

## Two new species of blackwater catfishes (Siluriformes: Siluridae and Clariidae) from the Natuna Archipelago, Indonesia

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**Abstract.** Two new species of blackwater catfishes are described from Pulau Natuna Besar of the Natuna Archipelago, Indonesia. *Silurichthys insulanus* (Siluridae), new species, differs from all congeners in having a combination of characters: eye diameter 8% HL; pectoral-fin length 16.0% SL; distinctly humped nuchal profile; 1 branched dorsal-fin ray; body depth at anus 16.0% SL; 54 anal-fin rays; caudal peduncle depth 5.7% SL; caudal fin asymmetrically forked, with 12 principal rays and upper lobe 1.1 times longer than lower lobe; and 50 vertebrae. *Clarias rennyae* (Clariidae), new species, is distinguished from all Southeast Asian congeners in having a combination of characters: anal-fin length 51.3–56.3% SL; body depth at anus 13.1–13.7% SL; head width 17.9–18.9% SL; distance between occipital process and dorsal-fin origin 6.8–8.9% SL; frontal fontanelle length 17.7–22.5% HL; anterior edge of pectoral spine with 19–31 irregular tiny asperities; and 65–68 total vertebrae. Both new species appear to be endemic to blackwater streams along the western coast of Pulau Natuna Besar.

**Key words.** *Clarias rennyae*, *Silurichthys insulanus*, taxonomy, Southeast Asia

### INTRODUCTION

The Natuna Archipelago consists of 272 islands located in the southernmost section of the South China Sea between the Malay Peninsula and the island of Borneo. The archipelago is part of the Riau Islands Province of Indonesia (Pratiwi & Elfidasari, 2020), and has historically been frequented by ships plying the Singapore-Hong Kong trade route. In recent years, discoveries of oil and natural gas deposits, as well as disputes over territorial sovereignty, has once again pushed the Natuna Islands into the international spotlight (Tan & Kastoro, 2004; Meyer et al., 2019).

The inland fish fauna of the Natuna Archipelago was poorly known up till 2002, when two expeditions were organised by the Raffles Museum of Biodiversity Research (now Lee Kong Chian Natural History Museum) of the National University of Singapore and the Lembaga Ilmu Pengetahuan Indonesia (Indonesian Institute of Sciences) to document the biodiversity of the Natuna and neighbouring Anambas Islands. These expeditions led to the first inventory of inland fishes from the Natuna and Anambas Islands (Tan & Lim,

2004). Fifty-five species of inland fishes were recorded from the Natuna Archipelago, of which 21 were restricted to fresh waters. Two freshwater species, viz. *Rasbora bunguranensis* and *Betta aurigans*, appear to be endemic to the Natuna Archipelago, specifically the largest island Pulau Natuna Besar (previously known as Pulau Bunguran or Bunguran Island).

Recent re-examination of material collected in 2002 revealed the presence of two undescribed species of freshwater catfishes from the families Siluridae and Clariidae. Both species appear to be endemic to blackwater streams along the western coast of Pulau Natuna Besar. The new species are herein described as *Silurichthys insulanus* and *Clarias rennyae*.

### MATERIAL AND METHODS

Methods for morphometric measurements and meristic counts follow Ng & Ng (1998) for *Silurichthys* and Ng (1999) for *Clarias*. Measurements were made point-to-point using dial calipers, and recorded to the nearest 0.1 mm. Counts and measurements were taken on the left side of the body whenever possible. Vertebrae and unpaired-fin rays were counted from radiographs, whereas paired-fin rays and gill rakers were counted under a dissecting microscope with transmitted light. TL is total length, SL is standard length, and HL is head length. Numbers in parentheses indicate number of specimens with an observed character state. Asterisks indicate counts for holotype. Institutional codes follow Sabaj (2020).

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**TAXONOMY**

**Order Siluriformes**

**Family Siluridae**

***Silurichthys insulanus*, new species**  
(Figs. 1, 2)

*Silurichthys marmoratus* (non Ng & Ng, 1998) – Tan & Lim, 2004: 109.

**Holotype.** MZB 17239, 41.9 mm SL; Pulau Natuna Besar: blackwater tributary of Sungai Sekeram, 3°50'29"N 108°03'47"E; D. Wowor et al., 18 March 2002.

**Diagnosis.** *Silurichthys insulanus* is distinguished from all congeners in having fewer branched dorsal-fin rays (1 vs. 2–3) and (except *S. gibbiceps*) a distinctly humped (vs. evenly curving) nuchal profile (Fig. 1). It is further distinguished from congeners by having the following unique combination of characters: eye diameter 8% HL; pectoral-fin length 16.0% SL; body depth at anus 16.0% SL; 54 anal-fin rays; caudal peduncle depth 5.7% SL; caudal fin asymmetrically forked, with 12 principal rays and upper lobe 1.1 times longer than lower lobe; and 50 vertebrae.

**Description.** Biometric data is given in Table 1. General body form as in Fig. 2. Body laterally compressed. Head somewhat depressed. Dorsal profile straight, descending gently from dorsal-fin origin to snout tip. Lateral line complete, extending to middle of caudal-fin base; minute, posteroventrally-directed branches visible, decreasing in size posteriorly. Anterior profile of snout rounded. Anterior pair of nostrils tubular and anteromedial to maxillary barbel base. Posterior pair of nostrils bordered by fleshy dorsal and ventral membranes and situated posteromedial to maxillary barbel base. Eyes small, subcutaneous; located in anterior half of head; visible dorsally, but not ventrally.

Mouth subterminal; gape horizontal or very slightly oblique. Well-developed rictal fold present, consisting of large and fleshy upper lobe joined at corner of mouth with lower lobe; lower lobe subtended by short submandibular groove.

Teeth villiform. Dentary teeth in slightly curved, elongate bands narrowing posteriorly, reaching from symphysis almost to mouth corners; premaxillary teeth in broader, slightly curved rectangular bands; vomerine teeth in a single crescent-shaped band.

