island. USNM 139372, Indonesia, north Borneo, Sebatik (=

Sebatik) Island. USNM 222971, Thailand, Central Merram Chao Phya (= Chao Phraya), Paknam. USNM 278470, Malaysia, Sabah, mangrove swamps on island opposite Sandakan, Borneo. USNM 279318, Malaysia, Johor, Muar, Indian Temple Creek. ZMA 113.702, Malaysia, Selangor, Kuala Langat. ZMUC P.781597-1608, 1610, 1611, Thailand, Phang Nga, northeast of Phuket Island.

*Periophthalmus weberi* Eggert, 1935: AUM 47584, Papua New Guinea, Western Province, Fly river, 15.8 km SW of Sturt Island. MCZR VP1011, Papua New Guinea, Western Province, lower Fly river. MSNG 54682, Papua New Guinea, Western Province, Fly river, Suki. MSNG 54683, Papua New Guinea, Western Province, Sturt Island. MSNG 54684, Papua New Guinea, Western Province, Fly river delta, Purutu Island.

*Periophthalmus* cf. *vulgaris* Eggert, 1935 (clade F in Polgar et al. 2014): MSNG 55627 (A-D), Indonesia, North Sulawesi, Bajo, Talawan River, 2005. MSNG 55628 (A-C), Indonesia, North Sulawesi, Bunaken Island, 2005. MSNG 55629, 55630, 55631, Indonesia, North Sulawesi, Likupang, 2005. MSNG 55632, Indonesia, North Sulawesi, Likupang, Marawuwung River. MSNG 55633, 55634, Indonesia, North Sulawesi, Wawontulap, Talonka River, 2005.

*Periophthalmus* cf. *vulgaris* Eggert (morphologically similar to the specimens of clade F in Polgar et al. 2014): USNM 356813, Brunei Darussalam, Sungai Penabai, where it enters Sungai Tutong, 1997. USNM 356814, Brunei Darussalam, Lubok Api-Api, Kuala Tutong, 1997.

*Periophthalmus* sp.: USNM 366713, 3 ex., Brunei Darussalam, Sungai Dalit, just above where it enters Sungai Belait, 1997 (catalogued as *P. gracilis*).

<sup>1</sup>Cited in Murdy (1989) as “FMNH uncatalogued” (Mary Ann Rogers, pers. comm.).

<sup>2</sup>Cited in Murdy (1989) as “ZUMC 78616-18” (Tammes Menne, pers. comm.).

<sup>3</sup>Determined as *P. novemradiatus* (= *P. variabilis sensu* Jaafar et al. 2009) by Murdy (1989).

<sup>4</sup>The lot of *P. minutus* ZMA 113.218 (in part), reported by Murdy (1989) from Java, is in fact from Flores, Mbawa (= Ma'u Mbawa) (Hielke Praagman, pers. comm.).

## Appendix 2. List of deposited museum specimens (all specimens were collected by G. Polgar in Brunei Darussalam, were fixed and preserved in 70% ethanol).

*Periophthalmus* cf. *vulgaris* Eggert (morphologically similar to the specimens included in clade F in Polgar et al. 2014):  
 UBDM MMe011213arg, 1 female, 50.5 mm SL; Meragang lagoon, Pemburungan Creek, 01 Dec 2013. UBDM MBe131013arg (A), 1 male, 43.3 mm SL; Pulau (= island) Bedukang, logs and debris in the mangrove pioneer shore (*Sonneratia* sp.); (B), 1 male, 48.3 mm SL; same site, high forest *Acrostichum* sp. ferns on *Thalassina* mounds, 13 Oct 2013. UBDM MBe070513arg (A), 1 female, 61.3 mm SL; Pulau Bedukang, mangrove pneumatophore zone; (B), 1 male, 48.4 mm SL; same site, pioneer mangrove forest, 07 May 2013. UBDM MBe270513arg, 1 ex., 34.8 mm SL; Pulau Bedukang, pioneer mangrove forest, 27 May 2013. UBDM MSe070813arg, 1 ex., 39.7 mm SL; Pulau Selirong, pioneer mangrove shore (*Rhizophora apiculata*), 07 Aug 2013. UBDM MSr300115arg, 1 male, 39.3 mm SL, Serasa, artificial jetty with rock breakwaters, 30 Jan 2015. UBDM MBs101013arg (A), 4 ex., 32.5-36.0 mm SL, Sungai (= river, creek) Besar, pioneer mangrove forest (*Sonneratia* sp.); (B), 2 ex., 32.9, 33.6 mm SL; same site, backforest and plant debris, 10 Oct 2013. UBDM MBs240513arg, 1 male 52.5 mm SL, Sungai Besar, pioneer mangrove forest, 24 May 2013. UBDM MBu081013arg, 2 males, 1 female, 46.3-53.7 mm SL; Sungai Bunga, *Rhizophora apiculata* forest, 08 Oct 2013. UBDM MSa150815arg, 1 ex., 40.3 mm SL; Sungai Salar, mangrove forest (*Rhizophora apiculata*, *Xylocarpus granatum*) along a tributary creek, 15 Aug 2015. UBDM MTu210214arg (A), 1 female, 50.9 mm SL,



