

THE FIVE SYMPATRIC MUDSKIPPERS (TELEOSTEI: GOBIOIDEA) OF PATTANI AREA, SOUTHERN THAILAND

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ABSTRACT

Five mud-kipper species were found near Pattani during our study in 1994: *Pseudapocryptes lanceolatus*, *Boleophthalmus boddarti*, *Periophthalmodon schlosseri*, *Periophthalmus novemradiatus* and *P. argentilineatus*. All were known to occur in Thailand, but only the first three species had been recorded before at Pattani. The species are described, as well as their spatial distribution and habitats. Burrows, behaviour and food were studied in the first three species. *P. lanceolatus* aestivates in narrow burrows in the bottom of dried up pools.

INTRODUCTION

Mudskippers are gobioid fishes belonging to several genera of the subfamily Oxudercinae. Their distribution is restricted to coastal marine and estuarine habitats in the Old World, mainly in SE Asia (MURDY, 1989). They live in mangrove swamps and bare, intertidal mud. They hide in burrows for a part of their life. Most of these fishes come out of the water during low tide. They crawl or jump over the exposed substrate and some even climb in trees. Their presence or absence can be used as an indication of certain characteristics of the habitat. However, many details of the life of these interesting fish species are still unknown due to taxonomic confusion in the past and the difficulty of studying and catching them in their muddy habitats.

The present paper resulted from research that was conducted during the workshop "The Life of the Mudskipper", held at Pattani campus of the Prince of Songkla University (PSU) from 21 March to 2 April 1994. A few data are included which were collected during preparation of the workshop or the weeks thereafter. The workshop was organised by the Faculty of Science and Technology of PSU in Pattani in cooperation with the Netherlands Institute for Sea Research (NIOZ), Texel. This paper describes the species found and compares their habitats, burrows, behaviour and food.

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THE STUDY AREA

The study was carried out in the coastal area of Pattani (about 06°50'N, 101°20'E) in the south-eastern part of peninsular Thailand. Here, the coast consists of a sand beach interrupted by Pattani Bay and several smaller estuaries. Pattani Bay is formed by a 22-km long sand spit, which runs parallel with the mainland in an east-west direction. The western end of the bay opens into the Gulf of Thailand. The Pattani and Yarring Rivers discharge into the bay. Bay and adjacent mainland coast are protected by the spit from the NE Monsoon resulting in sedimentation of silt and mud along this part of the coast.

The tides are of the mixed type. Tidal amplitudes are only 40 to 90 cm. The lowest ranges are found after full and new moon, the highest after first and last quarter. Mean sea level varies between June (lowest level) and December (highest level). This seasonal difference is about 45 cm according to the predicted sea levels in the tide tables.

MATERIALS AND METHODS

Mudskippers were caught by hand or with a dip net, tangle, casting net, or catapult, and brought to the laboratory. Their colours were noted. The surface of the fish was superficially dried with a piece of cloth to determine fresh body mass to 0.1 g on a digital balance. TL (total length: from snout to tip of caudal fin), SL (standard length: from snout to central base of caudal fin), diameter of the eye, height of first dorsal fin (from the base of the longest spine to its tip) were measured to 1 mm with a ruler. The numbers of fin rays were counted in the anterior (D_1) and in the posterior (D_2) dorsal fins, and in the anal and caudal fins. The body cavity was opened to determine the sex. The species were identified by means of the keys of KOUMANS (1953) and MURDY (1989). We followed MURDY (1989) for the nomenclature.

After dissection, the alimentary tracts were opened. Food clumps were broken up with a needle and diluted with water. Contents were examined with a microscope. The number of food items was estimated.

The spatial distribution of mudskippers was studied by visual inspection of all wetland habitats on 13 sites: Ban Bang Tawa, Ban Bang Plamo, Ban Rusamilae, PSU Pattani campus, Pattani River mouth, Ban Leam Nok, Ban Bana, Ban Tanyong Lulo, Ban Tosom, Ban Bang Pu, Ban Dato, Ban Budi, and the tip of Leam Pho (Fig. 1). The number of individuals of each species per 100 m² was counted. Transects were followed from the coast inland. Habitats were classified according to their substrate: sand, sandy mud, soft mud, or stiff mud; their connection with the sea: tidal, spring-tidal (only reached during spring-tides in winter), or non-tidal; their surroundings: open or enclosed; water depth and kind of vegetation. The physical properties of each habitat were described, and substrate types were noted. Temperature was measured by electronic temperature probe (Therm 2263-1, Ahlborn), salinity by light refraction (ATAGO salinometer S-10), soil pH with a Soil Tester (Takemura Electric Works Ltd), and water pH with a WTW 528 (TÜV, Germany) with Mettler probe.

We studied the architecture of the burrows of the common species. Burrows actively used by large, adult mudskippers were selected. A square frame of 1 m² with 1 dm²

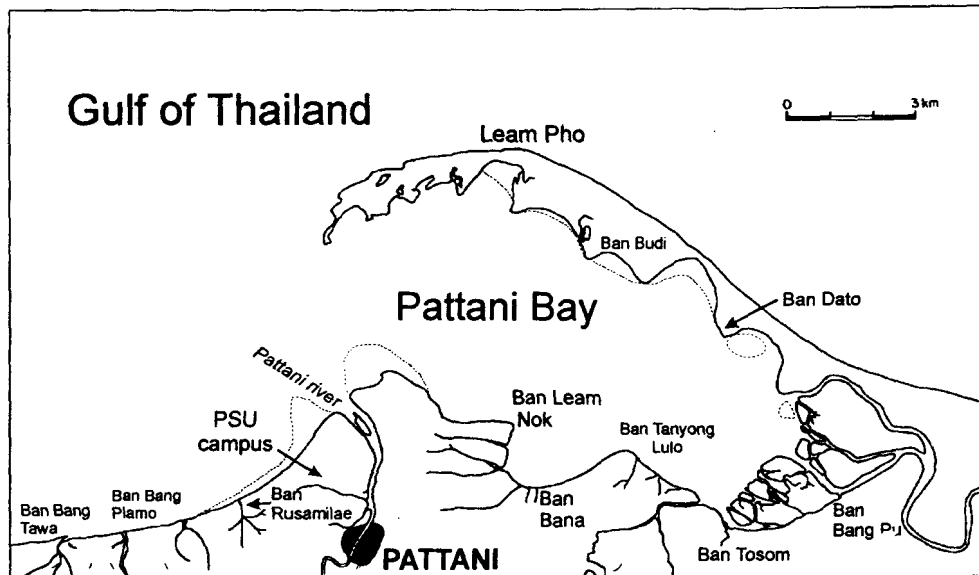


Figure 1. Map of the study area.

subdivisions was placed over the opening of a burrow and the position of the frame was fixed with four poles in the corners. The opening of the burrow was measured and a sketch was made of it. Thereafter, the frame was temporarily lifted and a layer of sediment was removed. The frame was then placed back on the poles and the position and depth of the exposed burrow measured again. This procedure was repeated until the whole burrow had been exposed, measured and drawn. For wide and deep burrows, a deep hole was made outside the frame. Water was removed from this hole with a bucket. In this way the water was drained from the burrow. The burrow was then filled with cement. The following day, the mud around the cement was removed and the dimensions of the cement cylinder were measured at different depths. Usually, tips of the branches and the deepest parts of burrows were not completely filled with cement. These parts were measured by hand after partly removing the water from the burrow.

