

**A NEW SPECIES OF MUDSKIPPER, *BOLEOPHTHALMUS POTI*
(TELEOSTEI: GOBIIDAE: OXUDERCINAE) FROM THE GULF OF PAPUA,
PAPUA NEW GUINEA, AND A KEY TO THE GENUS**

Gianluca Polgar

*Institute of Ocean and Earth Science, University of Malaya, Kuala Lumpur, Malaysia 50603
Department of Biology, University of Brunei Darussalam, Bandar Seri Begawan, Gadong, Negara Brunei Darussalam
Email: gianluca.polgar@gmail.com (Corresponding author)*

Zeehan Jaafar

Department of Biological Sciences, National University of Singapore, Singapore 117543

Peter Konstantinidis

Department of Comparative Zoology and Evolutionary Biology, Friedrich Schiller University, 07743 Jena, Germany

ABSTRACT. — *Boleophthalmus poti*, new species, is described from the Gulf of Papua, Papua New Guinea. It is distinguished from its congeners by a combination of characters, including: un-notched, flattened and horizontally disposed dentary teeth; pelvic-disc length ~10% of SL; D1 base length ~15% of SL; D2 base length ~40% of SL; ~5 interdorsal scale rows; ~110 lateral-scale rows; and the shape and colour pattern of the first and second dorsal fins.

KEY WORDS. — *Boleophthalmus*, taxonomy, oxudercine gobies, amphibious gobies, Fly River delta

INTRODUCTION

Boleophthalmus Valenciennes, 1837, is a genus of amphibious gobies, commonly known as mudskippers (Gobiidae: Oxudercinae; sensu Hoese, 1984) distributed in tropical and temperate intertidal habitats of the Indo-Pacific region, from the Persian Gulf eastward to the Gulf of Papua, and from southern Japan southward to northern Australia. The name *Boleophthalmus* refers to the capability of its members to rapidly raise their eyes above the level of their orbital cavities, as if the eyes were being ejected (Cuvier & Valenciennes, 1837), and is derived from the Greek βολε (ejected), and οφθαλμος (eye). This genus is characterised by the unique presence of a rectangular cartilage anterior to the pelvic spines, and by greatly thickened skin on the head and nape (Murdy, 1989). Five species are recognised within this genus: *B. birsongi* Murdy, 1989; *B. boddarti* (Pallas, 1770); *B. caeruleomaculatus* McCulloch & Waite, 1918; *B. dussumieri* Valenciennes, 1837; and *B. pectinirostris* (Linnaeus, 1758).

In the cladistic analysis conducted by Murdy (1989), the genera *Boleophthalmus*, *Periophthalmus* Bloch & Schneider, 1801, and *Periophthalmodon* Bleeker, 1874, were grouped in the same clade with the following shared characteristics: the abductor superficialis muscle of the

pectoral fin being divided into two sections (presumably aiding in terrestrial locomotion; Murdy, 1989; Eggert, 1929); and anteriorly enlarged neurocranial cavities, with a curved frontal interorbital bridge which overlaps with the ethmoid bones (Murdy, 1989). These three genera, along with the sister genus *Scartelaos* Swainson, 1839, exhibit true amphibious behaviour, being fully terrestrial for a portion of their daily cycle, and have dermal cups (sensu Murdy, 1989) below the orbits (dermal cups were later also observed in *Zappa confluentus* (Roberts, 1978) by Polgar et al. (2010).

Adult individuals of all species of *Boleophthalmus* typically live in open, non-vegetated areas of lower intertidal zones (Polgar & Crosa, 2009; Polgar et al., 2010). All congeners display a characteristic feeding behaviour in which the lower jaw is pressed on the wet substrate, typically soft intertidal mud, and the head is swept from side-to-side, thus scraping the biofilm on the substrate with the flat, and horizontally disposed dentary teeth (first author, pers. obs.). Analyses of gut contents and stable isotope signatures of *B. boddarti*, *B. dussumieri*, and *B. pectinirostris* indicate that these species feed mainly on epipelagic diatoms (e.g., Rodelli et al., 1984; Clayton & Wright, 1989; Yang et al., 2003). The species of *Boleophthalmus* share with the species of several related genera a significantly reduced premaxillary

ascending process, and a lack of connection between it and the palate-premaxillary ligament (Murdy, 1989). This condition, their elongate snout and jaws, and their slightly depressed heads appear to be adaptive to their feeding behaviour.

While carrying out ecological studies on amphibious gobies within the Fly River delta, Gulf of Papua, New Guinea, the senior author observed and collected an undescribed species of *Boleophthalmus*. The ecology and habitat differentiation of different size classes of this unidentified species were investigated by Polgar et al. (2010; as "*Boleophthalmus* sp."). This species is here described with the inclusion of a modified key to the genus, adapted from Murdy (1989).

MATERIAL AND METHODS

Specimens were collected by hand in tidally exposed burrows, seaward to the pneumatophore zones of pioneer mangrove shores dominated by *Sonneratia caseolaris* (L.) Engler, and along mud banks of intertidal creeks. They were transported alive to the laboratory, euthanized by rapid cooling (-25°C), fixed and preserved in 60–70% undenatured ethanol. Measurements were taken with vernier calipers to the nearest 0.1 mm and are expressed as a percentage of the fish standard length (SL), unless otherwise stated. Counts were made under a dissecting binocular microscope. Measurements and counts followed Murdy (1989), except as indicated below.

Head length was measured as the linear distance from the anteriormost part of the head, to the posteriormost margin of the opercular bones. Caudal-fin length was obtained by subtracting the value of the measurement of the standard length from the total length of the fish. Body width was measured as the transverse linear distance between the margins of the body at the base of the pectoral fins, measured immediately after the opercular margin. Murdy (1989) reported to measure pectoral-fin length following Hubbs & Lagler (1964: 25), thus measuring it as the linear "distance from the extreme base of the uppermost (...) ray to the farthest tip of the fin (...)". Pectoral fins' anatomy of mudskippers includes an enlarged muscular base, whose differential development appears as an adaptation to the amphibious lifestyle. Therefore, we here consider the pectoral fin to include both the radials and the muscular portion, and thus measured the pectoral-fin length as the linear distance from the dorsal point of insertion of the muscular base of the pectoral fin to its posteriormost tip. Measurements of pectoral-fin length following Hubbs & Lagler (1964) were also made, to allow for comparisons with other datasets. Accordingly, pectoral-fin height was measured as the linear vertical distance from the dorsal and the ventral points of insertion of the base of the pectoral fin, thus including the base. Measurements of the pectoral-fin height not including the base (i.e. from the extreme base of the dorsalmost ray to the extreme base of the ventralmost ray) were also included for comparisons. The pelvic-fin length was measured as the linear distance along

the longitudinal midline from the base of the pelvic spines to the distalmost tip of the pelvic disc.