Maxillary barbels slightly flattened, reaching to anterior third of anal fin. One pair of mandibular barbels present; located slightly anterolateral to gular fold; barbels flattened for most of length, reaching to middle of pectoral-fin base. Gill membranes separate and overlapping, free from isthmus. Branchiostegal rays 14. Gill rakers short and small; 0 + 4.

Distal margin of dorsal fin pointed, with i,1 rays; segments of first ray not co-ossified to form spine. Distal margin of

Table 1. Morphometric data for holotype of *Silurichthys insulanus*, new species.

	<b>Holotype MZB 17239</b>
Standard length/mm	41.9
<b>% SL</b>	
Predorsal length	27.4
Preanal length	32.2
Prepelvic length	27.4
Prepectoral length	17.4
Length of dorsal-fin base	1.2
Anal-fin length	64.0
Pelvic-fin length	8.4
Pectoral-fin length	16.0
Pectoral-spine length	5.0
Caudal-fin length	24.1
Body depth at anus	16.0
Caudal peduncle depth	5.7
Head length	19.8
Head width	11.5
Head depth	10.0
<b>% HL</b>	
Snout length	41
Interorbital distance	41
Eye diameter	8
Maxillary barbel length	306
Mandibular barbel length	117

pectoral fin broadly convex, with 8,i rays. Segments of the proximal two-thirds of first pectoral-fin element co-ossified, forming spine. Pectoral spine slender, without serrations on posterior edge of spine proper and proximal articulated segments. Distal margin of pelvic fin convex, with i,5 rays. Distal margin of anal fin straight, with 54 rays; joined to caudal fin for length of last anal-fin ray. Integument over anal fin thickened proximally for slightly more than half of ray lengths; fin-ray erector muscles extending along anterior edges of anal-fin rays, ventral-most extent of muscles that of thickened integument. Caudal fin forked, with upper lobe 1.1 times longer than lower lobe; principal rays i,6,4,i. Vertebrae 13+37=50.

Preserved colouration: Flanks and thickened integument over anal fin brown, with numerous dark patches forming faint mottled pattern. Dorsal surface and sides of head brown with numerous scattered dark spots, fading to cream on ventral surfaces of head, breast, and belly. Dorsal, anal, and caudal fins brown, distal margins very slightly hyaline. Pectoral and pelvic fins light brown, with hyaline inter-radial membranes.

**Distribution and habitat notes.** *Silurichthys insulanus*, new species, is only known from Pulau Natuna Besar of the Natuna Archipelago, Indonesia, where it occurs in heath-peat swamp forest habitat with acidic (pH ~3.4), tannin-stained black waters. Syntopic species include *Desmopuntius hexazona*, *Rasbora einthovenii*, *Trigonopoma gracile*, *Clarias*