Behaviour of the three common species was studied at sites with a high population density on the intertidal mudflat in front of the PSU campus, and in a ditch with a reduced tidal current in the campus. To make a comparison possible, the observations were carried out during low tide. Some additional observations were made on the mudflat of a nearly empty pond. An aquarium was used to observe in more detail the feeding behaviour of one of the species that usually foraged while under water.

Individuals were observed for 5-minute intervals in order to quantify some behavioural attributes. During each observation four parameters were noted: (1) the total amount of time in seconds (T_p) an individual spent feeding; (2) the number of times (x_p) the individual started feeding; (3) the number of times the individual turned to the left or the right along the longitudinal axis of its body; (4) the number of times any kind of interaction took place

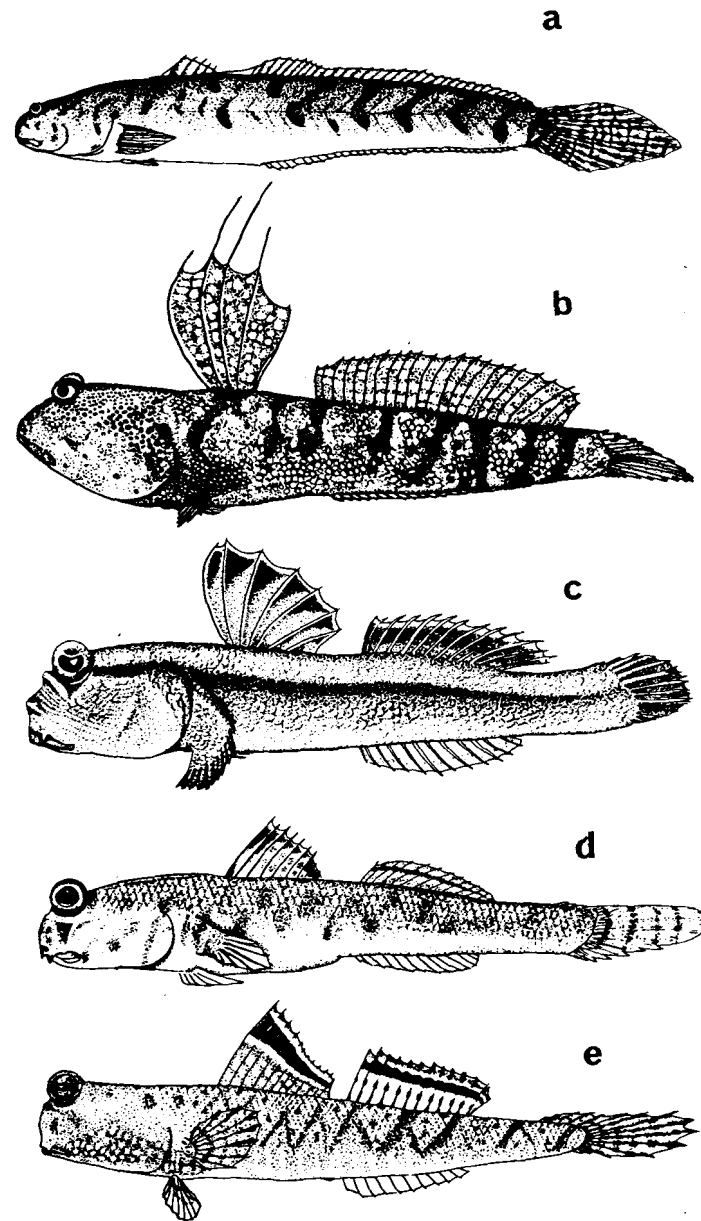


Figure 2. Appearance of (a) *Pseudapocryptes lanceolatus*, (b) *Boleophthalmus boddarti*, (c) *Periophthalmodon schlosseri*, (d) *Periophthalmus novemradiatus*, and (e) *Periophthalmus argentilineatus* from the study area. Drawn by C. Swennen after photographs of live specimens kept in bottles of water to show expanded fins.

between the observed individual and another. The ratio T_f/x_f was the average time in seconds spent per feeding bout and was calculated afterwards from our data. Time was determined with a stopwatch and numbers of times were scored with a counter. Observations were conducted one night during full moon to check if the species were active during the night. A flashlight was used during night observations, while a pair of binoculars was used for both day and night observations.

A preliminary test was conducted to study why the local people do not eat mudskippers. The participants of the workshop formed a panel for taste tests. They scored their relative preference for pieces of boiled meat of mudskippers and mullets (Mugilidae), the latter being a common and appreciated food.

RESULTS

Species Occurring in the Area

Five species were found (Fig. 2). Below we give short descriptions of the fish to avoid possible confusion about the identity of the species. Numbers refer to the average value of a specific meristic character, with ranges given in parenthesis.

Pseudapocryptes lanceolatus (Bloch & Schneider, 1801)

Figs. 2a, 3a, 7, and Tables 1 and 5

Colour: Light brown on the dorsum, paler on the flanks and whitish on the ventral side. Dark brown, irregular bars running slightly anteriorly from the back down along the sides. There were about 5 such bars on the posterior part, but only blotches in the front half of the body. The pattern of bars was more pronounced in young fish than in adults. The myomere system was clearly visible on the skin. Both dorsal fins (D_1 and D_2) with brownish blotches on the spines, rays and adjacent parts of the fin membranes. The other parts of the fin membranes were colourless and transparent. The caudal fin had dark, irregular vertical lines, 11 in the smallest and about 18 in the large specimens. The anal fin had no dark pigment.

We obtained 36 specimens. The dorsal fins were low and totally connected by a velum, which was decreasing in height towards D_2 . The scales are very small compared to those of the other species. Our specimens varied considerably in size: TL 13.2 (7.3–17.5) cm, SL 10.3 (5.5–13.7) cm, and fresh mass 12.8 (1.7–24.2) g.

Sex was determined in the 15 specimens with total length of more than 14 cm. There were 6 males and 9 females. At the end of March 1994, the ovaries were small in 7 females, but one female had ripe, yellow eggs in the ovary which filled most of the body cavity, and one female was spent. No differences were found in external characteristics, colouration, or size of males and females.

***Boleophthalmus boddarti* (Pallas, 1770)**

Figs. 2b, 3b, 4, 7, and Tables 1 and 5

Colour: Yellow-brown to dark brown, ventral paler. There were 4-8 dark brown, sometimes nearly black marks on the flanks. These were present as blotches anteriorly, gradually becoming broad bars posteriorly. Clear blue spots were scattered over the body. The spots were densest on the head and anterior part of body including base of pectoral fin, becoming less dense but larger on the sides of the body. D_1 and D_2 were brownish with large blue spots. Tips of fin rays bluish or yellowish, but both dorsal fins were yellowish in small specimens seen in the field.

We obtained 31 adult specimens of various sizes: TL 15.8 (6.0–20.1) cm, SL 12.9 (5.0–16.9) cm, fresh mass 40.1 (2.1–75.8) g.

The sample consisted of 18 males and 13 females. The third (longest) spine of D_1 was larger in females than in males (Fig. 4). No other sexual differences were observed. In 11 females caught in March (TL 15.3–19.4 cm) the ovaries were small and inactive. One female (TL 15.8 cm) was full of ripe, yellow eggs, which filled most of the body cavity, and another (TL 11.6 cm) had just spent. All 5 females caught in October were full of eggs.