The number of principal-caudal rays was counted as the number of branched caudal rays, plus two (Hubbs & Lagler, 1964; McDowall, 2003). Hubbs & Lagler (2004: 32) defined the lateral-line scale count as the "number of pored scales in the lateral line or the number of scales along the line in the position that would normally be occupied by a typical lateral line". As mudskippers do not have pored scales, we counted the number of "scale rows along side of body" (Hubbs & Lagler, 1964) between the landmarks defined by Hubbs & Lagler (2004), i.e., starting and including the first scale row overlying the posterior edge of the pectoral girdle, to the first scale row intersecting the scale column immediately anterior to the hypural crease, or overlapping it, if the middle of the scales' exposed fields lay anterior to the crease (Fig. 1). The "scales in a longitudinal series", or "longitudinal scales" were also counted to allow comparisons with Murdy's dataset (1989), counting from "the dorsoposterior attachment of the opercular membrane", then following "a posteroventral diagonal to the tip of the pectoral fin, and then in a straight line along the midline of the body to the posterior edge of the hypural plate, determined externally" (Murdy, 1989: 3, 84; Fig. 1). The transverse scales counted ventrally forward were counted from the origin of the anal fin, forward and up to the base of the first dorsal fin, or to its continuation along the dorsal midline. The number of interdorsal scale rows was counted from the posterior point of insertion of the first dorsal fin membrane to the point of insertion of the first element of second dorsal fin. The number of caudal peduncle scale rows was counted from the posterior point of insertion of the second dorsal fin membrane to the anterodorsal point of insertion of the caudal fin. The thick dermal papillae covering the head, nape and predorsal area prevented scale counts in these areas. Therefore, whenever counts crossed these areas, the papillae were conventionally counted as if they were scales. Fishes were sexed by examining the shape of the opening

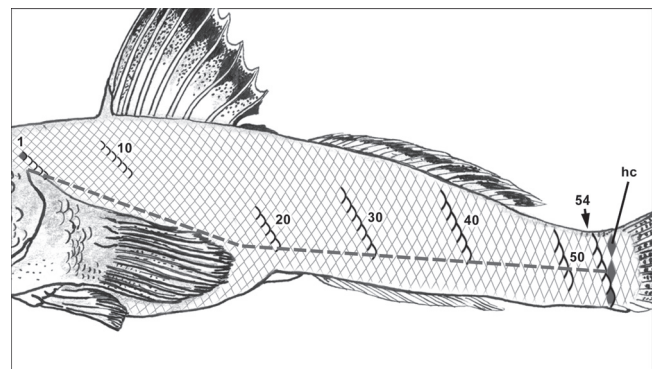


Fig. 1. Diagram of a mudskipper with 54 lateral scale rows (head to the left); 1 = scale overlapping the pectoral girdle (shaded); hc = scale column immediately before or overlapping with the hypural crease (shaded); scale rows (Hubbs & Lagler, 2004) are traced out at intervals of 10 rows; note that the rows can be detected and followed both above and below the lateral midline. For a comparison, Murdy's (1989) count of longitudinal scales (~ 70 scales are crossed by the dashed line) is also illustrated.

of the urogenital papilla: pointed in males, and spatulate in females (Miller, 1986).

One specimen (BMNH 2011.1.27.1; Fig. 3) was cleared and stained following the protocol by Taylor & Van Dyke (1985). The cartilaginous structures did not stain due to the initial preservation in ethanol, but cartilage could clearly be discriminated from other structures after the clearing process.

To explore the distribution of the measured specimens in a multivariate morphological space and select informative taxonomic descriptors, standard multivariate analyses were conducted on morphometric and meristic datasets (PCA and PCO, respectively; PAST; Hammer et al., 2001; Hammer & Harper, 2005). Following the method of Darroch & Mosimann (Darroch & Mosimann, 1985; Jungers et al., 1995), the morphometric matrix was first logarithmically transformed, and the arithmetic mean of all variables was subtracted from each variable, thus suppressing the size factor, defined as the geometric mean of all morphometric variables, and creating scale-free variables. Missing values (i.e., damaged caudal fins) were supported by mean value imputation (Hammer et al., 2001). Meristic data were logarithmically transformed, to standardise variances and obtain a scale-invariant covariance matrix (Jolicoeur, 1963; Strauss, 1985; Hammer & Harper, 2005).

Abbreviations used in this paper as follows – ABL: length of anal-fin base; AEL: number of elements of the anal fin; BD: body depth; BW: body width; CFL: caudal-fin length; CPR: number of principal-caudal rays; D1: first dorsal fin; D1BL: length of D1 base; D1D2: number of interdorsal scale rows; D1SP: number of elements of the first dorsal fin; D2: second dorsal fin; D2BL: length of D2 base; D2C: number of caudal peduncle scale rows; D2EL: number of elements of the second dorsal fin; HD: head depth; HL: head length; HW: head width; LPD: least caudal peduncle depth; NSR: number of lateral-scale rows; PCTHL: height of pectoral-fin base (left); PCTLL: pectoral-fin length (left); PCTRL: pectoral-fin rays (left); PCTRR: pectoral-fin rays (right); PLVL: pelvic-disc length; PRD: number of predorsal scales; SL: standard length; TL: total length; TRB: transverse scales counted ventrally backward; TRDB: transverse scales counted dorsally backward; TRF: transverse scales counted ventrally forward.

Specimens examined in this study are deposited in: Australian Museum, Sydney, Australia (AMS); Academy of Natural Sciences, Philadelphia, United States of America (ANSP); The Natural History Museum, London, United Kingdom (BMNH); Canadian Museum of Nature, Ottawa, Canada (CMN FI); Los Angeles County Museum, Los Angeles, United States of America (LACM); Civic Museum of Zoology of Rome, Italy (MCZR); Civic Museum of Natural History of Genoa, Italy (MSNG); National Science Museum, Tokyo, Japan (NSMT); Museums and Art Gallery of the Northern Territory, Darwin, Australia (NTM); Smithsonian National Museum of Natural History, Washington D.C., United States of America (USNM);

Museum für Naturkunde Humboldt Universität, Berlin, Germany (ZMB); Universität Hamburg, Biozentrum Grindel und Zoologisches Museum, Hamburg, Germany (ZMH); and Raffles Museum of Biodiversity Research, National University of Singapore, Singapore (ZRC).

A complete specimen (ZRC 52249, not included in the description of species) and fin-clips from the right pectoral fin of the specimens MSNG 56893, USNM 405556/3, ZRC 52240/2 were preserved in absolute ethanol for molecular analyses. All lengths are in SL, unless otherwise stated.

TAXONOMY

Family GOBIIDAE Cuvier & Valenciennes, 1837
Subfamily OXUDERCINAE Günther, 1861

Boleophthalmus poti, new species

(Figs. 2, 3, 5; Tables 1, 2)

Material examined. — Holotype: MSNG 56891, female, 89.9 mm SL; Papua New Guinea, Western Province, Fly river delta, Sisikura Island, 8°25'45.7"S, 143°36'24.0"E, coll. G. Polgar, A. Sacchetti & C. Tenakenai, 24 Sep.2007.

Paratypes: BMNH 2011.1.27.1, 1 female (cleared and stained), 108.2 mm SL; MSNG 56892, 1 male and 1 female, 89.6–104.5 mm SL; USNM 405556, 3 males, 80.5–105.8 mm SL; ZRC 52240 2 males and 1 female, 78.0–99.4 mm SL; same data as holotype. MSNG 56893, 1 male, 99.5 mm SL; Papua New Guinea, Western Province, Fly river delta, Purutu Island, Wapi Creek, 8°23'21.0"S, 143°31'23.4"E, coll. G. Polgar, A. Sacchetti & C. Tenakenai, 23 Sep.2007.

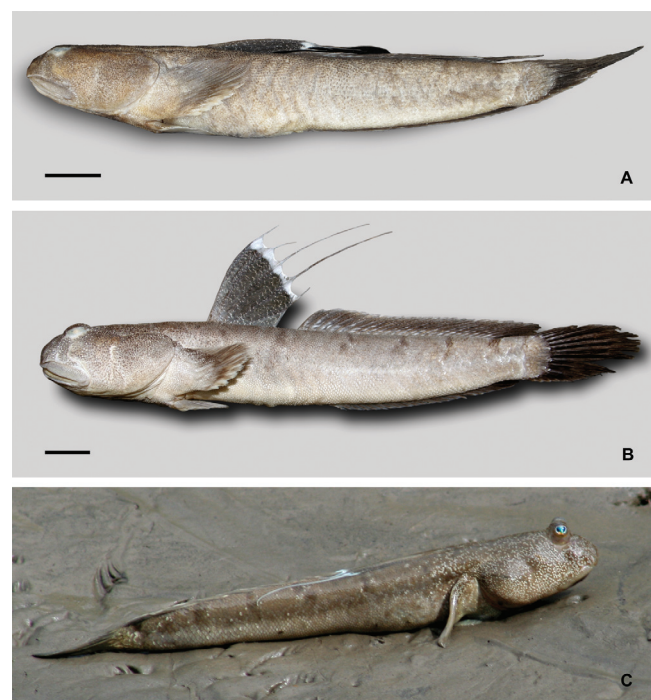


Fig. 2. *Boleophthalmus poti*: A, holotype, MSNG 56891; B, paratype, preserved specimen, female (108.2 mm) (BMNH 2011.1.27.1); C, an individual in its natural habitat, on the mud banks of Wapi Creek, Purutu Island, Fly River delta. Scale bars =10 mm.