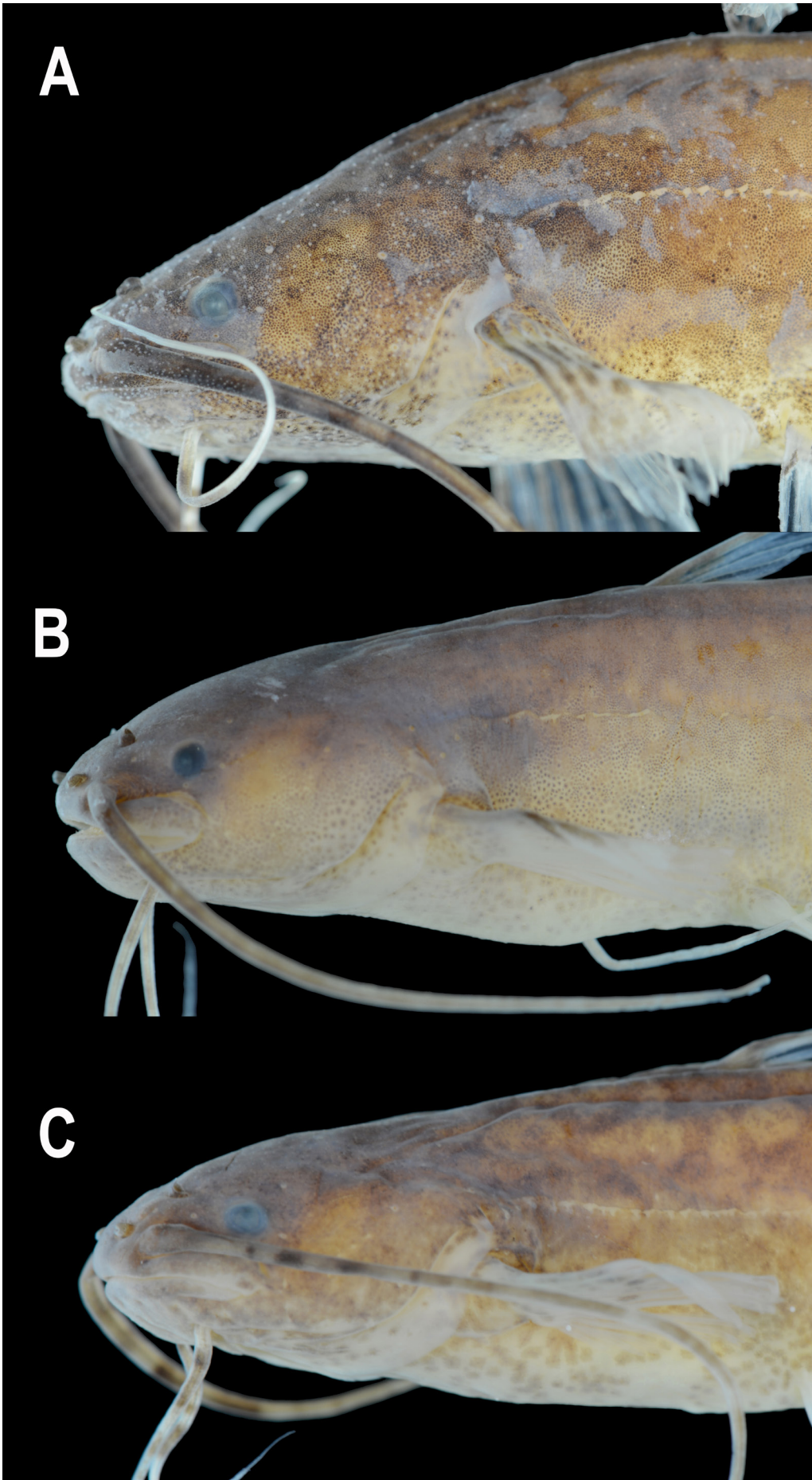


Fig. 1. Lateral views of head region of A) *Silurichthys insulanus*, new species, MZB 17239 holotype, 41.9 mm SL; B) *S. marmoratus*, ZRC 40107, 41.7 mm SL, Brunei; C) *S. gibbiceps*, ZRC 40328 paratype, 47.2 mm SL, Barito (not to scale).



Fig. 2. Lateral view of *Silurichthys insulanus*, new species, MZB 17239 holotype, 41.9 mm SL (composite of the same fish, top with black background, bottom with white background).

*rennyae*, new species, *Dermogenys colletei*, *Hemiramphodon pogonognathus*, *Brachygnathus doriae*, *Betta aurigans*, and *Luciocephalus pulcher*.

**Etymology.** The specific epithet comes from the Latin adjective *insulanus*, *-a*, *-um*, which means “of or belonging to an island”. The name is used in reference to the only location this species is known from (an island).

**Remarks.** In addition to the number of branched dorsal-fin rays and the nuchal profile, *Silurichthys insulanus* is further distinguished from *S. citatus* in having a longer pectoral fin (16.0% SL vs. 12.6–14.2), a more slender caudal peduncle (5.7% SL vs. 6.5–7.6) and an asymmetrically-forked caudal fin with distinct lobes (vs. obliquely truncate without distinct lobes), from *S. exortivus* in having (vs. lacking) dorsal and pelvic fins, and more principal caudal-fin rays (7+5 vs. 4+5), from *S. gibbiceps* in having a smaller eye (diameter 8% HL vs. 10–14), a longer pectoral fin (16.0% SL vs. 13.0–14.8), a more slender caudal peduncle (5.7% SL vs. 6.3–8.8), more branchiostegal rays (14 vs. 10) and gill rakers (0+4 vs. 0+2), and from *S. hasseltii* in having a smaller eye (diameter 8% HL vs. 11–18). It further differs from *S. indragiriensis* in having a smaller eye (diameter 8% HL vs. 10–15) and a shorter upper lobe of the caudal fin relative to the lower lobe (1.1 times vs. 1.4–1.6), from *S. ligneolus* in having a deeper body (depth at anus 16.0% SL vs. 9.1–11.0), more anal-fin

rays (54 vs. 44–45), vertebrae (50 vs. 46–48), and principal caudal-fin rays (7+5 vs. 7+3–4), and an asymmetrically-forked caudal fin with distinct lobes (vs. obliquely truncate without distinct lobes), and from *S. marmoratus* in having a smaller eye (diameter 8% HL vs. 10–13), a longer pectoral fin (16.0% SL vs. 12.4–14.9), and a more slender caudal peduncle (5.7% SL vs. 6.3–9.5). *Silurichthys insulanus* is also distinguished from *S. phaiosoma* in having a smaller eye (diameter 8% HL vs. 11–14) and a shorter upper lobe of the caudal fin relative to the lower lobe (1.1 times vs. 1.4–1.6), from *S. sanguineus* in having a deeper body (depth at anus 16.0% SL vs. 9.2) and caudal peduncle (5.7 vs. 4.2), fewer vertebrae (50 vs. 57), more principal caudal-fin rays (7+5 vs. 7+4), and an asymmetrically-forked caudal fin with distinct lobes (vs. obliquely truncate without distinct lobes), and from *S. schneideri* in having a longer pectoral fin (16.0% SL vs. 12.7–14.8), and fewer anal-fin rays (54 vs. 58–68) and vertebrae (50 vs. 53–55).

**Comparative material.** *Silurichthys exortivus*: MZB 17240, 60.6 mm SL; Borneo: Kalimantan Timur, Mahakam River drainage, Belayan River system, REA Plantations, Long Buluh Damai Estate, 0°14'29"N 116°19'14"E.

*Silurichthys gibbiceps*: ZRC 40328 (5 paratypes), 47.2–75.2 mm SL; Borneo: Kalimantan Tengah, Barito basin, Sungei Paku-merah, 0°35'10"N 115°11'24"E.

*Silurichthys marmoratus*: ZRC 40107 (9), 34.5–52.4 mm SL;

Borneo: Brunei Darussalam, Belait District, peat swamp from next to Sungai Sepan. ZRC 40110 (1), 56.5 mm SL; Borneo: Brunei Darussalam, Tutong District, Sungai Ratuan Uluh, 200 km behind base camp at Tasik Merimbun, 4°34'53"N 114°21'24"E. ZRC 41849 (1), 97.8 mm SL; Borneo: Sarawak, Serian market.

Additional comparative material used is listed in Ng & Ng (1998) and Ng & Tan (2011).

## Order Siluriformes

### Family Clariidae

#### *Clarias rennyae*, new species

(Figs. 3, 4)

*Clarias leiakanthus* (non Bleeker, 1851) – Tan & Lim, 2004: 109 (part).

**Holotype.** MZB 17237, 108.0 mm SL; Pulau Natuna Besar: blackwater tributary of Sungai Sekeram (3°50'28.6"N 108°03'47.1"E) (W13); D. Wowor et al.; 18 March 2002.