Note: Some authors (e.g. MACNAE, 1968; BISWAS ET AL., 1979; DATTA & DAS, 1980; PATEL ET AL., 1985; CHEW & IP, 1992) spell the species name as *boddaerti*, but this is not in accordance with the nomenclatural rules. PALLAS (1770) indeed named the species after his friend Mr. Pieter Boddaert, but the spelling *boddarti* is clearly not a slip of the pen, because the author used the name *G. boddarti* three times in his paper. Boddaert (1730–1796) was a Dutch author who translated and popularised several scientific books. The latinized spelling of his name is Boddartus (see the declensional form in the Latin description of PALLAS (1770)).

***Periophthalmodon schlosseri* (Pallas, 1770)**

Figs. 2c, 3c, 7, and Tables 1 and 5

Colour: Yellowish-grey rather dark at the dorsum above a dark brown stripe. The stripe starts near the eye, becoming wider on the body. The stripe was complete or blotched. Some fish showed no stripe, or had one with irregular borders, while others had stripes with straight borders. Pale blue spots on the cheek and the sides. Dorsal fins with a dark brown stripe and pale margins.

We obtained 11 specimens. The height of D_1 was 4.0 (3.5–4.5) cm in adults. Spines and rays were mixed in D_2 . All specimens caught were rather large: TL 25.6 (20.9–27.4) cm, SL 22.2 (18.1–24.0) cm, fresh mass 164.4 (103.2–218) g. However, small specimens of about 10 cm were seen in the field.

The sample caught in March contained 4 males and 7 females. No external differences between the sexes were found. The ovaries of 6 females had bright yellow eggs which filled most of the body cavity. One female had just spent. The single adult female caught in October was filled with eggs.

***Periophthalmus novemradiatus* (Hamilton, 1822)**

Figs. 2d, 3d, 7, and Tables 1 and 5

Colour: Yellowish grey on dorsum, ventrally lighter. Reddish-brown blotches more or less in two rows over the upper half of the sides. D_1 with red on tips of spines. Margin pale, followed by a row of dark gray or black blotches on the membranes between the spines; proximal part whitish with red blotches. Prominent black spot in posterior part and smaller spot in frontal part of the fin. D_2 with pale margin and a broad black subterminal band bordered by white lines; proximal part with bright reddish spots. Caudal fin with red-brown spots on the rays; anal fin yellowish.

We obtained 7 specimens, all small: TL 6.0 (4.7–7.0) cm, SL 4.9 (3.9–5.9) cm, and the fresh mass was 1.7 (0.8–2.9) g. Only a few specimens were sexed. Testes and ovaries were only slightly developed in March 1994.

***Periophthalmus argentilineatus* Valenciennes, 1837**

Figs. 2e, 3e, 7, and Tables 1 and 5

Colour: Dark grey or dark brown on dorsum and flanks, ventrally nearly white. A series of dark spots forming a more-or-less zig-zag line over the flanks. About 14 silvery, vertical bars on the sides, not connected dorsally or ventrally. Several small blue dots on the operculum and silvery scales on the sides. D_1 with a broad white margin with some red spots followed by a broad greyish stripe; proximal part brownish and pale. D_2 had broad reddish blotches along the outer margin, followed by a broad black stripe with narrow white borders; proximal part pale with dark red blotches. Caudal fin pale or yellowish with several brownish spots on the rays. Anal fin uncoloured.

We obtained 11 specimens. The pelvic fins were separated and had no frenum. The animals were small: TL 4.5 (4.0–4.7) cm, SL 3.6 (3.2–3.8) cm, and fresh mass was 0.76 (0.6–0.9) g. Only a few animals were sexed; females had unripe eggs in small ovaries in March.

Spatial Distribution and Habitats

Mudskippers appeared to be restricted to the coastal zone and were only found on wet sediments or in shallow water near the shoreline. They were not present on sand beaches, in permanent freshwater habitats, salt pans or shrimp ponds.

B. boddarti and *P. schlosseri* were mainly seen on exposed, soft intertidal mud, bare mud in tidal pools, and also on narrow borders of tidal creeks and canals. Both species occurred also among scattered young mangrove trees, but only *P. schlosseri* was found in dense mangrove forests. *P. lanceolatus* was also restricted to muddy sediments, but this species mainly occurred in non-tidal waters or in habitats in which tidal influences were restricted. There was a gradient from the intertidal mudflat with only *B. boddarti* and *P. schlosseri* inland where the first two species became less numerous and numbers, of *P. lanceolatus* increased. The latter species was found up to 1.5 km behind the shore line (Fig. 5).

The frequencies of occurrence are given according to study plots in the various habitats

Table 1. Means and ranges of counts for fin elements in first dorsal (D_1), second dorsal (D_2), caudal (C), and anal fins (A) of mudskipper species found in Pattani area. Comparable data of Murdy (1989) are given in italics. The fin elements in D_1 were spines (not segmented and not branched). The elements in the other fins were rays (segmented and branched), except the anterior ones which were usually spines. However, we found in some specimens the first element unbranched, but nevertheless segmented. Similar spinous structures were found among the other elements in a few cases. Therefore the difference between spines and rays is vague in mudskipper fins.

Species	N	D_1	D_2	Anal fin	Caudal fin*
<i>P. lanceolatus</i>	36	5	32.0 (30-33)	29.8 (29-31)	18.2 (18-19)
	12	5	31.3 (29-33)	29.3 (28-31)	17
<i>B. boddarti</i>	31	5	25.3 (25-26)	25.2 (25-26)	±18
	20	5	24.5 (24-26)	24.5 (24-26)	17
<i>P. schlosseri</i>	11	8.5 (7-11)	12.5 (8-14)	13.1 (13-14)	±19
	10	8.0 (6-9)	12.7 (12-13)	12.7 (12-14)	14-17
<i>P. novemradiatus</i>	7	9.4 (9-10)	12.2 (13-14)	12.8 (12-13)	±18
	10	9.3 (9-11)	13.1 (13-14)	13.7 (12-14)	17
<i>P. argenteolineatus</i>	11	13.3 (9-16)	12.3 (11-14)	11.6 (11-13)	16.2 (14-17)
	20	13.9 (11-16)	12.0 (10-13)	11.0 (9-12)	17

* The outer elements in the caudal fin were often small and mistakes may be made in the counts.

Table 2. Frequency of occurrence of *Pseudapocryptes lanceolatus*, *Boleophthalmus boddarti*, and *Periophthalmodon schlosseri* in different habitats around Pattani. N = number of plots studied.

Habitats	N	<i>P. lanceolatus</i>	<i>B. boddarti</i>	<i>P. schlosseri</i>
Intertidal mudflats	24	0	24	10
Mangrove forests	10	0	5	9
Tidal creeks and pools	16	2	16	9
Non-tidal ditches	8	8	7	1
Spring tidal pools	18	17	3	1

(Table 2). Densities could only be determined on a few sites and only for large specimens: up to 21 per 100 m² for *P. lanceolatus*, up to 13 per 100 m² for *B. boddarti*, and up to 1 per 100 m² for *P. schlosseri*.

The median salinity in occupied habitats was 25‰. However, salinity was zero in a tidal creek due to freshwater flow during low tide, and a maximum of 35‰ was found in a pool. The median pH of the water was 7.6 (7.1–8.1), decreasing to 6.3 in mangroves and some creeks. The pH values in the muddy sediments were lower with a median of 5.6 (6.7–3.8). Temperature of the water in tidal habitats varied between 28.7 and 31.9 °C, while a maximum of 36.8 °C was measured in a pool.