Non-type material: ZRC 51367, 2 ex., 35–50 mm, Purutu Island, Fly River delta, Papua New Guinea, 2007; ZRC 52249, 1 ex., 80.4 mm, same data as holotype.

Diagnosis. — *Boleophthalmus poti* is similar to *B. birdsongi* and *B. caeruleomaculatus*, sharing with these species unnotched, flattened and horizontally disposed dentary teeth. It is distinguished from these species (and all remaining congeners) by having elongate D1 fin spines, protruding from the fin margin, in both sexes and the following unique features of dorsal-fin colouration in live individuals: D1 with clearly demarcated sky-blue to whitish marginal band; interradial membranes of D1 greenish-brown, spotted with whitish to yellowish speckles, sometimes fused into broken, narrow and wavy lines; interradial membranes of D2 grey to pale brown, darker posteriorly, pale grey distally, with a very thin white margin and columns of 0–5 whitish spots between adjacent rays; D2 rays darker than interradial membranes.

Description. — General body shape as in Figs. 2, 5C. Meristic and morphometric data are presented in Tables 1, 2. Head subcylindrical, about as wide as deep; body subcylindrical in thoracic region, becoming slightly compressed caudally; mouth subterminal, with jaw extending posteriorly to vertical point immediately posterior to posterior margin of eye. Lower jaw containing 2–8 caninoid teeth and 14–37 distally flattened, anteriorly directed and horizontally displaced teeth on each side. One recurved, canine tooth on both sides of mandibular symphysis, internal to the anterior margin of mandible (Fig. 3). Posterior interorbital pore present. Anterior nare positioned at tip of triangular pendulous flap overhanging upper lip; posterior nare as slit immediately in front of anterior margin of eye. Anterior oculoscapular canal pores anterior to posterior nares, at ~1/3 the distance from eye to upper lip. Gill opening extending for ~4/5 of height of pectoral-fin base. All first-dorsal fin spines protruding from fin margin: elements III–V elongate, element IV longest in both sexes (Figs. 2B, 5C). In larger specimens, adpressed

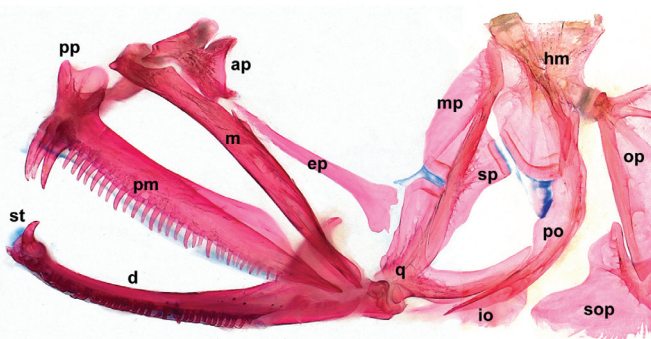


Fig. 3. *Boleophthalmus poti*, BMNH 2011.1.27.1. Lateral view of the suspensorium. Abbreviations: ap = autopalatine; d = dentary; ep = ectopterygoid; hm = hyomandibular; io = interopercle; m = maxilla; mp = metapterygoid; op = opercle; pm = premaxilla; po = preopercle; pp = ascending processes of the premaxilla; q = quadrate; sop = subopercle; sp = symplectic; st = symphyseal tooth. Scale bar = 1 mm. the original image was reversed horizontally.

pectoral fin reaching a vertical point anterior to terminus of D1. Caudal fin ovate; pelvic fins completely fused into round disc with large pelvic frenum connecting pelvic spines, and basal membrane connecting innermost pelvic rays.

Live colouration. — Background colouration of dorsolateral portion of body and head yellowish-brown to greyish (Figs. 2C, 5C); ventral portion greyish and paler; in some individuals, isthmus, throat and thoracic region dark grey; scattered tiny whitish speckles covering head, extending anteriorly and dorsally from snout to insertion of D1; 8–10 subvertical, saddle-like, bilaterally asymmetrical and irregular dark brown bars on dorsum (2–3 before D1, 2 in front and behind D1, and 4–5 below D2), saddle-like bars never extending below lateral midline; one horizontal, darker, irregular brownish band 1/3 width of body depth may be present on sides above lateral midline and below saddle-like bars, coursing from pectoral fins to caudal peduncle; sparse whitish speckles present on flanks; several scales on caudal peduncle with whitish margins. Caudal fin with grey interradial membranes and black rays. Anal fin with blackish rays and darkened inter-radial membrane, posterior portion more densely pigmented. Pectoral fins with translucent interradial membranes and pale brown rays, muscular base with similar colouration to body. Pelvic fins with translucent interradial membranes and pale brown rays, proximally dark grey, both dorsally and ventrally.

Preserved colouration. — Body colouration dorsally and laterally greyish, ventrally paler (Fig. 2A, B); isthmus, throat and thoracic regions grey, dark grey in some individuals. Small white speckles and vertical dark bars visible in preservation; on fins, live brown colour becoming grey and yellow whitish; live whitish pigmentation remains in preservation; other traits as in vivo.

Distribution. — *Boleophthalmus poti* is presently known only from the delta of the Fly River, in the Gulf of Papua (Fig. 4).

Etymology. — The indigenous people of the Wapi villages of Purutu Island, the type locality, call this species ‘poti’, that in their language means ‘spotted’ and refers to the numerous tiny whitish spots present on the head of this species.

Remarks. — Freshly dead individuals of *B. poti* less than 5 cm SL (e.g., ZRC 51367) have a transparent, indistinct margin of D1, a much less densely pigmented D2 with columns of brownish spots on a transparent background, hyaline pelvic fins, scattered dark brown spots on the head and flanks on the anterior third of the body, and some irregular brown blotches on flanks, roughly corresponding to the dorsal saddle-like bands observed in larger specimens.

Boleophthalmus birdsongi was the only congener reported previously to possess flattened dentary teeth, lacking notches (Murdy, 1989) but examination of all congeners revealed this tooth type is also present in *B. caeruleomaculatus* and *B. poti*.

Table 1. Meristic data for *Boleophthalmus poti* (n = 10; the cleared and stained paratype BMNH 2011.1.27.1 is not included).

	Holotype MSNG 56891	Range (holotype plus paratypes)
Fin-ray counts		
First dorsal fin	5	5
Second dorsal fin	26	23–26
Anal fin	25	24–26
Pectoral fin (left/right)	19/19	18–19/18–20
Principal-caudal rays	17	16–18
Scale counts		
Number of lateral-scale rows	97	97–119
Number of longitudinal scales	106	102–114
Transverse scales counted ventrally backward	39	31–39
Transverse scales counted dorsally backward	39	37–42
Transverse scales counted ventrally forward	40	39–46
Predorsal scales	58	58–69
Number of interdorsal-scale rows	4	3–6
Number of caudal-peduncle scale rows	9	4–9

Boleophthalmus poti differs from *B. birdsongi* (Fig. 5A) in having fewer interdorsal scale rows (3–6 vs. 6–9, respectively; Tables 1, 3), a longer D1 base (13–15% SL vs. 10–13% SL, respectively; Murdy, 1989; Tables 2, 4), and

in the colouration of the unpaired fins: in the latter species, D1 is proximally black and distally blue; D2 has a narrow whitish basal portion, proximally and medially black, and a yellowish to whitish marginal band.