Sungai Tutong, *Rhizopora apiculata* forest, near tide pools; (B), 1 male, 36.6 mm SL; same site, *Nypa fruticans* forest, 21 Feb 2014. UBDM MTu300713arg, 1 male, 1 ex., 37.6-43.1 mm SL, Sungai Tutong, *Nypa fruticans* forest, 30 Jul 2014.

*Periophthalmus gracilis* Eggert: UBDM MBe070513gra, 2 males, 32.6, 34.8 mm SL; Pulau Bedukang, high mangrove inlet, 07 May 2013. UBDM MBe131013gra (A), 1 female, 40.5 mm SL; Pulau Bedukang, logs and debris in the mangrove pioneer shore (*Sonneratia* sp.); (B), 2 males, 32.4, 32.8 mm SL; same site, high forest *Acrostichum* ferns on *Thalassina* mounds, 13 Oct 2013. UBDM MBm050514gra, 1 male, 35.3 mm SL; Pulau Berambang, 05 May 2014. UBDM MPe270513gra, 1 ex., 25.2 mm SL; Pulau Pepataan, pioneer mangrove shore, 27 May 2013. UBDM MSe070813gra, 1 ex., 30.2 mm SL; Pulau Selirong, pioneer mangrove shore (*Rhizopora apiculata*), 07 Aug 2013. UBDM MTm151013gra, 1 female, 38.2 mm SL; Sungai Belayang, tide pools on the vegetated banks (*Nypa fruticans*) of the river, 15 Oct 2013. UBDM MBu081013gra, 1 male, 1 female, 34.1, 35.5 mm SL; Sungai Bunga, high mangrove shore, 08 Oct 2013. UBDM MSa150815gra, 1 ex., 38.5 mm SL; Sungai Salar, mangrove forest (*Rhizophora apiculata*, *Xylocarpus granatum*) along a tributary creek, 15 Aug 2015. UBDM MTu210214gra, 1 female, 37.8 mm SL; Sungai Tutong, *Nypa fruticans* forest, 21 Feb 2014.

*Periophthalmus malaccensis* Eggert: UBDM MSe170414mal, 1 ex., 54.7 mm SL; Pulau Selirong vegetated creek banks (*Rhizophora apiculata*), 17 Apr 2014. UBDM MBu081013mal, 1 female, 83.0 mm SL; Sungai Bunga, high mangrove shore (*Rhizopora apiculata*), 08 Oct 2013. UBDM MBu111013mal, 2 males, 83.1, 90.3 mm SL (head dissected); Sungai Bunga, high mangrove shore (*Rhizopora apiculata*), 11 Oct 2013.

*Periophthalmodon schlosseri* (Pallas): UBDM MUb131013sch (A), 1 female, 109.8 mm SL; Ujong Bukit, mudflat with sparse *Avicennia*

sp. trees, around stilt houses; (B), 1 male 205.0 mm SL (head dissected), same site and habitat, 13 Oct 2014.

**Museums' abbreviations:** AMS = Australian Museum, Sydney, New South Wales, Australia. AUM = Auburn University Natural History Museum, Auburn, Alabama, U.S.A. BMNH = Natural History Museum, London, U.K. FMNH = Field Museum of Natural History, Chicago, Illinois, USA. MCZ = Museum of Comparative Zoology, Harvard University, Ichthyology Department, Cambridge, Massachusetts, U.S.A. MCZR = Museo Civico di Zoologia, Comune di Roma, Roma, Italy. MSNG = Museo Civico di Storia Naturale di Genova 'Giacomo Doria', Genova, Italy. NSMT = National Science Museum, Zoology Department, Division of Fishes, Tokyo, Japan. NTM = Museums and Art Galleries of the Northern Territory, Ichthyology, Darwin, Northern Territory, Australia. RMNH = Naturalis - National Natuurhistorisch Museum, Leiden, Netherlands. UBDM = Universiti Brunei Darussalam Museum, Zoological Collection. USNM = Smithsonian Institution National Museum of Natural History, Department of Vertebrate Zoology, Division of Fishes, Washington D.C., U.S.A. ZMA = Universiteit van Amsterdam, Faculty of Science, Zoologisch Museum, Amsterdam, The Netherlands. ZMUC = Københavns Universitet, Zoologisk Museum, Vertebrater, Fiskesamlingen, Copenhagen, Denmark. ZRC = Zoological Reference Collection, Department of Life Sciences, Faculty of Science, National University of Singapore, Singapore.