The two smaller species *P. novemradiatus* and *P. argentilineatus* were only found in a few localities: near the bridge over the small estuary near Ban Panare, in a narrow tidal ditch near the saltpans of Ban Tanyong Lulo, and in a ditch and tidal creek near Ban Bang Tawa. A few individuals of *P. novemradiatus* were also found in two ditches between Ban Rusamilae and the mouth of Pattani River. The habitats had muddy borders with pieces of stiff clay, mangrove stems, waste and other solid objects. In places where both small species were observed, young specimens of *B. boddarti* or *P. lanceolatus* also often occurred, while *P. schlosseri* was always absent. Besides inhabiting less open areas, the behaviour of *P. novemradiatus* and *P. argentilineatus* also differed from the other species. When disturbed, individuals of the three larger species disappeared into their holes or into water, while both small species usually came out of the water and hid between or climbed up mangrove roots, or climbed the sides of fishing boats. As the distribution of these species was limited to small areas and their density was low, no special attention was paid to them.

The Burrows

We measured four burrows of *B. boddarti* and four of *P. schlosseri* in the intertidal mudflat along the PSU campus, and 15 of *P. lanceolatus* in the mud of a spring-tide pool near Ban Bang Tawa. No burrows could be found which with certainty belonged to *P. novemradiatus* or *P. argentilineatus*. Although the burrows showed individual differences, each of the three species clearly had a particular burrow architecture.

Burrows of *P. schlosseri* were found in bare, intertidal mud or between mangrove trees. Some were situated so high in the intertidal zone that they were not reached by the tides for several days. The opening of a burrow of *P. schlosseri* was always conspicuous. The surface of the mud around the burrow was raised by deposition of sediment that the fish had removed from its burrow. The sediment wall, up to 6 cm high, often had a rim of mud pellets on top. The opening including the sediment wall had an area of up to 0.8 m². Inside the wall was a water-filled pool with a diameter of about 50–60 cm and a depth of about 15 cm. In the centre of the pool, a shaft with a diameter of about 15 cm went down to a depth of about 2 m. The shafts had one or two branches with a length of up to 1.5 m at a depth of 80–100 cm. These branches were more or less horizontal or went slightly upwards. These branches sometimes had a secondary branch (Fig. 6a).

Burrows of *B. boddarti* were only found in bare, intertidal mud. The openings were simple holes in the mud slightly wider than the body of their occupant. The central shaft went down to a depth of 65 cm, but had one or two branches 20 to 30 cm below the surface. The branches had secondary and sometimes tertiary branches. Some of them had

openings to the surface; others ended blindly or had a narrow opening made by a crustacean or polychaete worm. The whole gallery system covered an area of up to 1 m² (Fig. 6b).

The burrows of *P. lanceolatus* were subtidal or near low water level. They were most numerous, however, in the bottom of spring-tide pools. These pools are dry in summer when the sea level is so low that even spring tides do not reach them. The burrows of *P. lanceolatus* had simple openings as wide as the body diameter of their owners. The openings were inconspicuous and difficult to detect. When the pool dried out, the animals stayed active till the mud became stiff. We were able to study the burrows in more detail when the surface layer of the mud was dry and cracked. The openings were then totally closed by heaps of mud pellets, which stuck together when the mud dried. In depressions, where the water had stayed longer, they had first made small funnels surrounded by pellets. The funnels had a diameter of 3–8 cm and looked like funnels of *P. schlosseri* in miniature before the entrances were closed. The opening of the shaft could be found by removing the dry heap of pellets. The greyish, oxidised mud of the walls of the shafts strongly contrasted with the subsurface mud, which was bluish and anaerobic. The upper shaft walls were grey and dry, deeper down black and somewhat damp. However, the deepest parts of the burrows were far above the level of the groundwater. The fish could be found by digging the burrows; most had their heads upwards. They were inactive and covered by a thick layer of mucous. Only after some time of exposure, or after being touched, did they make eel-like movements. The shafts were generally vertical, but some had a small horizontal part at the bottom. There were no branches and we found only one fish per hole (Fig. 6c). The burrows of small fish were only 20 cm, deep, while larger fish had burrows as deep as 60 cm.

Close observations in the field showed that the burrows of *B. boddarti* were at least partly constructed by mouth excavation. However, when the opening were covered by the rising tide, we often observed plumes of mud coming out of them. This suggests that the fish was removing soft mud by body movements. The burrows of *P. schlosseri* were excavated by mouth. Several times fish were seen coming up with a mouthful of solid bluish mud which they ejected along the rim of the pool. In pools, *P. lanceolatus* made their burrows by body movements and plumes of mud suspension came out of the openings which fish had entered. However, it became clear that they excavated the deeper layers by mouth, judging from the heaps of pellets on and around the openings of the burrows that had been made when their pool dried out.

Behaviour

Feeding

Feeding of *B. boddarti*, *P. schlosseri* and *P. lanceolatus* was observed over two days for a total of 300, 205 and 295 minutes, respectively. *B. boddarti* grazed the surface layer of the exposed mudflat by moving the head left and right, while it slowly went forward. The head was raised when the food was swallowed. *P. lanceolatus* took small bites of mud under water, then sifted the mud through its gills. *B. boddarti* started feeding on average one time per minute, while *P. lanceolatus* started almost 10 bouts per minute. The average time spent per bout was 3.4 seconds for *B. boddarti* and 0.2 seconds for *P. lanceolatus* (Table 3). The feeding behaviour of *P. lanceolatus* was confirmed in an aquarium. The

Table 3. Total time (in seconds per 5 minutes) spent on feeding, total number of turns around the longitudinal axis, and total number of interactions for *Pseudapocryptes lanceolatus*, *Bolephthalmus boddarti* and *Periophthalmodon schlosseri*. N = the number of observed individuals, each observed for 5 minutes. X, average; SD, standard deviation of the mean. All other parameters are explained in Material and Methods.

Species	N	Feeding						Turning		Inter- actions
		T _f (s)		x _f		T _f /x _f (s)		Total number of times		Total number of times
		X	SD	X	SD	X	SD	Left	Right	n
<i>P. lanceolatus</i>	59	11.6	7.5	46.2	22.4	0.2	0.1	0	0	50
<i>B. boddarti</i>	60	17.4	10.6	5.1	3.2	3.4	1.8	13	17	117
<i>P. schlosseri</i>	41	0	0	0	0	-	-	7	11	2

percentage of time spent feeding was almost the same for *B. boddarti* and *P. lanceolatus*, but the species clearly differed in x_f and T_f/x_f . Feeding was not observed for *P. schlosseri* (Table 3). *P. schlosseri* mostly lay immobile on the mudflat or on the wall around its burrow. This behaviour might be related to a hunting strategy.

In the aquarium *P. lanceolatus* showed a second type of feeding, namely direct filtering of the water by rapid movements of its gills, approximately 6–10 beats per second, whereas for breathing a rate of 2–3 beats per second was used. Another remarkable phenomenon was that *P. lanceolatus* often locked its operculum while standing on its tail in the water. The reason for this behaviour remained unclear.

In an artificially emptied pool, *B. boddarti* and *P. lanceolatus* were observed in mixed populations on exposed soft mud covered by a film of diatoms. Here *P. lanceolatus* took little bites of the mud as noted earlier in feeding under water. However, we saw it also moving the head left and right, almost as *B. boddarti* did. It was remarkable that *P. lanceolatus* came out of the water at this site. They jumped high up on their tails when returning to the water, whereas *B. boddarti* walked back with its pectoral fins.