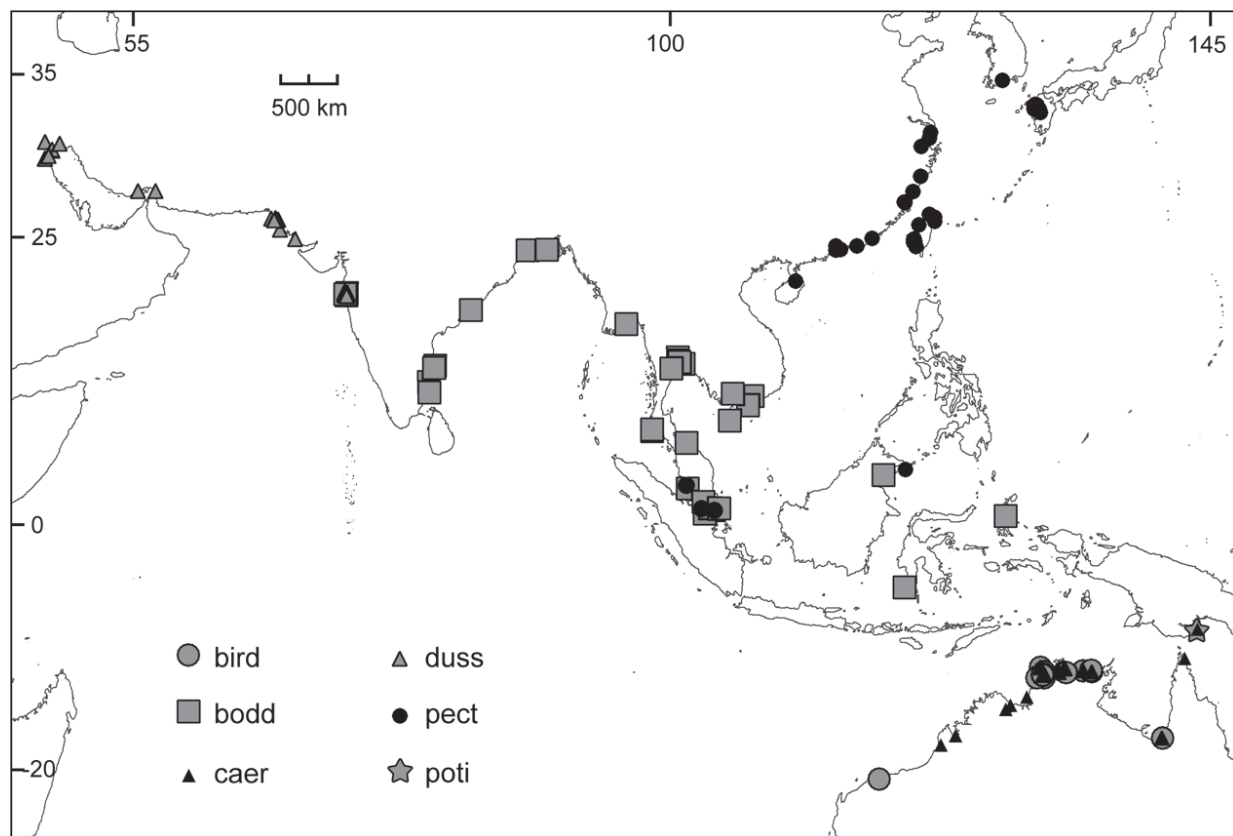


Fig. 4. Geographical distribution of the species of *Boleophthalmus*: point data; bird = *Boleophthalmus birdsongi*; bodd = *Boleophthalmus boddarti*; caer = *Boleophthalmus caeruleomaculatus*; duss = *Boleophthalmus dussumieri*; pect = *Boleophthalmus pectinirostris*; poti = *Boleophthalmus poti*. Data from Murdy, 1989; Swennen et al., 1995; Rainboth, 1996; Takita et al., 1999; Nakabo, 2002; Nanami & Takegaki, 2005; Chen et al., 2007; Froese & Pauly, 2007; Ocean Biogeographic Information System, 2007; Baeck et al., 2008; Global Biodiversity Information Facility, 2008; Larson et al., 2008; Polgar & Crosa, 2009. Data in online databases were verified by comparison with museum material and published references.

Table 2. Morphometric data for *Boleophthalmus poti* (n = 10; the cleared and stained paratype BMNH 2011.1.27.1 is not included).

	Holotype MSNG 56891	Range (holotype plus paratypes)
Total length (mm)	112.5	94.4–133.0
Standard length (mm)	89.9	78.0–105.8
In % SL		
Head length	25.4	24.4–26.4
Body depth	12.2	10.6–13.5
Body width	10.6	9.3–10.6
Length of D1 base	14.7	12.7–15.3
Length of D2 base	41.9	39.7–42.9
Length of anal-fin base	38.5	36.7–39.7
Least caudal-peduncle depth	6.9	6.9–8.0
Pectoral-fin length, base included/not included (left)	17.9/14.7	15.2–21.0/13.8–18.0
Pectoral-fin height, base included/not included (left)	11.7/7.7	10.7–12.5/6.3–7.7
Pelvic-disc length	12.2	11.2–12.3
Caudal-fin length	25.1	21.0–25.7
In % head length		
Head depth	49.1	47.6–52.7
Head width	53.1	48.3–58.5

Boleophthalmus poti differs from *B. caeruleomaculatus* (Fig. 5B) in the smaller number of lateral-scale rows (97–119 vs. 130–151, respectively; Tables 1, 3), a shorter D2 base (40–43% SL vs. 43–48% SL, respectively) and a shorter pelvic disc (11–12%SL vs. 16–18%SL, respectively; Tables 2, 4; Murdy, 1989), in body colouration, which in the latter species includes sky-blue speckles on head, dorsum and flanks, and a sky-blue patch of skin below the orbits, and in the colouration of the unpaired fins: *B. caeruleomaculatus* lacks distinct marginal bands and has sky-blue spots on the interradiial membranes, arranged in series along the whole length of rays.

Boleophthalmus caeruleomaculatus also attains a larger size than the other two species (maximum recorded size = 165 mm, vs. 111 mm and 106 mm of *B. birdsongi* and *B. poti*, respectively; Murdy, 1989; Takita et al., 2011; this study), and exhibits sexual dimorphism in the D1: females have elongated spines III–V, the IV being the longest one.

Multivariate analyses of meristic and morphometric datasets (n = 25; Tables 3, 4; Hammer et al., 2001) showed that *B. birdsongi*, *B. caeruleomaculatus*, and *B. poti* are morphologically distinct (Fig. 6A, B). Consistent with the above results, the length of D1 base and the pelvic fin length had higher PC1 and PC2 loadings (>0.5; Fig. 6B).

Boleophthalmus poti is traditionally consumed and used as bait in the delta of the Fly River, together with the other mudskipper species *B. caeruleomaculatus* and *Periophthalmodon freycineti* Quoy & Gaimard (Polgar & Lim, 2011).

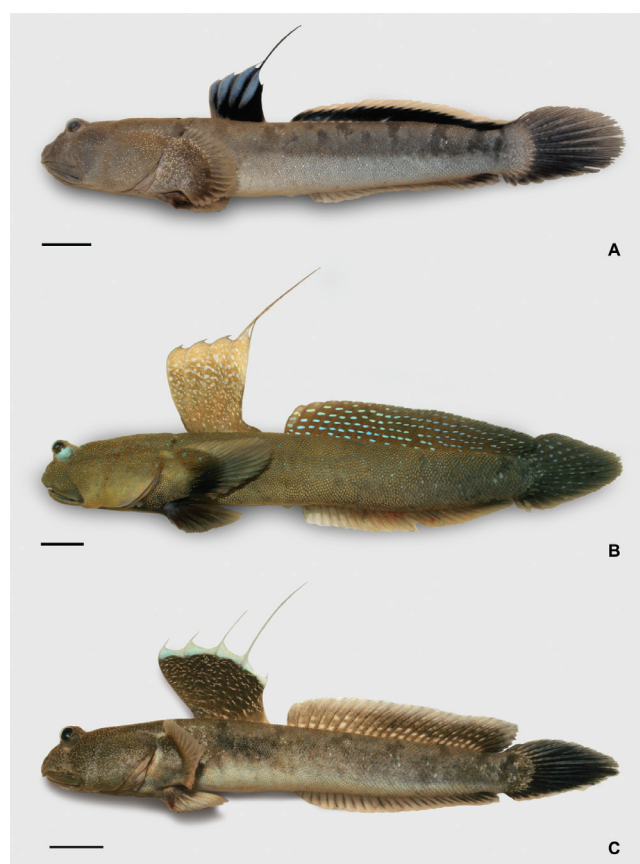


Fig. 5. Shape and colouration of freshly dead species of *Boleophthalmus* with un-notched dentary teeth: A, female of *B. birdsongi* (95 mm; ZRC 52250); B, female of *B. caeruleomaculatus* (106 mm; MSNG 54689); and C, paratype, male of *B. poti* (83.4 mm; USNM 40566). Scale bars = 10 mm.