**Paratypes.** ZRC 62074, 157.9 mm SL; ZRC 62075, 115.1 mm SL; MZB 17238, 84.6 mm SL; Pulau Natuna Besar: blackwater tributary of Sungai Sekeram (3°50'28.6"N 108°03'47.1"E) (W12); D. Wowor et al.; 18 March 2002.

**Diagnosis.** *Clarias rennyae* is distinguished from all other Southeast Asian congeners by the following suite of characters: anal-fin length 51.3–56.3% SL, body depth at anus 13.1–13.7% SL, head width 17.9–18.9% SL, distance between occipital process and dorsal-fin origin 6.8–8.9% SL, frontal fontanelle length 17.7–22.5% HL, anterior edge of pectoral-fin spine with 19–31 irregular tiny asperities, and 65–68 total vertebrae.

**Description.** General body form as in Fig. 3. Morphometric measurements are shown in Table 2. Body cylindrical, tapering towards caudal peduncle. Skin smooth. Lateral line median, starting just behind operculum and ending at caudal peduncle. Openings to secondary sensory canals arranged regularly on upper flanks of the body in vertical branches above the lateral line, visible as 12–17 vertical rows of 2–6 tiny white spots.

Head depressed, dorsal profile slightly convex, egg-shaped when viewed from the top, snout narrow. Occipital process narrow; round or slightly triangular with rounded tip. Frontal fontanelle around twice (1.9–2.4×) as long as wide, with anterior margin reaching imaginary line between orbits. Occipital fontanelles oval, around 1.5 times as long as wide; anterior margin slightly before pectoral fin insertion. Four pairs of barbels with fleshy base, tapering towards the tips. Mouth subterminal with fleshy lips. Eyes small and subcutaneous. First branchial arch with 15 (1), 16 (1), 20\* (1) gill rakers.

Dorsal fin with long base, spanning posterior four-fifths of body, with 72\* (2) or 73 (2) rays. Anal fin with long base, spanning posterior three-quarters of body, with 58 (1), 59\* (1), 60 (1), or 64 (1) rays. Posterior extremities of dorsal and anal-fin base extending beyond anterior margin of the hypural complex. Caudal fin rounded, with 8+7 (2) or 9+7\* (2) rays. Dorsal, anal and caudal fins covered with thick layer of skin. Pectoral fin with a small spine, and 8 (1) or 9\* (3) rays; anterior edge of pectoral-fin spine with 19\* (1), 24 (1), 27 (1), or 31 (1) irregular tiny pointed asperities at proximal end, distal end smooth. Pelvic fin with I,5 (4) rays, originating at anterior third of body.

Vertebral formula: 20 + 45 = 65 (1), 21 + 45 = 66\* (2), 21 + 47 = 68 (1).

Preserved colouration: Body dark brown on dorsum and sides, fading to cream on the underside. Dorsal, anal, and caudal fins dark brown, distal margins very slightly hyaline. Pectoral and pelvic fins light brown, with hyaline inter-radial membranes.

**Distribution and habitat notes.** *Clarias rennyae*, new species, is only known from Pulau Natuna Besar of the Natuna Archipelago, Indonesia, where it occurs in heath-peat swamp forest habitat with acidic (pH ~3.4), tannin-stained black waters. Syntopic species as listed above.

A second species of walking catfish we tentatively identify as *C. leiakanthus*, was also collected from Pulau Natuna Besar. Both species are not syntopic, however, with *C. rennyae* only recorded from blackwater streams on the western side of the island, whereas *C. leiakanthus* was only caught from a rocky clearwater stream (near a waterfall habitat) draining the eastern slope of the island. Additionally, *C. rennyae* can be distinguished from *C. leiakanthus* by a wider head (head width 17.9–18.9% SL vs. 17.2–17.9% SL in *C. leiakanthus*) and a narrower suborbital snout width (50.4–53.8% HL vs. 54.5–55.4% HL in *C. leiakanthus*), giving the appearance of a more tapered snout when viewed dorsally, as well as falcate pectoral fins (vs. rounded pectoral fins in *C. leiakanthus*) (Fig. 4).

**Etymology.** The species is named for the late Renny Kurnia Hadiaty (21 August 1960–30 January 2019), a dear friend and colleague who passed away too soon. Renny was a leading expert on the taxonomy of Indonesian freshwater fishes, and was Curator of Fishes and Head of the Ichthyology Laboratory at the Museum Zoologicum Bogoriense, Lembaga Ilmu Pengetahuan Indonesia (Indonesian Institute of Sciences).

**Remarks.** Twenty-one Southeast Asian *Clarias* species are currently recognised (Ng & Kottelat, 2014), viz. *C. batrachus* (Linnaeus, 1758); *C. fuscus* (La Cèpède, 1803); *C. nieuhofii* Valenciennes, in Cuvier & Valenciennes, 1840; *C. meladerma* Bleeker, 1846; *C. leiakanthus* Bleeker, 1851; *C. macrocephalus* Günther, 1864; *C. olivaceus* Fowler, 1904; *C. batu* Lim & Ng, 1999; *C. anfractus* Ng, 1999; *C. planiceps* Ng, 1999; *C. microstomus* Ng, 2001; *C. intermedius* Teugels, Sudarto & Pouyaud, 2001; *C. insolitus* Ng, 2003; *C. nigricans*

Table 2. Morphometric data for *Clarias rennyae*, new species.