Turning

B. boddarti and *P. schlosseri* regularly turned or rolled their bodies around the longitudinal axis while on the exposed mudflat. Turning occurred both to the left and to the right (Table 3). *P. lanceolatus* did not turn while under water in the ditch. However, specimens turned their body frequently while feeding on an exposed mudflat in an artificially emptied pool.

Interactions

We saw two interactions between an individual of *P. schlosseri* under observation and another *P. schlosseri*. They chased each other from their territories. *B. boddarti* individuals displayed a whole spectrum of territorial behaviours: they looked towards each other, moved towards or away from each other, raised their heads, raised one or both dorsal fins (flagging), fought with open mouth and raised fins, or retreated into their burrows. *P. lanceolatus* showed no elaborate territorial behaviour. Specimens only interacted when their living area became too crowded, pushing each other away to free some space for themselves. Besides showing a less ritualised territorial behaviour than *B. boddarti*, *P. lanceolatus* (Table 3) interacted less notwithstanding a higher density. In a nearly empty pool, *B. boddarti* and *P. lanceolatus* individuals were about equally numerous, but although they frequently showed intraspecific aggression, interactions between different species were not observed.

B. boddarti and *P. lanceolatus* were active during the day. During the night, most individuals of *B. boddarti* were in their burrows, and the ones present on the mudflat generally were immobile. On the other hand, *P. schlosseri* was 2–3 times more common on the flat during low tide at night than during the day. The individuals of *P. schlosseri* present, however, were not more active than during the day (night observations were conducted only once).

Food and Feeding Apparatus

The species differ in number and form of teeth, length and shape of the intestinal tract, and in foods eaten. The characteristics of the feeding apparatus and the stomach contents are summarised in Table 4. *P. boddarti* and *B. lanceolatus* are clearly herbivorous. They have numerous small teeth and long intestines. The largest species, *P. schlosseri*, appears to be carnivorous. This species has fewer but larger teeth and a shorter intestine than the two herbivorous species.

Taste

The taste panel scored the order of preference in taste and texture of boiled fish. Preliminary results showed the lowest preference for mullet, while *P. lanceolatus* scored highest. *B. boddarti* and *P. schlosseri* got intermediate ratings. However, the relative differences were slight and statistically not significant.

DISCUSSION AND CONCLUSIONS

Three of our species (*P. lanceolatus*, *B. boddarti* and *P. schlosseri*) were reported from Pattani by JOHNSTONE (1903). Since that time no further information on the mudskippers of the area seems to have been published. *P. novemradiatus* and *P. argentilineatus* have not been reported before, but MURDY (1989) found samples of both species in the U.S. Museum of Natural History, Washington D.C., which had been collected on sites in the upper Gulf of Thailand.

Table 4. Characteristics of the mouth, alimentary tract, and the contents of stomach and intestines of adult *Pseudapocryptes lanceolatus*, *Bolephthalmus boddarti*, and *Periophthalmodon schlosseri*.

	<i>P. lanceolatus</i>	<i>B. boddarti</i>	<i>P. schlosseri</i>
Teeth in upper jaw	A single row of about 35 caninoid teeth, the 12 median ones longest	A single row of about 40 caninoid teeth, the 10 median ones longest	Two rows of caninoid teeth. First row of about 10 large teeth, behind this row is a second row of about 8 small teeth
Lower jaw	About 25 caninoid teeth. The median ones upright, the others more or less horizontally outwards directed	About 30 spatulate teeth. The two median ones larger and upright, the others horizontally outwards directed	About 10 caninoid teeth
Gill rakers	Brush-shaped	Brush-shaped	Knob-like
Gill filament	Feather-like	Feather-like	Thread-like
Colour of peritoneum	Black	Black	Flesh-coloured
Stomach	Straight and small	Straight and small	J-shaped and large
Intestinal length (from oesophagus to rectum)	>body length	>body length	<body length
Stomach content	About 70% diatoms and 30% filamentous algae. The latter had the largest volume. Further a few crustaceans, some detritus and mud particles	About 97% diatoms. Further blue green algae, a few nematodes some detritus and sediment particles	Shrimps, crabs, fish (only scales and bones found), copepods
Intestine content	Empty diatom scales and unidentifiable debris	Empty diatom scales and unidentifiable debris	Small chalk particles and unidentifiable debris

The five sympatric mudskipper species of Pattani differ in several respects. *P. lanceolatus* and *B. boddarti* are herbivorous, grazing on diatoms and blue-green algae. The few small animals that were found in their stomachs may have been accidentally swallowed and there is no reason to consider them omnivorous. Their high ingestion rate is also typical of herbivorous fish (HORN, 1989). The horizontally placed, spatulate teeth in the lower jaw seem to be adapted for scraping microalgae from the surface of soft sediments. Their long and flexible gill rakers may function in filtering food particles out of sediments and probably also out of water as our observations of *P. lanceolatus* suggest. Both herbivorous species have small stomachs and relatively long intestines. Their peritoneum is black, perhaps to exclude penetration of light and so prevent photosynthesis