Table 3. Meristic dataset of the PCO analysis for *B. birdsongi*, *B. caeruleomaculatus*, and *B. poti*. The cleared paratype (BMNH 2011.1.27.1) is not included.

	DISP	D2EL	AEL	PCTRL	PCTRR	CPR	NSR	TRB	TRDB	TRF	PRD	D1D2	D2C
<i>B. birdsongi</i>	5	25	23	19	19	17	109	37	37	44	55	7	7
<i>B. birdsongi</i>	5	24	24	20	19	17	121	42	43	46	57	9	8
<i>B. birdsongi</i>	5	24	24	20	19	18	128	36	44	44	50	8	7
<i>B. birdsongi</i>	5	24	24	19	19	18	109	40	39	43	50	6	8
<i>B. birdsongi</i>	5	25	24	19	19	17	102	39	39	43	56	8	9
<i>B. birdsongi</i>	5	24	23	19	19	18	109	39	41	41	50	8	12
<i>B. birdsongi</i>	5	25	24	20	19	18	103	36	39	45	50	7	9
<i>B. birdsongi</i>	5	24	23	19	19	19	115	39	45	48	60	8	5
<i>B. birdsongi</i>	5	24	23	19	19	19	106	35	40	48	65	7	7
<i>B. birdsongi</i>	5	24	23	19	19	17	114	35	37	45	65	9	9
<i>B. birdsongi</i>	5	24	24	19	19	17	110	39	40	48	65	9	10
<i>B. caeruleomaculatus</i>	5	28	27	20	20	17	151	35	40	46	50	7	8
<i>B. caeruleomaculatus</i>	5	27	27	20	20	17	139	37	46	46	54	6	8
<i>B. caeruleomaculatus</i>	5	27	26	19	19	18	131	40	39	49	60	5	9
<i>B. caeruleomaculatus</i>	5	28	27	18	20	17	130	32	41	54	62	5	5
<i>B. poti</i>	5	26	25	19	19	17	97	39	39	40	58	4	9
<i>B. poti</i>	5	25	25	19	20	17	100	34	40	39	62	5	7
<i>B. poti</i>	5	25	25	18	18	17	108	36	39	40	65	3	9
<i>B. poti</i>	5	26	25	18	18	17	101	38	38	44	62	3	7
<i>B. poti</i>	5	24	24	19	19	18	106	33	38	46	69	5	7
<i>B. poti</i>	5	25	25	19	19	17	104	35	37	46	64	6	6
<i>B. poti</i>	5	25	25	19	19	17	119	35	42	43	63	5	5
<i>B. poti</i>	5	26	26	19	19	17	108	31	38	42	59	6	6
<i>B. poti</i>	5	25	24	19	19	17	108	36	38	44	62	4	4
<i>B. poti</i>	5	23	24	19	19	16	107	32	41	45	60	5	5

Table 4. Morphometric dataset of the PCA for *B. birdsongi*, *B. caeruleomaculatus*, and *B. poti*; measurements are in mm. HW was not included in this analysis, since it varies with the degree of expansion of the opercles; SL and TL were also not included, since they do not convey information about shape. The cleared paratype (BMNH 2011.1.27.1) is not included; ? = missing values (damaged caudal fins).

		ABL	BD	BW	CFL	D1BL	D2BL	HD	HL	HW	LPD	PCTLL	PCTHL	PLVL	SL	TL
<i>B. birdsongi</i>	AMS I. 24686-015	29.3	11.9	9.7	19.7	8.2	32.5	11.7	21.5	13.6	6.7	16.3	8.6	11.6	76.1	95.8
<i>B. birdsongi</i>	AMS I. 25511-005/1	28.8	11.9	11.1	18.7	8.8	31.7	13.2	22.2	14.0	7.1	16.5	8.7	11.2	78.0	96.7
<i>B. birdsongi</i>	NTMS11362-032/1	37.9	15.5	12.6	25.9	12.2	39.6	15.7	28.7	15.1	9.4	20.7	11.8	15.2	99.1	124.9
<i>B. birdsongi</i>	NTMS11362-032/2	40.1	17.1	13.1	27.9	12.9	45.3	16.7	29.7	14.6	9.7	21.6	13.1	13.8	108.2	136.0
<i>B. birdsongi</i>	NTMS11362-032/3	38.8	14.2	13.4	26.1	10.6	41.0	16.5	30.0	18.3	9.4	23.2	11.8	14.2	102.7	128.8
<i>B. birdsongi</i>	NTMS11362-032/4	26.3	11.2	8.9	18.5	7.8	27.5	11.7	21.9	10.9	6.4	14.4	8.7	9.5	72.8	91.3
<i>B. birdsongi</i>	NTMS10694-006/1	29.9	12.8	10.0	21.0	9.3	34.9	13.4	23.3	13.3	7.2	16.0	8.9	12.1	81.0	102.0
<i>B. birdsongi</i>	NTMS10421-001/1	39.1	18.4	15.1	26.6	11.2	41.4	16.9	30.0	17.1	9.8	22.6	12.4	15.9	99.9	126.4
<i>B. birdsongi</i>	NTMS10421-001/2	37.9	17.6	14.5	26.5	12.2	40.6	16.9	30.9	19.8	9.6	22.8	14.1	14.9	102.7	129.2
<i>B. birdsongi</i>	ZRC 52252/1	36.1	16.1	14.4	26.0	12.5	38.3	16.1	29.1	15.2	9.0	17.7	11.3	14.6	95.1	121.1
<i>B. birdsongi</i>	ZRC 52252/2	41.0	17.2	17.2	29.5	12.7	43.5	16.2	31.6	16.3	9.6	21.1	12.1	14.7	106.3	135.8
<i>B. caeruleomaculatus</i>	MCZR VP1016	57.2	20.9	17.3	36.0	21.0	61.4	20.0	38.0	18.7	12.4	37.2	15.9	24.7	136.4	172.4
<i>B. caeruleomaculatus</i>	MCZR VP1017	62.8	20.8	17.1	39.3	24.6	68.5	20.2	39.8	18.7	14.5	33.6	16.0	24.5	146.1	185.4
<i>B. caeruleomaculatus</i>	AMS I. 18393-001/1	67.8	25.6	21.6	50.7	27.3	71.6	27.1	44.9	26.8	15.5	41.4	19.2	28.0	159.3	210.0
<i>B. caeruleomaculatus</i>	AMS I. 14325	74.0	29.1	21.9	41.6	29.1	72.8	25.3	46.6	22.1	16.2	33.8	21.4	28.7	162.7	204.3
<i>B. poti</i>	MSNG 56891	34.6	11.0	9.5	22.6	13.2	37.7	11.2	22.8	12.1	6.2	16.1	10.5	11.0	89.9	112.5
<i>B. poti</i>	MSNG 56892/1	39.4	13.0	9.9	?	14.6	42.5	13.3	26.8	14.1	8.0	21.4	12.4	12.9	104.5	?
<i>B. poti</i>	MSNG 56892/2	34.3	12.1	8.5	23.0	12.6	37.8	11.6	23.4	11.9	7.2	16.3	11.2	10.8	89.6	112.6
<i>B. poti</i>	MSNG 56893	39.1	11.9	10.2	?	14.3	42.5	13.2	25.3	14.5	7.8	20.4	11.3	12.0	99.5	?
<i>B. poti</i>	USNM 405556/1	40.1	12.8	9.8	27.2	14.5	45.4	13.5	25.8	13.1	8.0	19.4	11.8	12.1	105.8	133.0
<i>B. poti</i>	USNM 405556/2	31.7	8.5	7.9	20.0	10.2	32.4	9.9	20.3	9.8	5.7	13.9	8.8	9.7	80.5	100.5
<i>B. poti</i>	USNM 405556/3	32.1	9.2	8.6	19.8	10.8	34.2	10.8	20.5	12.0	6.2	16.1	8.9	9.8	83.4	103.2
<i>B. poti</i>	ZRC 52240/1	39.5	11.3	9.6	23.0	13.6	41.6	12.7	25.6	13.2	7.3	20.9	11.6	11.8	99.4	122.4
<i>B. poti</i>	ZRC 52240/2	32.3	10.6	8.8	20.8	13.5	36.2	11.1	23.3	12.4	6.2	13.4	9.5	10.2	88.1	108.9
<i>B. poti</i>	ZRC 52240/3	28.8	9.8	8.3	16.4	10.2	31.0	9.9	20.0	10.6	5.7	14.1	9.2	8.7	78.0	94.4