**Appendix 3. Study sites (Figure 1; Table 1).**

- Site 1. Pemburungan Creek. Mangrove creek, 10-20 m wide at its mouth, flowing into the South China Sea. The creek crosses the Meragang coastal lagoon, which is almost completely isolated from the sea by a ~ 100 m-wide coastal ridge.
- Site 2. Pulau (= island) Bedukang. Transect (~ 100 m) along the intertidal gradient, positioned on the west coast of the island. The transect included a pioneer mangrove shore dominated by *Sonneratia* sp., and a mangrove-creek network dominated by *Rhizophora apiculata*, and halophytic ferns of the genus *Acrostichum* colonising mud mounds built by crustaceans of the genus *Thalassina* (*Thalassina* mounds).
- Site 3. Pulau Berembang. Patch of nypah forest (*Nypa fruticans*) with *Thalassina* mounds colonised by *Acrostichum* ferns, at ~ 300 m from the northeastern coast of the island.
- Site 4. Pulau Pepataan. Pioneer mangrove forest (*Avicennia alba*, *Rhizophora apiculata*) along the northern coast of the island, at 5-20 m from the first line of trees.
- Site 5. Pulau Selirong, site A. Banks of the Sungai Melimbai creek, at ~ 5 km from its confluence with the creek Aloh Besar, which delimits the southern coast of Selirong island. The site was ~ 4 km from the coastline. The creek banks were colonised by a ~ 30 m-wide stand of *Rhizophora apiculata*, followed by patches of *Acrostichum* ferns, and a steep transition (2-3 m wide) to a backforest swamp with *Pandanus* palms.
- Site 6. Pulau Selirong, site B. Area ~ 1 km south of the mouth of the Aloh Besar, along the marine fringe of a stand of *Rhizophora apiculata*, at 5-10 m from the first line of trees.
- Site 7. Serasa jetty. Artificial strip of land ~ 5 m wide, projecting for ~ 100 m into the sea, and protected on both sides by 2-3 m of rocky breakwaters.
- Site 8. Sungai (= river) Belayang. Bank of a tributary of the Belayang river, which is a tributary of the Kibi river. The bank was covered by a ~ 50 m fringe of *Nypa fruticans*, and was positioned at ~ 8 km from the coastline.
- Site 9. Sungai Besar. Tract of coast on the western bank of the Brunei Bay, colonised by a 100 m-long and ~ 15 m-wide mangrove fringe (*Sonneratia* sp.), located ~ 100 m north of the mouth of a small river (= Sungai Besar).
- Site 10. Sungai Bunga. Tract of coast on the western bank of the Brunei Bay, at the mouth of the Brunei river and in front of the northern tip of Berembang island. The area included a 50-350 m intertidal zone, including an unvegetated mudbank; a pioneer mangrove fringe (*Sonneratia* sp. and *Rhizophora apiculata*); a middle mangrove forest dominated by *Rhizophora apiculata*; a high forest dominated by *Acrostichum* ferns and *Thalassina* mounds; and a transition to the backforest, with thorny palms, *Pandanus* sp. and *Hibiscus* sp.
- Site 11. Sungai Salar. Mangrove forest (*Rhizophora apiculata*, *Xylocarpus granatum*) and mud banks of a tributary of Sungai Salar, at < 5 m from the water's edge.
- Site 12. Sungai Tutong. *Nypa fruticans* forest, forming a ~ 100 m-wide fringe, along the southern bank of the mouth of the Tutong river.
- Site 13. Ujong Bukit. Mud bank on the western bank of the Kedayan river, which after ~ 450 m flows into the lower tract of the Brunei river, at ~ 12 km from the western coast of the Brunei Bay. The area is occupied by a small village made of stilt houses.