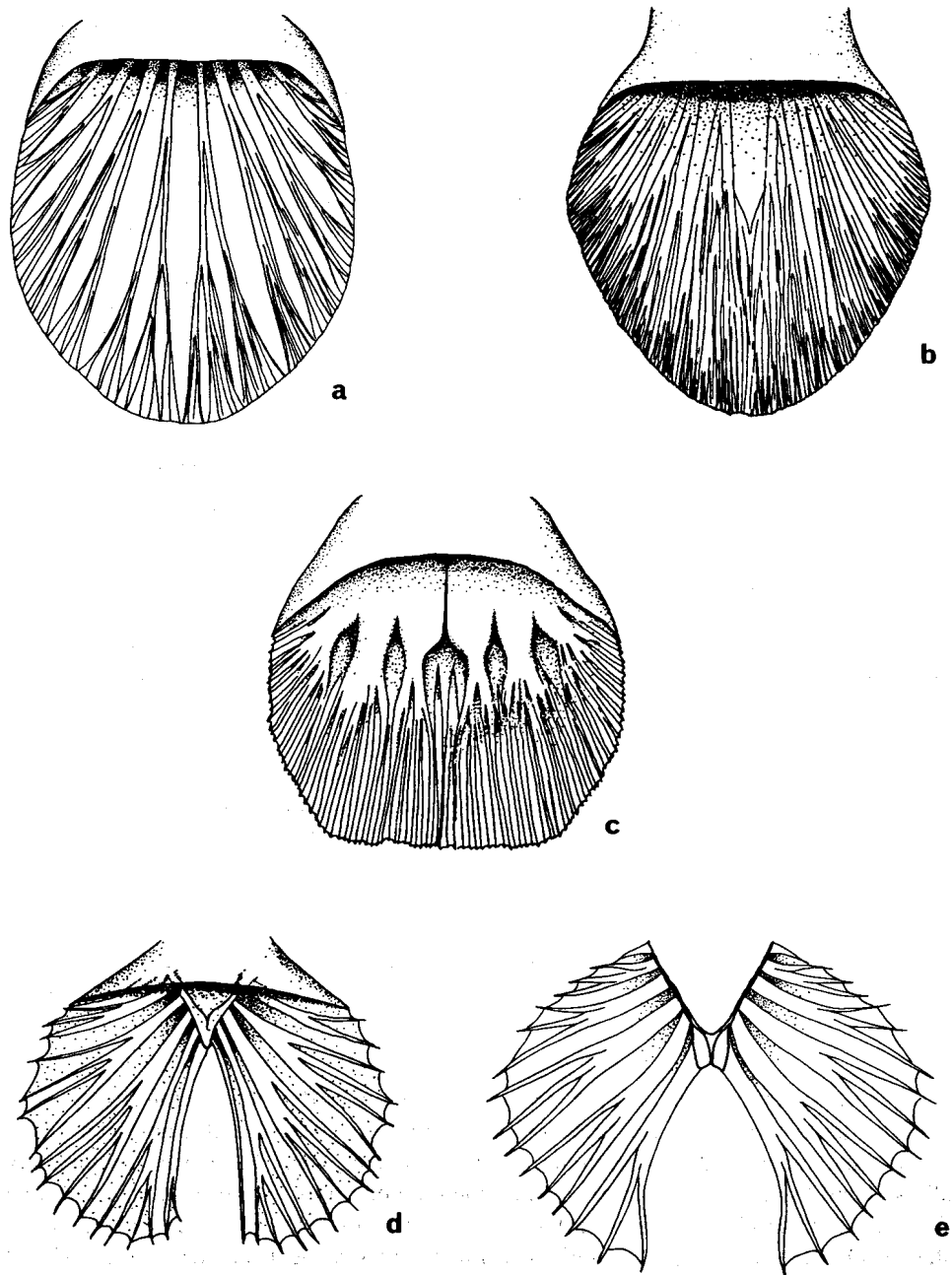


Figure 3. Pelvic fins of (a) *Pseudapocryptes lanceolatus*, (b) *Boleophthalmus boddarti*, (c) *Periophthalmodon schlosseri*, (d) *Periophthalmus novemradiatus*, and (e) *Periophthalmus argentilineatus* from the study area. Drawn by Samart Detsathit.

and release of oxygen in the alimentary tract. *P. schlosseri* appears to be a predator of rather large prey, including fish. Characteristics include the large eyes, strong pointed teeth, short gill rakers, large stomach and short intestine. They seem to lie in wait for moving prey, but we did not see actual feeding. It is plausible that also *P. novemradiatus* and *P. argentilineatus* are predators. Stomachs of *P. novemradiatus* contained claws of pistol shrimps (*Alpheus* spp.).

P. lanceolatus is the most aquatic of the species and has the longest caudal fin in relation to body size (Table 5). This species also has a more slender body than the others (Fig. 2), which is reflected in the relation between standard length and body mass (Fig. 7). The pelvic fins are fully united in the species confined to soft mud (*P. lanceolatus*, *B. boddarti* and *P. schlosseri*), and most slender and soft in the most aquatic species among them (Fig. 3). These fins are separate in species living on more solid substrates (*P. novemradiatus* and *P. argentilineatus*). The pelvic fins of *P. argentilineatus* even lack a frenum, which may be an adaptation for climbing up rough roots. The diameter of the eyes is much smaller in the herbivorous *P. lanceolatus* and *B. boddarti* than in the carnivorous species (Table 5), but larger in the more terrestrial *B. boddarti* than in the more aquatic *P. lanceolatus*.

All species depend on, or can endure, daily fluctuations in water level. Foraging seems to be restricted to periods of low tide. Only *P. lanceolatus* proved also to feed under water and thrive well without regular tides. They were densest in temporary pools. This species appeared to aestivate when the water disappeared by evaporation. They were found torpid in their narrow burrows under a layer of cracked, dry mud. It was not clear whether the other species can survive in their burrows when the openings are not regularly flooded. Some burrows of *P. schlosseri* were so high in the intertidal zone that the sea did not reach them for a few months. Such burrows in dry mud seemed deserted. However, since we later found aestivation in *P. lanceolatus*, we wonder if some individuals of *P. schlosseri* also stayed in their burrow for months, or if they had migrated to lower parts of the intertidal zone. In India, *Periophthalmus* (most probably *Periophthalmodon schlosseri* was meant) has been reported to aestivate in the bed of dried-up pools at considerable depth (HORA, 1933).

Table 5. Eye diameter as percentage of standard length of fish and length of caudal fin as percentage of total length of fish.

Species	Eye % SL	Caudal % TL
<i>Pseudapocryptes lanceolatus</i>	2.3	22.0
<i>Boleophthalmus boddarti</i>	3.1	14.0
<i>Periophthalmodon schlosseri</i>	4.0	12.4
<i>Periophthalmus novemradiatus</i>	6.4	18.1
<i>Periophthalmus argentilineatus</i>	6.4	18.7

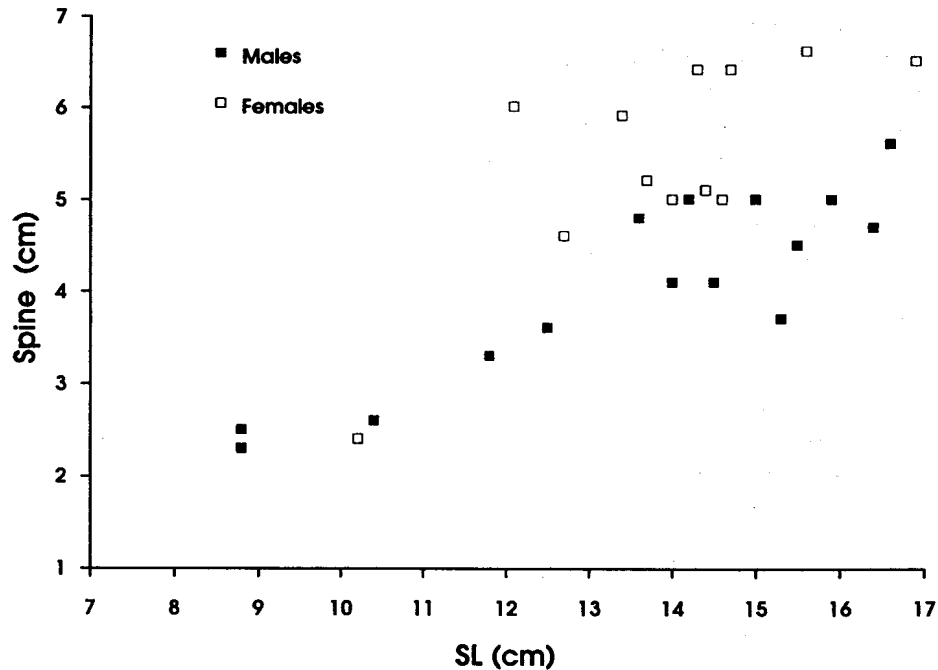


Figure 4. Sexual difference in length of longest (3rd) spine in first dorsal fin of adult *Boleophthalmus boddarti*.

The architecture of the burrows differed among the species (Fig. 6). There also appear to be regional differences. In India, the burrows made by *P. lanceolatus* for aestivation reach a depth of 1.8 m and penetrate the water table (HORA, 1936 quoted by ATKINSON & TAYLOR, 1991). Similar burrows in Pattani were much shorter and did not reach water. This may be an adaptation to differences in the severity of the dry seasons, which are short in Pattani. A drawing of the burrow of *P. schlosseri* from Java (VERWEY, 1930) is similar to the burrows studied by us, but the Indonesian ones were not branched. At first glance there seems to be a considerable difference between the burrows of *B. boddarti* studied by CLAYTON & VAUGHAN (1986) in Kuwait and those found in Pattani. However, the fish from Kuwait is not *B. boddarti* but *B. dussumieri* (CLAYTON, 1993).