KEY TO THE GENUS *BOLEOPHTHALMUS*

This key is adapted from Murdy (1989). Colouration patterns and size of D1 refer to larger specimens.

1. Flattened, horizontal dentary teeth lacking notches 2
 - Flattened, horizontal dentary teeth notched 4
2. Length of D1 base is equal or less than 13% SL; tip of adpressed pectoral fin reaching a vertical point slightly posterior to terminus of D1; D1 membrane proximally black and distally blue in vivo, without spots, completely black in preserved material; D2 with a black, broad medial band, bordered by a narrow whitish basal band and a broad yellowish to whitish marginal band, hyaline on preservation (northern Australia) *B. birdsongi* Murdy
 - Length of D1 base is equal or more than 13% SL; tip of adpressed pectoral fin reaching a vertical point anterior to terminus of D1; D1 membrane with spots or speckles, not black in preserved material; D2 membrane without black medial bands, and with no marginal bands 3
3. Pelvic-fin length is equal to, or greater than, 16% SL; lateral scale rows more than 125; D1, D2 with no distinct marginal band; D1, D2 and caudal fin with series of sky-blue spots, becoming whitish or semi-transparent on preservation, along the whole length of rays; sky-blue skin fold below eyes, not visible upon preservation (northern Australia and Gulf of Papua) *B. caeruleomaculatus* McCulloch & Waite
 - Pelvic-fin length is equal to, or less than, 12% SL; lateral scale rows less than 120; D1 membrane with numerous tiny yellowish speckles (whitish on preservation) and a distinct whitish to sky-blue marginal band (whitish on preservation); D2 with few whitish spots in the proximal portion; caudal fin with no spots or speckles (Gulf of Papua) *B. poti*, new species

4. Longitudinal scales fewer than 80; dorsal margin of pectoral fin black, retained after preservation; in vivo, D1 bright yellow in smaller specimens; dark saddle-like bars often extending below the midline in the posterior third of the body, visible in preserved material (eastern and western coasts of India, Sunda Shelf, eastward to Sulawesi and the Moluccas) *B. boddarti* (Pallas)
 - Longitudinal scales more than 80; pectoral fin with no dark margin; D1 never yellow in vivo; dark saddle-like bars or blotches on flanks never extending below midline, except on the hypural plate 5
5. Length of caudal fin equal to, or greater than 22% SL; dark brown spots on D1, body and head (darker than background), visible in preservation (Arabian Sea and Persian Gulf) *B. dussumieri* Valenciennes
 - Length of caudal fin equal to or less than 22% SL; in vivo, scattered sky-blue spots on D1, body and head (paler than background), often not visible in preservation; black elongate blotches may be present in the distal portion of D1, visible in preservation (Sunda Shelf eastward and northward to southern Japan) *B. pectinirostris* (Linnaeus)

Comparative material. — *Boleophthalmus birdsongi*: NTM S. 10421-001, paratypes, 1 female and 1 ex., 100–103 mm SL; Australia, Northern Territory, Darwin, east arm of Elizabeth River mouth, 1987; NTM S. 10694-006, paratypes, 1 male and 1 female, 61–81 mm SL; Australia, Northern Territory, Darwin, Gunn Point, Mangrove Creek, 1982; NTM S. 11362-032, paratypes, 2 males and 2 females, 73–108 mm SL; Australia, Northern Territory, Millingimbi, northeast of Darbilla Creek, 1984; AMS I. 24686-015, 1 male, 76 mm SL; Australia, Northern Territory, Darwin, main channel of Ludmilla Creek; AMS I. 24689-002, 1

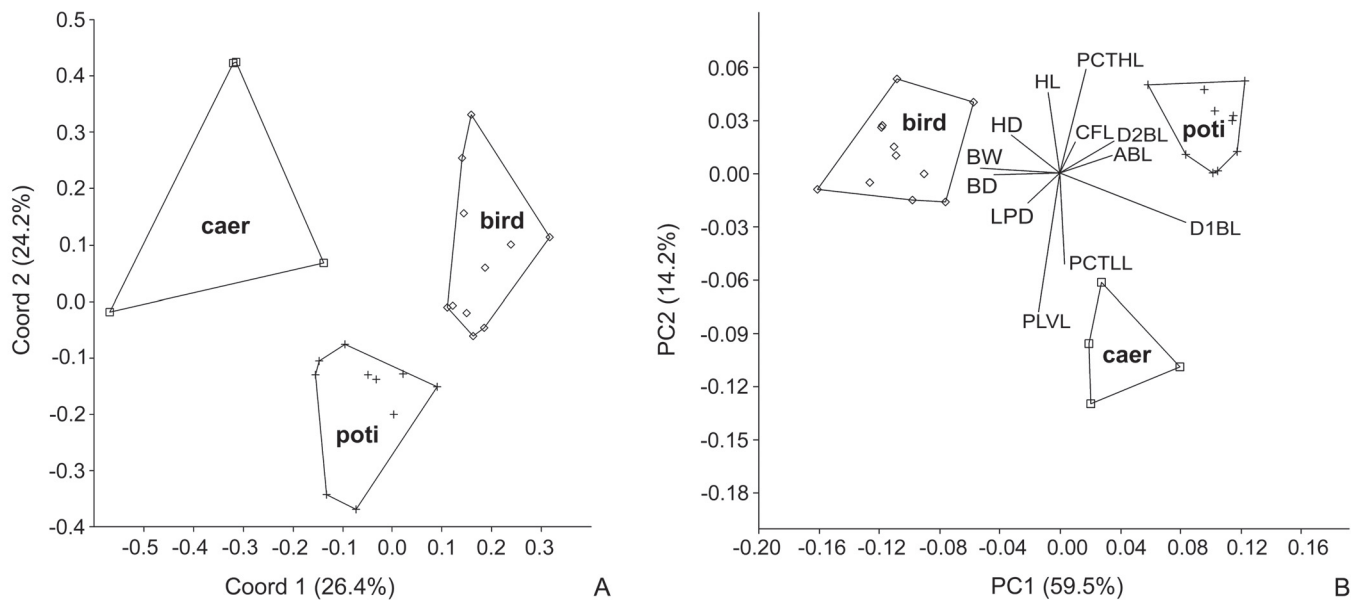


Fig. 6. Multivariate morphological analyses of the three species of *Boleophthalmus* without notched dentary teeth, supporting the separation of the examined specimens in 3 morphologically distinct groups. A: PCO scatter plot of meristic characters, after logarithmic transformation. The two coordinate axes Coord 1 and Coord 2 explained the highest percentage of total variance (in parentheses); closed lined (convex hulls) delimit clusters of specimens of the same species. B: PCA distance biplot of morphometric characters after Darroch & Mosimann transformation (1985). The two principal component axes PC1 and PC2 explained the highest percentage of total variance (in parentheses); closed lines (convex hulls) delimit clusters of specimens of the same species; the variables are projected onto the scattergram as vectors, graphically visualising their PCA loadings, or the degree they enter into the principal components. PLVL separates caer from bird and poti, while D1BL separates bird from caer and poti. bird = *B. birdsongi* (n = 11); caer = *B. caeruleomaculatus* (n = 4); poti = *B. poti* (n = 10). See Tables 3, 4 for the dataset.