	Holotype	Paratypes (n = 3)
Standard length/mm	108	84.6–157.9
<b>% SL</b>		
Predorsal length	34.6	30.7–34.9
Preanal length	50	45–48.6
Prepelvic length	43.1	38.6–42.6
Prepectoral length	20.6	19.1–20.7
Dorsal fin length	66.6	67.7–71.5
Anal fin length	51.3	51.7–56.3
Pelvic fin length	8.4	8.5–8.7
Pectoral fin length	14.5	13.4–14.9
Pectoral spine length	10.3	9.3–10.9
Caudal fin length	19.2	17.7–19.9
Distance between occipital process and dorsal fin	8.5	6.8–8.9
Caudal peduncle depth	6.3	6.1–6.8
Body depth at anus	13.1	13.4–13.7
Head length	26.1	24–26.3
Head width	18.2	17.9–18.9
Head depth	12.4	12.3–12.9
<b>% HL</b>		
Snout length	25	23–24
Interorbital width	44	44–46
Eye diameter	6	6–8
Occipital process length	12	8–11
Occipital process width	23	22–27
Nasal barbel length	94	99–104
Maxillary barbel length	163	164–169
Inner mandibular barbel length	92	85–101
Outer mandibular barbel length	133	131–135
Frontal fontanelle length	18	18–23
Frontal fontanelle width	9	8–10
Occipital fontanelle length	11	9–11
Occipital fontanelle width	7	6–7

Ng, 2003; *C. kapuasensis* Sudarto, Teugels & Pouyaud, 2003; *C. pseudoleiacanthus* Sudarto, Teugels & Pouyaud, 2003; *C. sulcatus* Ng, 2004; *C. pseudonieuhofii* Sudarto, Pouyaud & Teugels, 2004; *C. gracilentus* Ng, Dang & Nguyen, 2011; *C. microspilus* Ng & Hadiaty, 2011; and *C. serniosus* Ng & Kottelat, 2014. These can be broadly divided into two artificial species groups based on their morphology, with the more elongate/anguilliform species (81–101 dorsal fin rays, 74–84 total vertebrae) being placed into the *C. nieuhofii* species group, and the less elongate species (53–77 dorsal fin rays, 54–71 total vertebrae) being placed into the *C. batrachus* species group (Sudarto et al., 2003; Ng et al., 2011). Presently, the *C. nieuhofii* species group comprises *C. nieuhofii*, *C. nigricans*, *C. pseudonieuhofii*, and *C. gracilentus*, whereas the *C. batrachus* species group comprises the remaining 17 Southeast Asian species. *Clarias rennyae*, with 72–73 dorsal fin rays and 65–68 total vertebrae, falls into the *C. batrachus* species group.

*Clarias rennyae* differs from *C. anfractus* in having a longer frontal fontanelle (18–23% HL vs. 10–16) and a pectoral spine with a smooth anterior margin along distal two-thirds and tiny pointed asperities along proximal one-third (vs. irregular outline along entire anterior margin), from *C. batrachus* in having a longer anal fin (51.3–56.3% SL vs. 43.3–50.7) and more vertebrae (65–68 vs. 54–61), and from *C. batu* in having a shorter distance between the occipital process tip and dorsal fin origin (6.8–8.9% SL vs. 9.9–11.8), a deeper body (depth at anus 13.1–13.7% SL vs. 9.0–11.4) and a longer frontal fontanelle (18–23% HL vs. 13–16). It can be differentiated from *C. fuscus* by a greater distance between the occipital process and dorsal fin origin (6.8–8.9% SL vs. 4.8–6.5) and more vertebrae (65–68 vs. 53–57), from *C. gracilentus* by a shorter anal fin (51.3–56.3% SL vs. 60.0–63.9), a deeper body (depth at anus 13.1–13.7% SL vs. 8.2–11.7), a wider head (17.9–18.9% SL vs. 11.9–12.9) and fewer vertebrae (65–68 vs. 80–84), and from *C. insolitus* by a shorter distance between the occipital process and dorsal fin origin (6.8–8.9% SL vs. 10.3–12.4), a deeper body



Fig. 3. *Clarias rennyae*, new species, holotype, MZB 17237, 108 mm SL; Indonesia: Natuna Islands, Pulau Natuna Besar (composite of dorsal, lateral, and ventral views).

(depth at anus 13.1–13.7% SL vs. 9.9–11.5), a wider head (17.9–18.9% SL vs. 14.0–15.6) and a pectoral spine with tiny asperities on the anterior edge (vs. prominent serrations). *Clarias rennyae* can be distinguished from *C. intermedius* by a greater distance between the occipital process and dorsal fin origin (6.8–8.9% SL vs. 1.8–3.8), a more slender body (depth at anus 13.1–13.7% SL vs. 14.0–18.1) and more vertebrae (65–68 vs. 61), from *C. kapuasensis* by a more slender body (depth at anus 13.1–13.7% SL vs. 14.4–18.0) and a pectoral spine with tiny asperities on the anterior edge (vs. a smooth edge), and from *C. leiacanthus* by a wider head (17.9–18.9% SL vs. 17.2–17.9) and a longer frontal fontanelle (18–23%

HL vs. 9–16). It further differs from *C. macrocephalus* in having a longer anal fin (51.3–56.3% SL vs. 46.4–50.2), a greater distance between the occipital process and dorsal fin origin (6.8–8.9% SL vs. 2.2–5.1), a more slender body (depth at anus 13.1–13.7% SL vs. 16.8–19.2) and a greater number of vertebrae (65–68 vs. 57–61), from *C. meladerma* in having a greater distance between the occipital process tip and dorsal fin origin (6.8–8.9% SL vs. 2.1–4.8) and a pectoral spine with tiny asperities on the anterior edge (vs. prominent serrations), and from *C. microspilus* in having a longer anal fin (51.3–56.3% SL vs. 47.4–50.5), a more slender body (depth at anus 13.1–13.7% SL vs. 14.9–18.9),