The two large species (*B. boddarti* and *P. schlosseri*) usually withdrew into their burrows before the opening became flooded. The fish stayed there (as far we could see) till the area became exposed again. The burrows of these species were part of their territories, acting as a wetting place and as shelter against predators. Some mudskippers (*Boleophthalmus* spp., *Periophthalmus* spp. and perhaps *Periophthalmodon* spp.) seem to use their burrows for egg incubation (MACNAE, 1968; CLAYTON, 1993), but we failed to find evidence of this. *P. schlosseri* used the wall around the opening as an observation post. The wide entrances make its burrow a trap for small fish, crabs, and shrimps. However, a local

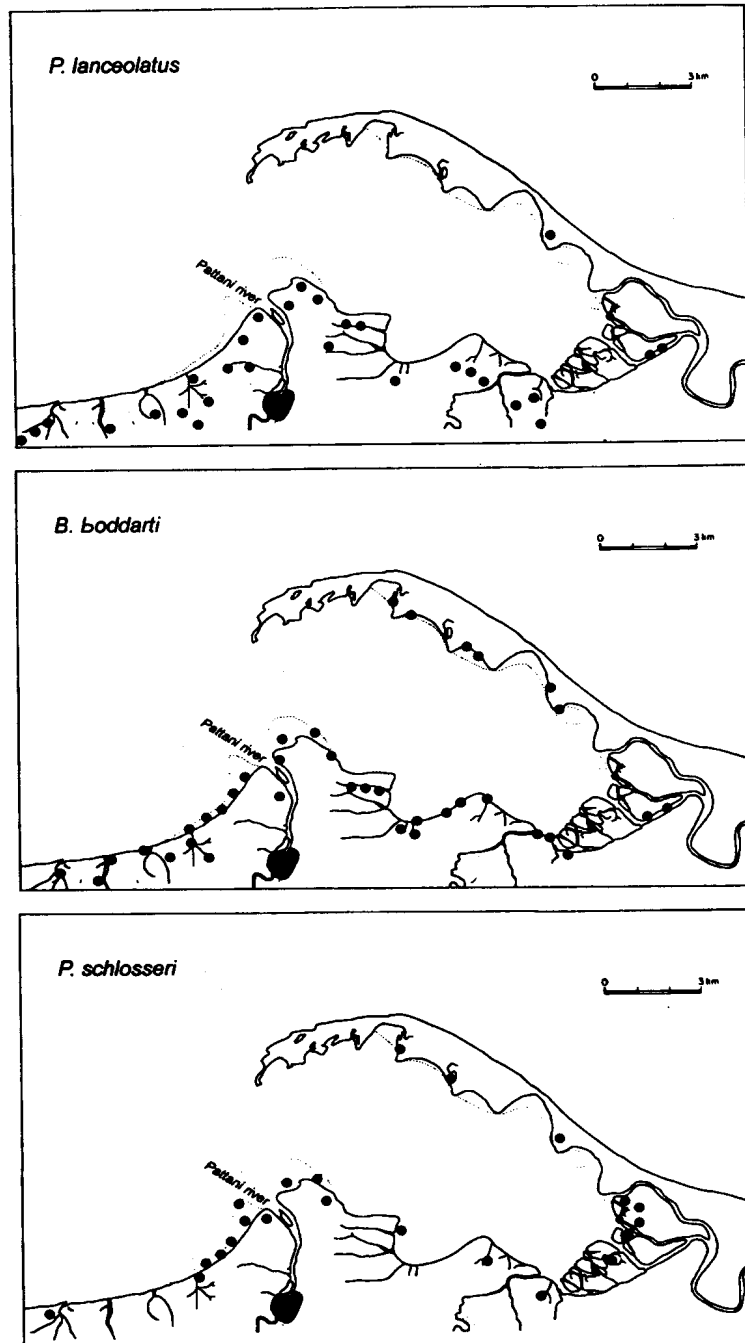


Figure 5. Distribution of the three common mudskipper species near Pattani.

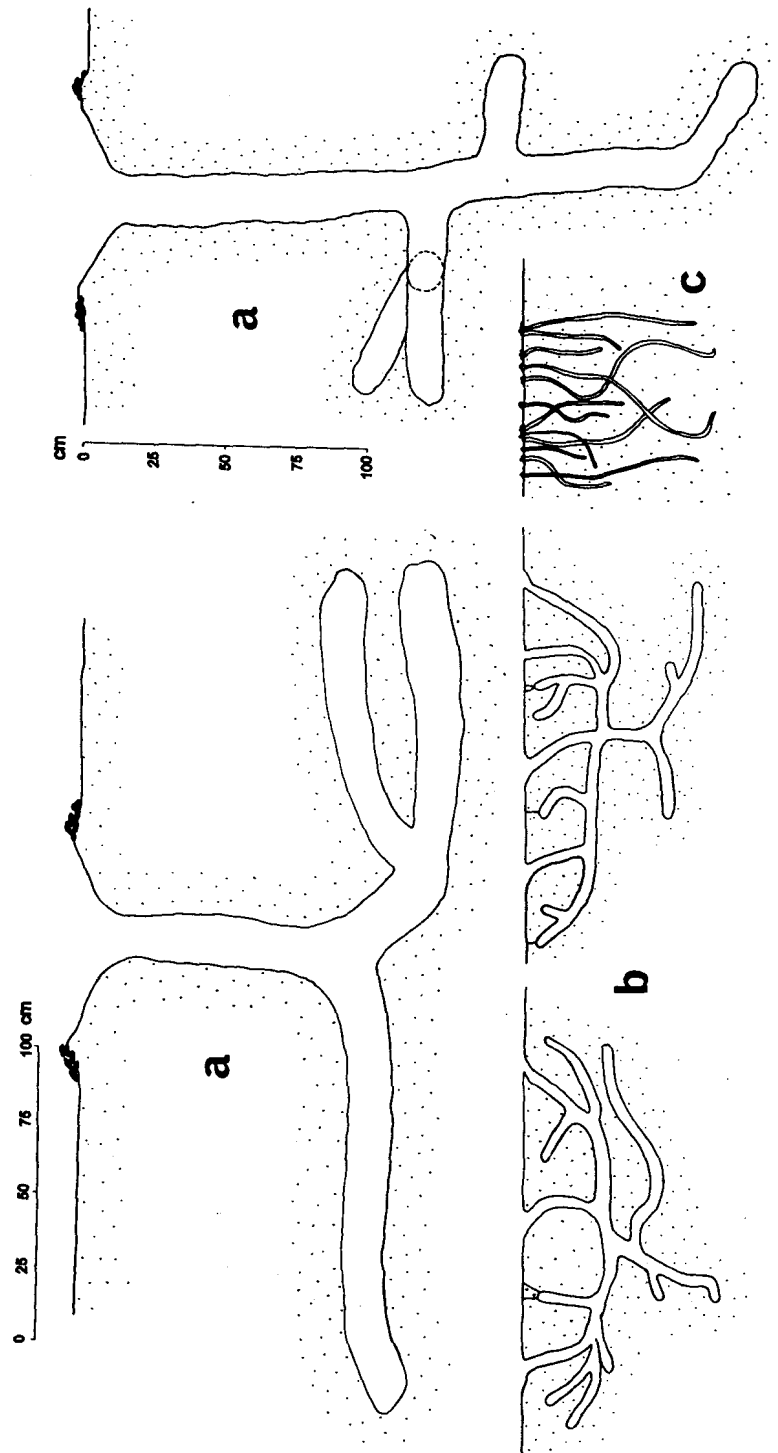


Figure 6. Burrows of adult mudskippers drawn at the same scale. Curvature and direction of the branches are drawn in the same plane, but lengths and diameters are correctly presented. (a) *Periophthalmodon schlosseri*, (b) *Boieophthalmus boddarti*, (c) *Pseudoporryptes lanceolatus*. Drawn by Witool Chaipakdi.