male, 67 mm SL; Australia, Northern Territory, Darwin, mouth of Buffalo Creek; AMS I. 25511-005, 1 male, 78 mm SL; Australia, Northern Territory, Darwin, 1 km east of Cossacks, Cossack mangroves; ZRC 52250, 1 ex., 87 mm SL; Australia, Northern Territory, Darwin, Buffalo Creek, 2007; ZRC 52252, 1 male and 1 female, 95–106 mm SL; Australia, Northern Territory, Darwin, Sadgroves Creek, 2007; ZRC 52287, 5 ex., 16.5–58.5 mm SL; Australia, Northern Territory, Darwin, 2001.

Boleophthalmus boddarti: ZMB 2145, syntypes of *Gobius striatus* Bloch & Schneider, 1801, 2 ex., 115–128 mm SL; India, Tamil Nadu, Tranquebar [=Tharangambadi], 1800; ANSP 85017, 5 ex., 84–99 mm SL; India, Maharashtra, Bombay [=Mumbai], 1924; ANSP 77540, 1 ex., 86 mm SL; India, Tamil Nadu, Madras [=Chennai], 1922; MSNG 54124, 1 ex., 108 mm SL; Malaysia, Selangor, Sungai [=River] Sementa Besar, 1996; MSNG 54636, 1 ex., 95 mm SL; Bangladesh, Khulna, Bagerhat, Mongla Upazila, 2008; MSNG 54637, 2 ex., 61–103 mm SL; Malaysia, Johor, Tanjung [=Cape] Piai, 2006; ZMH 19369, 3 ex., 35–53 mm SL; India, Maharashtra, Bombay [=Mumbai], 1929.

Boleophthalmus caeruleomaculatus: AMS I. 14325, paratype, 1 male, 163 mm SL; Australia, Northern Territory, Adelaide River, 1917; AMS I. 18393-001, 1 male, 159 mm SL; Australia, Northern Territory, Arnhem Land, Liverpool River mouth; AMS I. 21219-001, 2 ex., 41–64 mm SL; Australia, Northern Territory, Shoal Bay, False Creek; AMS IB.2836, 1 male, 111 mm SL; Australia, Western Australia, Forrest River Mission; MCZR VP1016, 1 male, 136 mm SL; Papua New Guinea, Western Province, Fly River delta, Sisikura Island, coll. G. Polgar, A. Sacchetti a& C. Tenakenai, 24 Sep.2007; MCZR VP1017, 1 female, 146 mm SL; locality, collectors and date as previous entry; MSNG 54689, 1 female and 1 male, 106–134 mm SL; locality, collectors and date as previous entry.

Boleophthalmus dussumieri: CMN FI 1979-0145, 1 male, 122 mm SL; Iran, Hormozgan, Geru river, Minab to Jask road, 1976; LACM 38125-6, 1 ex., 110 mm SL; Pakistan, Sind, Karachi fish market, 1978; MSNG 54638, 1 ex., 112 mm SL; Iran, Hormozgan, Bandar Khamir, 2005; MSNG 54639, 2 ex., 87–115 mm SL; Kuwait, Khor Subiyah, 2006; ZRC 52246, 8 ex., 58–137 mm SL; Pakistan, Ambro Creek, 2006.

Boleophthalmus pectinirostris: MSNG 54640, 1 ex., 76 mm SL; China, Guangdong, Qi'ao Island, 2006; MSNG 54641, 1 male and 1 female, 117–156 mm SL; Malaysia, Johor, Tanjung [=Cape] Piai, 2006; MSNG 54642, 1 male, 156 mm SL; locality as previous entry, 2007; NSMT-P 33716, 4 ex., 55–61 mm SL; Japan, Kyushu, Udo, 1990; NSMT-P 54457, 3 ex., 164–179 mm SL; Malaysia, Selangor, Kampung [=Village] Yu, 1997; NTM S. 11173-001, 2 ex., 143–144 mm SL; Taiwan, Kaohsiung fish farm, 1982; NTM S. 15524-001, 5 ex., 77–112 mm SL; Indonesia, Sumatra, Pulau [=Island] Bengkalis, 1994; ZRC 51102, 5 ex., 92–117 mm SL; China, Fujian Province, Xiamen, Guang Yu Island, 2007; ZRC 52255, 2 females, 150–158 mm SL; Malaysia,

Johor, Tanjung [=Cape] Piai, 2006; ZRC 52257, 1 ex., 63 mm SL; Malaysia, Selangor, Sementa, 2010.

ACKNOWLEDGEMENTS

The authors wish to thank the Ok Tedi Mining Limited (OTML) and its Environment Department for air and water transportation and laboratory facilities; the captain and crew of the R.V. Tahua Chief; M. T. Rau, C. Tenakenai and his team of the Sturt station for their invaluable assistance in the field; and the people of the Fly River delta, with particular reference to Agua, David, and the residents of the new and old Wapi villages. We are grateful to all museum curators who facilitated the loan of specimens or provided digital images of comparative materials: Mark McGrouther, Australian Museum; John G. Lundberg and Mark Sabaj Pérez, Academy of Natural Sciences; Brian Coad and Sylvie Laframboise, Canadian Museum of Nature; Rick Feeney, Los Angeles County Museum; Massimo Capula, Civic Museum of Zoology of Rome; Giuliano Doria, Civic Museum of Natural History of Genoa; Gento Shinohara, National Science Museum, Tokyo; Helen K. Larson, Museums and Art Gallery of the Northern Territory, who also hosted the first author in Darwin, Australia; Sandra J. Raredon, Smithsonian National Museum of Natural History; Peter Bartsch, Museum für Naturkunde Humboldt Universität; Ralf Thiel, Universität Hamburg, Biozentrum Grindel und Zoologisches Museum; and Kelvin Lim, Raffles Museum of Biodiversity Research, who also hosted the first two authors in the Raffles Museum, Singapore. This study was partially funded by a Ph.D. grant to the senior author in Ecological Sciences, University of Rome “La Sapienza”, Italy and to the second author by the Department of Biological Sciences, National University of Singapore.

LITERATURE CITED

- Baeck, G. W., T. Takita & Y. H. Yoon, 2008. Lifestyle of Korean mudskipper *Periophthalmus magnuspinnatus* with reference to a congeneric species *Periophthalmus modestus*. *Ichthyological Research*, **55**: 43–52.
- Bleeker, P., 1874. Esquisse d'un système naturel des Gobioides. *Archives Néerlandaises des Sciences Exactes et Naturelles*, **9**: 289–331.
- Bloch, M. E. & J. G. Schneider, 1801. *M.E. Blochii, Systema Ichthyologiae Iconibus CX Illustratum. Post Obitum Auctoris Opus Inchoatum Absolvit, Correxerit, Interpolavit Jo. Gottlob Schneider, Saxo. Berolini. Sumtibus Auctoris Impressum et Bibliopolio Sanderiano Commissum*. 584 pp.
- Chen, S., W. Hong, Q. Zhang & Y. Su, 2007. Why does the mudskipper *Boleophthalmus pectinirostris* form territories in farming ponds? *Journal of the Marine Biological Association of the United Kingdom*, **87**: 615–619.
- Clayton, D. A. & J. M. Wright, 1989. Mud-walled territories and feeding behaviour of *Boleophthalmus boddarti* (Pisces, Gobiidae), on the mud flats of Kuwait. *Journal of Ethology*, **7**: 91–95.
- Cuvier, G. & A. Valenciennes, 1837. *Histoire Naturelle des Poissons. Tome Douzième. Suite Du Livre Quatorzième. Gobioides. Livre Quinzième. Acanthoptérygiens A Pectorales Pédiculées*. Levrault, Strasbourg. 507 pp.