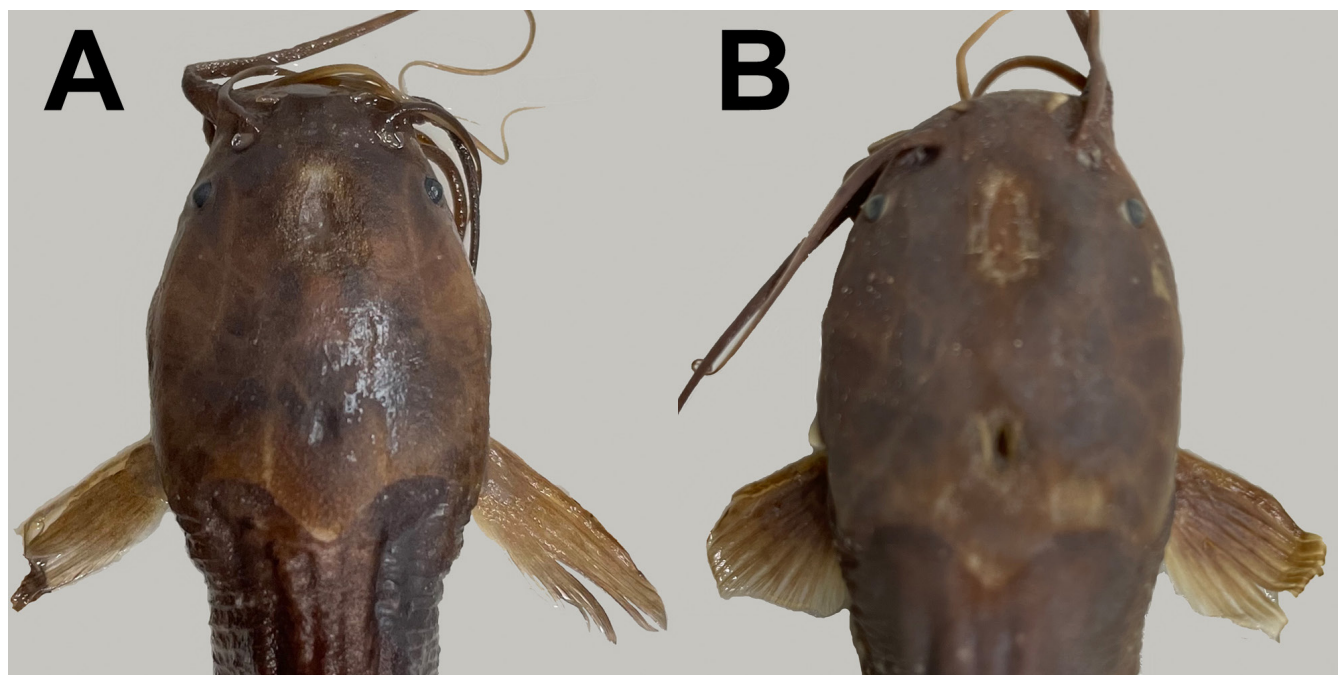


Fig. 4. Dorsal views showing differences in head and pectoral fin morphology between A) *C. rennyae*, new species, holotype, MZB 17237, 108 mm SL, Pulau Natuna Besar, and B) *C. leiacanthus*, ZRC uncat., 133.8 mm SL, Pulau Natuna Besar (not to scale).

a longer frontal fontanelle (18–23% HL vs. 12–17), more vertebrae (65–68 vs. 60–62), and a pectoral spine with tiny asperities (vs. prominent serrations).

*Clarias rennyae* is further distinguished from *C. microstomus* by a shorter distance between the occipital process and dorsal fin origin (6.8–8.9% SL vs. 12.8–13.1), a wider head (17.9–18.9% SL vs. 16.2–17.2), a longer frontal fontanelle (17.7–22.5% HL vs. 8.3–10.9), a greater number of vertebrae (65–68 vs. 61–64) and a pectoral spine with tiny asperities on the anterior edge (vs. a smooth edge), from *C. nieuhoffii* by a shorter anal fin (51.3–56.3% SL vs. 59.7–66.8) and a wider head (17.9–18.9% SL vs. 11.7–15.8), and from *C. nigricans* by a shorter anal fin (51.3–56.3% SL vs. 59.6–63.8), a deeper body (depth at anus 13.1–13.7% SL vs. 10.4–13.0), a wider head (17.9–18.9% SL vs. 11.7–12.3), a longer frontal fontanelle (18–23% HL vs. 9–14), fewer vertebrae (65–68 vs. 76–83) and a pectoral spine with tiny asperities on the anterior edge (vs. a few large serrations). It is further differentiated from *C. olivaceus* by a longer frontal fontanelle (18–23% HL vs. 10–17), a greater number of vertebrae (65–68 vs. 60–63) and a pectoral spine with tiny asperities (vs. prominent serrations), from *C. planiceps* by a wider head (17.9–18.9% SL vs. 15.7–17.6), a longer frontal fontanelle (18–23% HL vs. 11–18) and a pectoral spine with tiny asperities on the anterior edge (vs. prominent serrations), and from *C. pseudoleiacanthus* by a greater distance between the occipital process and dorsal fin origin (6.8–8.9% SL vs. 4.5–5.6), a more slender body (depth at anus 13.1–13.7% SL vs. 15.7–18.2) and a pectoral spine with tiny asperities on the anterior edge (vs. a smooth edge). Lastly, *C. rennyae* differs from *C. pseudonieuhoffii* in having a deeper body (13.1–13.7% SL vs. 11.0–12.9), a wider head (17.9–18.9% SL vs. 12.7–14.3) and a longer frontal fontanelle (18–23% HL vs. 10–15), from *C. serniosus* in having a longer anal

fin (51.3–56.3% SL vs. 46.2–50.1), a more slender body (13.1–13.7% SL vs. 16.2–16.5), more vertebrae (65–68 vs. 57) and a pectoral spine with tiny asperities on the anterior edge (vs. a smooth edge), and from *C. sulcatus* in having more vertebrae (65–68 vs. 62–64).