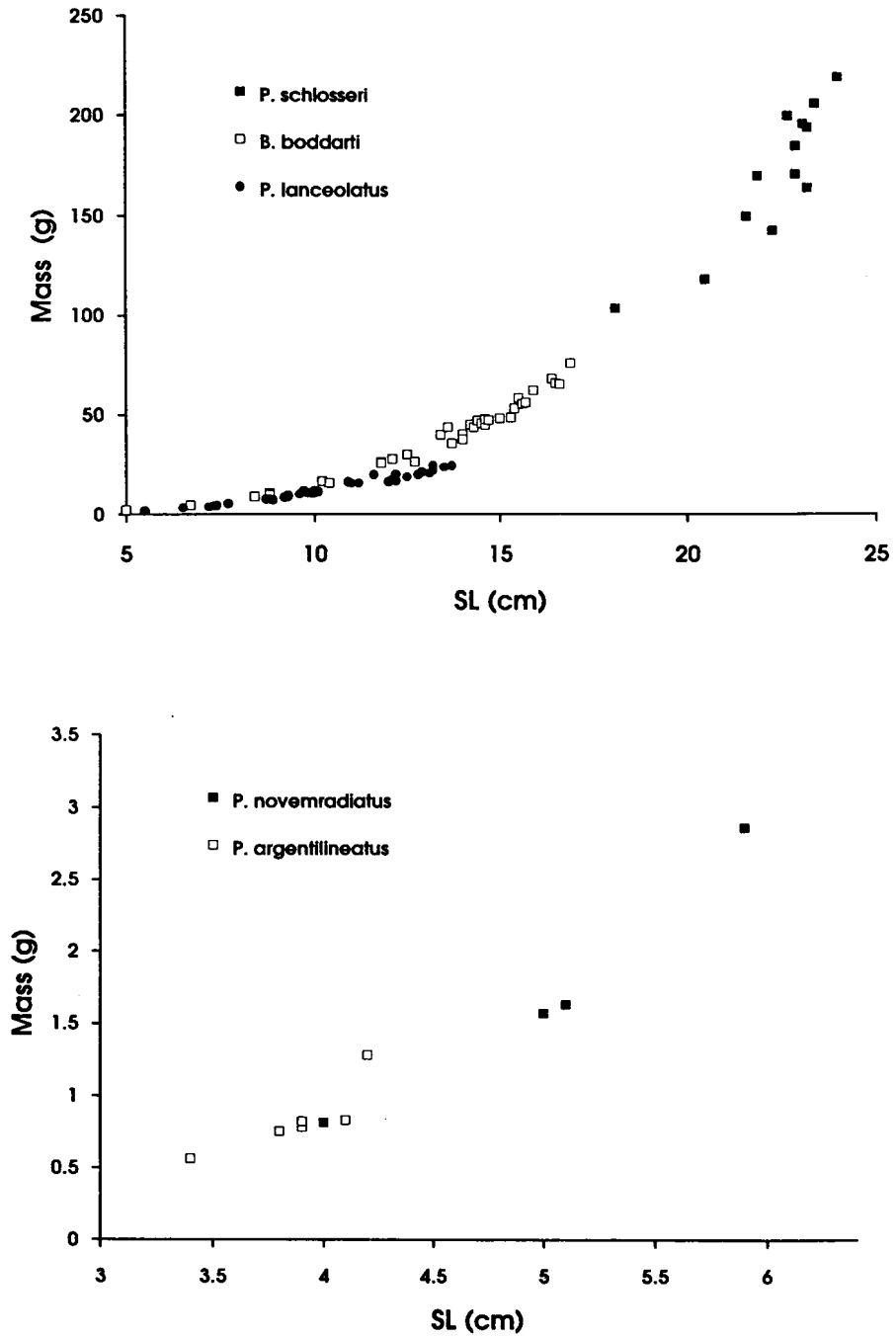


Figure 7. Relation between standard length and fresh mass of the mudskippers caught.

fisherman, requested to fish with hooked bait in the burrows, reported that *P. schlosseri* did not touch the bait. The narrow burrows of *P. lanceolatus* seemed to be built only for aestivation. In pools, the fish appeared to hide in any kind of hole or made a new burrow by pushing the body into the soft mud while removing the sediment by body movements.

Turning is an obvious behaviour in mudskippers. It was formerly believed to help the aeration of the water around the gills, but some authors thought it was a reaction to biting mosquitos (MACNAE, 1968). The turning behaviour was studied in some detail by IP ET AL. (1991) in Singapore. Their study indicates that the behaviour may serve to moisten the dorsal surface of the fish after evaporation in the air. These authors state that *B. boddarti* frequently turned, but that *P. schlosseri* exhibited no turning behaviour. This is in contrast with our observations. We found that *B. boddarti*, *P. schlosseri* and *P. lanceolatus* frequently turned to one side on exposed mud. In the water none of our species turned, probably because there was no need to, which is in agreement with the general conclusion of IP ET AL. (1991).

Interaction behaviour appeared highly developed in *B. boddarti*, a species feeding by side to side movements of the head while skimming benthic diatoms from the mud. They cleared small feeding-gardens around their burrows and threatened competitors with a whole repertoire of displays. *B. boddarti* is also the most colourful species with the largest dorsal fins. It is remarkable that the anterior dorsal fin is higher in females than in males (Fig. 4). The function of this sexual difference remains unclear. The other herbivorous species, *P. lanceolatus*, which usually fed submerged in turbid water, seemed not to need a feeding territory. Intraspecific interactions were not observed. However, because juveniles and small species were not observed on sites where adults of *P. schlosseri* occurred, we suspect that these carnivores may devour all small mudskippers in their vicinity. Only large individuals of the herbivorous *B. boddarti* were observed in such sites.

B. boddarti and *P. schlosseri* are not taken as food by the local population in Pattani area. Only *P. lanceolatus* is rarely eaten in a few villages. From other sites in Thailand, SMITH (1945) reported about bamboo traps to catch *Periophthalmus* spp. He stated, moreover, that *B. boddarti* is caught in seines, bag nets and traps for local consumption and for sale in the larger market towns. *B. pectinirostris* is considered a delicacy and is even cultured in Japan and Taiwan (CHEN, 1990). Our taste panel rated mudskipper meat above that of mullet, which is favored food in Pattani. Therefore, that mudskippers are neglected as food is certainly not due to low appreciation of its taste. Probably, fish protein is sufficiently available in Pattani that it is not considered rewarding to catch small fish in soft mud.

Our study shows that the sympatric mudskipper species differ in various aspects (anatomical, physiological, behavioural). This also holds for the accumulation of heavy metals. *B. boddarti* and *P. schlosseri*, from the mudflat in front of the PSU campus, had accumulated significantly different amounts of the heavy metals copper, zinc, cadmium and lead (EVERAARTS ET AL., 1994). This stresses the importance of identification to the lowest taxonomic level when closely related organisms are studied.

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