- Darroch, J. N. & J. E. Mosimann, 1985. Canonical and principal components of shape. *Biometrika*, **72**: 241–252.
- Eggert, B., 1929. Die Gobiidenflosse und ihre Anpassung an das Landleben. *Zeitschrift für Wissenschaftliche Zoologie*, **133**: 411–440.
- Froese, R. & D. Pauly (eds.), *FishBase*. World Wide Web electronic publication. www.fishbase.org. (Accessed Jun.2007).
- Global Biodiversity Information Facility (GBIF) Data Portal, 2008. World Wide Web electronic publication. www.gbif.net. (Accessed Apr.2008).
- Günther, A., 1861. *Catalogue of the Fishes in the British Museum. First Order: Acanthopterygii, Volume 3*. Taylor and Francis, London. x + 586 pp.
- Hammer, Ø., D. A. T. Harper & P. D. Ryan, 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, **4**: art. 4, 9 pp. http://palaeo-electronica.org/2001_1/past/issue1_01.htm.
- Hammer, Ø. & D. A. T. Harper, 2005. *Palaeontological Data Analysis*. Blackwell Publishing, Oxford. 351 pp.
- Hoese, D. F., 1984. Gobioidae: Relationships. In: Moser, H. G., W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. & S. L. Richardson (eds.), *Ontogeny and Systematics of Fishes*. American Society of Ichthyologists and Herpetologists, Special Publications no. 1. Allen Press, Lawrence Kansas. Pp. 588–591.
- Hubbs, C. L. & K. F. Lagler, 1964. *Fishes of the Great Lakes Region*. The University of Michigan Press, Ann Arbor. 213 pp.
- Hubbs, C. L. & K. F. Lagler, 2004. *Fishes of the Great Lakes Region, Revised Edition*. The University of Michigan Press, Ann Arbor. 332 pp.
- Jolicoeur, P., 1963. The multivariate generalisation of the allometry equation. *Biometrics*, **19**: 497–499.
- Jungers, W. L., A. B. Falsetti & Ch. E. Wall, 1995. Shape, relative size, and size-adjustments in morphometrics. *Yearbook of Physical Anthropology*, **38**: 137–161.
- Larson, H. K., Z. Jaafar & K. K. P. Lim, 2008. An annotated checklist of the gobioid fishes of Singapore. *Raffles Bulletin of Zoology*, **56**: 135–155.
- Linnaeus, C., 1758. *Systema Naturae Per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, Cum Characteribus, Differentiis, Synonymis, Locis (Pisces)*. 10th Edition. Laurentii Salvii, Holmiae. 824 pp.
- McCulloch, A. R. & E. R. Waite, 1918. Descriptions of two new Australian gobies. *Records of the South Australian Museum*, **1**: 79–82.
- McDowall, R. M., 2003. Protocols for enumerating the principal caudal fin rays of fishes. *New Zealand Journal of Zoology*, **30**: 259–261.
- Miller P. J., 1986. Reproductive biology and systematic problems in gobioid fishes. In: Uyeno T., R. Arai, T. Taniuchi & K. Matsuura (eds.), *Pacific Fish Biology: Proceedings of the 2nd International Conference on Indo-Pacific Fishes*. Ichthyological Society of Japan, Tokyo. Pp. 640–647.
- Murdy, E. O., 1989. A taxonomic revision and cladistic analysis of the oxudercine gobies (Gobiidae: Oxudercinae). *Records of the Australian Museum, Supplement*, **11**: 1–93.
- Nakabo, T. (ed.), 2002. *Fishes of Japan with Pictorial Keys to the Species. English edition I, II*. Tokai University Press, Hadano. 1800 pp.
- Nanami, A. & T. Takegaki, 2005. Age and growth of the mudskipper *Boleophthalmus pectinirostris* in Ariake Bay, Kyushu, Japan. *Fisheries Research*, **74**: 24–34.
- Ocean Biogeographic Information System (OBIS), World Wide Web electronic publication. www.iobis.org. (Accessed Dec.2007).
- Pallas, P. S., 1770. *Spicilegia Zoologica Quibus Novae Imprimis et Obscurae Animalium Species Iconibus, Descriptionibus Atque Commentariis Illustrantur. Tomus I*. Prostant apud Gottl. August. Lange, Berolini. 558 pp.
- Polgar, G. & G. Crosa, 2009. Multivariate characterization of the habitats of seven species of Malayan mudskippers (Gobiidae: Oxudercinae). *Marine Biology*, **156**: 1475–1486.
- Polgar, G. & R. Lim, 2011. Mudskippers: Human use, ecotoxicology and biomonitoring of mangrove and other soft bottom intertidal ecosystems. In: Metras, J. N. (ed.) *Mangroves: Ecology, Biology and Taxonomy*. Nova Science Publishers, Hauppauge. Pp. 51–86.
- Polgar, G., A. Sacchetti & P. Galli, 2010. Differentiation and adaptive radiation of amphibious gobies (Gobiidae: Oxudercinae) in semi-terrestrial habitats. *Journal of Fish Biology*, **77**: 1645–1664.
- Quoy, J. R. C. & J. P. Gaimard, 1824–25. Description des Poissons. Chapter IX. In: Freycinet, L. de. (ed.), *Voyage Autour Du Monde... Exécuté Sur Les Corvettes De L. M. «L'Uranie» Et «La Physicienne» Pendant Les Années 1817, 1818, 1819 et 1820*. Voyage Uranie, Zool., Paris. 1–328 pp.
- Rainboth, W., 1996. *Fishes of the Cambodian Mekong. FAO Species Identification Field Guide for Fishery Purposes*. FAO, Rome. 310 pp.
- Roberts, T. R., 1978. An ichthyological survey of the Fly River in Papua New Guinea with descriptions of new species. *Smithsonian Contributions to Zoology*, no. **281**. 72 pp.
- Rodelli, M. R., J. N. Gearing, P. J. Gearing, N. Marshall & A. Sasekumar, 1984. Stable isotope ratio as a tracer of mangrove carbon in Malaysian ecosystems. *Oecologia*, **61**: 326–333.
- Strauss, R. E., 1985. Evolutionary allometry and variation in body form in the South American catfish genus *Corydoras* (Callichthyidae). *Systematic Zoology*, **34**: 381–396.
- Swainson, W., 1839. *Natural History and Classification of Fishes, Amphibians and Reptiles. Volume II*. Longman, Orme, Brown, Green & Longmans and John Taylor, London: 452 pp.
- Swennen, C., N. Ruttanadukul, M. Haver, S. Piummongkol, S. Prasertsongscum, I. Intanai, W. Chaipakdi, P. Yeesin, P. Horpet & S. Detsathit, 1995. The five sympatric mudskippers (Teleostei: Gobioidae) of Pattani area, southern Thailand. *Natural History Bulletin of the Siam Society*, **42**: 109–129.
- Takita, T., Agusnimar & B. Ali Ahyudin, 1999. Distribution and habitat requirements of oxudercine gobies (Gobiidae: Oxudercinae) along the Straits of Malacca. *Ichthyological Research*, **46**: 131–138.
- Takita, T., H. Larson & A. Ishimatsu, 2011. The natural history of mudskippers in northern Australia, with field identification characters. *The Beagle. Records of the Museums and Art Galleries of the Northern Territory*, **27**: 189–204.
- Taylor, W. R. & C. C. Van Dyke, 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, **9**: 107–120.
- Yang, K. Y., S. Y. Lee & G. A. Williams, 2003. Selective feeding by the mudskipper (*Boleophthalmus pectinirostris*) on the microalgal assemblage of a tropical mudflat. *Marine Biology*, **143**: 245–256.