**Comparative material.** *Clarias batrachus*: ZRC 2585 (4), 170.3–247 mm SL; Tjilebut, West Java. – MZB 15517 (1), 187.5 mm SL; S. Cipayang, Gn. Ciremai Timur; Kuningan, Jawa Barat. – MZB 20621 (1), 199 mm SL; Situ Mangabolong, kel Srengseng Sawah, kec. Jagakarsa, kotip Jakarta Selatan. – MZB 1270 (1), 167.2 mm SL; Java: Ciangeke, Semplak, Bogor. – MZB 1457 (1), 226.1 mm SL; Caringin, Citarik, Pelabuhan Ratu, West Java. – MZB uncat. (1), 195 mm SL; Batavia. – MZB 10070 (1), 158 mm SL; S. Cimanuk, Kp. Sipon, Ds. Bayongbong, Garut, Jawa Barat. – MZB 4033 (2), 200.5–218 mm SL; Rawa Pening, Jawa-Tengah. – MZB 4190 (1), 224.4 mm SL; Ambarawa, Jawa Tengah. – MZB 2447 (1), 190.8 mm SL; Telaga Menggen, Womosobo, Jawa-Tengah. – MZB 1237 (2), 221–221.9 mm SL; S. Blawi, 10 km utara Lamongan. – MZB 1451 (3), 173.9–192.7 mm SL; Java: Riv. Bersini, Gemuk Mas, Jembero, East Java. – MZB 1358 (1), 170 mm SL; East Java: Riv. Kuwayangan, Ngantang-Malang.

*Clarias fuscus*: Data from Arai & Hirano (1974).

*Clarias intermedius*: Data from Teugels et al. (2001).

*Clarias kapuasensis*: Data from Sudarto et al. (2003).

*Clarias leiacanthus*: ZRC 37758 (10), 49.1–129.5 mm SL; Borneo: Sarawak, Bako National Park, Ulu Assam, stream I. – ZRC 39744 (12), 155.0–326.7 mm SL; Borneo: Sarawak, Serian market, from Batang Kerang. – ZRC 40551 (3), 191.7–206.0 mm SL; Borneo: Sarawak, Miri, from pasar malam next to bus station, purportedly from Sungai Bakung. – ZRC 42697 (8), 20.4–95.8 mm SL; Brunei: Belait district, 2 streams near old padi fields ca. 200 m downstream



of Kampung Melilas (4°15'24.3"N, 114°39'40.2"E). – ZRC 40131 (1), 97.7 mm SL; Java: Java Barat, Bogor, tributary of Cipinang Gading. – ZRC 39105 (4), 37.0–150.0 mm SL; Sumatra: Riau, stream near Pangkalankasai, 43 km from Rengat on Rengat–Jambi road. – ZRC 41523 (5), 175.1–255.7 mm SL; Sumatra: Jambi, Angso Duo market. – ZRC 11678–11679 (2), 109.8–202.9 mm SL; Singapore: Nee Soon Swamp Forest. – ZRC 39985 (5), 23.8–177.5 mm SL; Malaysia: Johor, Pontian, Kampung Parit Tekong. – ZRC 39961 (2), 56.9–120.7 mm SL; Malaysia: Johor, 3–4 km towards Kukup after Sri Bunian turnoff. – ZRC 2596 (2), 93.4–109.5 mm SL; Malaysia: Pahang, Kuala Tahan. – ZRC 25669 (1), 124.8 mm SL; Malaysia: Pahang, 69 km on Mersing–Kuantan road. – ZRC uncat. (2), 133.8–214.1 mm SL; Pulau Natuna Besar: stream under last wooden bridge towards waterfall from Ranai (DW0207).

*Clarias macrocephalus*: ZRC 30465 (1), 197.2 mm SL; Malaysia: Pahang, Sg. Jelai. – ZRC uncat. (1), 280 mm TL; Malaysia: Perak, Sg. Sungkai Mati. – ZRC uncat. (1), 205 mm SL; Thailand: Phuket province, Thalang district. – MARNM 5887 (1), 139.5 mm SL; Thailand: Chiang Rai province, Teung district, Ing River. Additional data from Teugels et al. (1999).

*Clarias meladerma*: ZRC uncat. (1), 160 mm TL; Malaysia: Langkawi, stream along Persiaran Langkawi Indah 12, near intersection with Langkawi Highway.

*Clarias nieuhoffii*: Data from Sudarto et al. (2004).

*Clarias pseudoleiacanthus*: Data from Sudarto et al. (2003).

*Clarias pseudonieuhoffii*: Data from Sudarto et al. (2004).

For a list of additional material examined, see Ng (1999, 2001, 2003a, b, 2004), Lim & Ng (1999), Tan & Ng (2000), Ng & Hadiaty (2011), Ng et al. (2011), Ng & Kottelat (2008, 2014).

## DISCUSSION

Freshwater fish species and endemic diversity are extremely high in Sundaic Southeast Asia, with more than 900 species and 500 endemics documented thus far (Chong et al., 2010; Hubert et al., 2015). Around 350 species are only known from a single island or island-group, with insular endemism being highest on Borneo (267 endemics) (Tan, 2006), followed by Sumatra (58 endemics) (Wargasasmita, 2017), Java and Bali (21 endemics) (Dahrudin et al., 2017), the Natuna Archipelago (4 species) (Tan & Lim, 2004; current study), and islands off the Malay Peninsula (3 species) (Lim & Ng, 1999; Ng, 2004).

Hall (2013) hypothesised that geological and climatic processes during the early to mid-Miocene (15–20 Ma) effectively split the Southeast Asian landmass into two major components—Indochina and (an extended) Borneo—which in the latter, facilitated the early accumulation of lineages which would later develop into Sundaland's distinct biota. Coupled with its prolonged emergent history and periodic connectivity with the other (younger) Greater Sunda islands throughout the Miocene and Plio-Pleistocene, this has led to the hypothesis that Borneo was the major diversification hotspot and origin

of lineage dispersal within Sundaland (De Bruyn et al., 2014). Subsequently, climate-induced Pleistocene eustatic sea level oscillations further played a disproportionately large role in the diversification of Sundaland's insular fish diversity, by facilitating colonisation events (from Borneo into surrounding islands) during periods of low sea levels (glacial maxima) interspersed with periods of isolation and in situ diversification when sea levels rose (glacial minima) (Sholihah et al., 2021). Despite intermittent connectivity between islands throughout the Pleistocene, the high insular endemism within Sundaland may be in part explained by some lineages evolving specialised habitat requirements (e.g., blackwater stenotopics) or poor dispersal capabilities (e.g., producing fewer but larger offspring) during periods of isolation, which consequently limited penetration into dispersal corridors (typically savanna or seasonal forests) when connectivity was restored during glacial periods. This model of “founder effect” speciation has been postulated to drive the high insular endemism of Southeast Asian halfbeaks from the family Zenarchopteridae and blackwater lineages of walking catfishes from the family Clariidae (De Bruyn et al., 2013; Sholihah et al., 2021).

Given that the basal divergence between temperate and tropical Siluridae lineages (the latter to which *Silurichthys* belongs) has been estimated to have occurred around 5 Ma (Bornbusch, 1995), and that the first vicariance event between Southeast Asian mainland and Sundaic *Clarias* lineages occurred around 6.37 Ma (Sholihah et al., 2021), we can infer that both new species *S. insulanus* and *C. rennyae* were likely to have emerged sometime during the Plio-Pleistocene (5 Ma onwards). This period was marked by large climate-induced fluctuations in global sea levels, and the Natuna Archipelago was intermittently connected to northwestern and western Borneo via the North Sunda River when sea levels were >50 m below present levels (Voris, 2000). As blackwater siluriform lineages generally exhibit a limited ability to disperse over large stretches of unsuitable habitats (Sholihah et al., 2021), we speculate that both species originate from blackwater lineages that are currently extant on northwestern and western Borneo. Representatives of these lineages, which *S. insulanus* and *C. rennyae* may be sister taxa to, include *S. marmoratus* and *S. phaiosoma*, and *C. leiacanthus* and *C. pseudoleiacanthus*, respectively (Ng & Ng, 1998; Sudarto et al., 2003).

Currently, both *Silurichthys insulanus* and *Clarias rennyae* are only known from a single locality within heath-peat swamp forests along the western coast of Pulau Natuna Besar, with an estimated area of occupancy of less than 10 km<sup>2</sup>. However, given that there is no precise information on current population trends and threats, we are unable to accurately assess the extinction risks faced by both species (IUCN, 2012). Giam et al. (2012) highlighted that the conversion of peat swamp forests for agricultural land use poses the biggest threat to blackwater stenotopic fishes across Sundaland. While nearly 70% of forests on Pulau Natuna Besar has been logged to some extent by the late 20<sup>th</sup> century, large-scale logging operations were halted by the early 2000s and there are currently no future plans for

Table 3. Endemic freshwater fishes known from Sundaic islands under 2,000 km<sup>2</sup> in area (NA = not assessed).

Species	IUCN conservation status	Main reference
<b>Cyprinidae</b>		
<i>Rasbora bunguranensis</i>	DD	Tan & Lim, 2004
<i>Rasbora dies</i>	DD	Kottelat, 2008
<i>Sundadanio atomus</i>	EN	Conway et al., 2011
<i>Sundadanio axelrodi</i>	VU	Conway et al., 2011
<i>Sundadanio gargula</i>	VU	Conway et al., 2011
<b>Barbuccidae</b>		
<i>Barbucca elongata</i>	NA	Vasil'eva & Vasil'ev, 2013
<b>Nemacheilidae</b>		
<i>Speonectes tiomanensis</i>	CR	Tan et al., 2015
<b>Clariidae</b>		
<i>Clarias batu</i>	CR	Lim & Ng, 1999
<i>Clarias gracilentus</i>	NA	Ng et al., 2011
<i>Clarias sulcatus</i>	CR	Ng, 2004
<b>Osphronemidae</b>		
<i>Betta aurigans</i>	DD	Tan & Lim, 2004
<i>Betta miniopinna</i>	CR	Tan & Tan, 1994
<i>Betta spilotogena</i>	EN	Ng & Kottelat, 1994
<i>Parosphromenus bintan</i>	VU	Kottelat & Ng, 1998
<i>Parosphromenus deissneri</i>	EN	Kottelat & Ng, 1998
<i>Parosphromenus juelinae</i>	NA	Shi et al., 2021

palm oil plantations, owing to high transportation costs to and from this remote island. Nonetheless, small-scale illegal logging has been reported to be widespread in the past (Lammertink et al., 2003), although the current magnitude of this threat is unknown. Further research is needed to elucidate population trends and potential threats to these species, and clearly identify their extinction risks.

It is sobering to also note that coastal (low-lying) habitats in which many of the small-island (here defined as those under 2,000 km<sup>2</sup> in area fide Falkland, 1993) endemic fish species are found are highly vulnerable to the effects of sea-level rise (SLR) caused by climate change, with up to 15% of the coastal habitats on Southeast Asian islands estimated to be destroyed by an SLR of 1 m through inundation and coastal erosion (Wetzel et al., 2012). Another insidious, but no less severe, effect of SLR is the rapid landward (and upward) extension of tidal creek systems and saltwater intrusion into low-lying coastal freshwater habitats, which can lead to habitat destruction far exceeding that of shoreline retreat alone (Knighton et al., 1991). Although freshwater fish biodiversity in small islands in Sundaic Southeast Asia has not been well-studied, 16 endemic freshwater fish species have been identified, with a large majority being found in low-elevation habitats and more than half assessed as being in a threatened category (Table 3). Given their highly localised distributions and the paucity of inland refugia habitats (particularly for species stenotopic to blackwater habitats), we expect many of these species to face extinction with increasing SLR. At the moment, research and conservation of many, if not all,

Sundaic small-island endemic fishes are woefully inadequate, there is the urgent need to consider the combined impacts of multiple stressors (e.g., land conversion, SLR) in future conservation plans.

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