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# *Channa kelaartii*, a valid species of dwarf snakehead from Sri Lanka and southern peninsular India (Teleostei: Channidae)

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## Abstract

The dwarf snakehead *Channa gachua* (Hamilton, 1822) (type locality Bengal) has been reported from a vast range, from Iran to Taiwan, and northern India to Sri Lanka. Here, adopting an integrative taxonomic approach, we show that the Sri Lankan snakehead previously referred to as *C. gachua* is in fact a distinct species, for which the name *C. kelaartii* (Günther, 1861) is available. Widely distributed in streams and ponds throughout Sri Lanka's lowlands, and also recorded here from the east-flowing drainages of southern peninsular India, *C. kelaartii* is distinguished from all the other species of the *C. gachua* species group by the combination of head shape, dorsal- and anal-fin ray counts, scale counts, the presence of pelvic fins, and live adult coloration. Further, *C. kelaartii* is genetically distinct from topotypical *C. gachua* by an uncorrected pairwise distance of 7.9–8.8 % for the mitochondrial *cytochrome c oxidase subunit 1* (*cox1*) gene.

## Key words

*Channa gachua*, integrative taxonomy, DNA barcoding, biogeography, Western Ghats-Sri Lanka biodiversity hotspot.

## Introduction

The *Channa gachua* group of snakehead fishes (Britz, 2008, hereafter the 'Gachua group') currently comprises some 20 valid species in addition to several undescribed taxa (Rüber *et al*., 2020). Members of this group are mostly small to medium sized (100–250 mm SL), though some, such as *C. barca* (Hamilton, 1822) and *C. aurantimaculata* Musikasinthorn, 2000, can reach 400–900 mm SL (Rüber *et al*., 2020). With the exception of *C. aurantipectoralis* Lalhlimpuia, Lalronunga & Lalramliana, 2016 members of the Gachua group are united in exhibiting an alternating pattern of dark and light concentric bands on the pectoral fin (Britz, 2008; Lalhlimpuia *et al*., 2016; Britz *et al*., 2019), a character absent in other channids. The monophyly of this group is supported also by the molecular phylogeny of Rüber *et al*. (2020). The Gachua group has a wide range across southern Asia, from eastern Iran, across India and Sri Lanka, Myanmar, Singapore, and on to Java and Taiwan, with the highest diversity reported in the Eastern Himalaya Biodiversity Hotspot (Kottelat, 2013; Conte-Grand *et al*., 2017; Rüber *et al*., 2020). Several of the group's constituent species are narrow-range endemics.

GÜNTHER (1861: 472) described, from a series of 13 specimens sent to him from Sri Lanka, *Ophiocephalus kelaartii* (*Ophiocephalus* is an incorrect subsequent spelling of *Ophicephalus* Bloch, which is a synonym of *Channa* Scopoli: see MYERS & SHAPOVALOV, 1932; KOTTELAT, 2013). In his synopsis of species, GÜNTHER (1861: 469) grouped *C. kelaartii* together with *C. gachua* on the basis of their having moderate or larger-sized scales on the dorsal surface of the head, lacking an ocellated spot in the adult state, and possessing 29–37 dorsal-fin rays. He distinguished *O. kelaartii* from *O. gachua*, however, only by stating: 'This species is allied to *O. gachua*, differing from it by its longer caudal fin.' DAY (1878) relegated *C. kelaartii* to the synonymy of *C. gachua*, while DERANIYAGALA (1945) recognized the Sri Lankan taxon as a subspecies, *C. gachua kelaartii*, which he differentiated from *C. g. gachua* by its smaller size. There has been no specimen-based critical appraisal of the validity of *C. kelaartii* since then, with most subsequent authors (e.g., PETHIYAGODA, 1991; JAYARAM, 2010) following the synonymy proposed by DAY (1878).

Recent DNA-barcoding studies and molecular phylogenies have revealed that the Sri Lankan species hitherto identified as *Channa gachua* is distinct genetically from the other members of the Gachua group (CONTE-GRAND *et al*., 2017; RÜBER *et al*., 2020). These studies have not, however, provided a morphological characterization of the Sri Lankan species or evaluated its geographic distribution.

Here, within an integrative taxonomic framework (DAYRAT, 2005; PADIAL *et al*., 2010), and based on fresh collections in Sri Lanka and India, we provide a reappraisal of the identity and distribution of the dwarf snakehead hitherto identified as *Channa gachua* in Sri Lanka.

## Materials and Methods

Measurements were taken point to point using calipers, to the nearest 0.1 mm. Measurements and counts follow MUSIKASINTHORN (1998) and BRITZ (2008), except that the predorsal scale count is given as the number of scales between the basal scale (DERANIYAGALA, 1929) of the head and the origin of the dorsal fin. X-radiographs were taken of two specimens of *Channa kelaartii* from Sri Lanka. In addition, four specimens of *C. kelaartii* and two specimens of *C. gachua* were cleared and stained following the methods of TAYLOR & VAN DYKE (1985). Values in parentheses after a count represent the frequency of that count.

Specimens referred to in the text are deposited in the following institutions: BMNH, Natural History Museum, London; DZ, Evolutionary Ecology and Systematics Lab, Department of Molecular Biology and Biotechnology, University of Peradeniya, Peradeniya; and WHT, collection of the Wildlife Heritage Trust of Sri Lanka now at National Museum of Sri Lanka. Abbreviations: Ma, million years ago; ka, thousand years ago.

DNA was acquired from ethanol-preserved muscle tissues or fin clips of 11 specimens of *Channa kelaartii* representative of the major bioclimatic regions of Sri Lanka (Table 1). A DNeasy Blood & Tissue Kit protocol (Qiagen, UK) was used to extract DNA. A 654 base pair fragment of the mitochondrial *cytochrome c oxidase subunit 1* (*cox1*) was amplified using the DNA barcoding primer pair FishF1 and FishR1 (WARD *et al*., 2005) following the methods of SUDASINGHE *et al*. (2018a). BLAST (ALTSCHUL *et al*., 1990) was used to check the genetic affinity of the newly generated sequences with those available in GenBank. Comparative genetic data for *cox1* of the Gachua group were obtained from GenBank based on confidently identified specimens (CONTE-GRAND *et al*., 2017; BRITZ *et al*., 2019). ClustalW in MEGA v. 7.0 (KUMAR *et al*., 2016) was used to align the *cox1* dataset, from which uncorrected pairwise genetic distances were calculated. To explore the demographic histories of *C. kelaartii*, nucleotide diversity and haplotype diversity, neutrality tests, Tajima's D (TAJIMA, 1989) and Fu and Li's F test (FU & LI, 1993) were conducted using DNASP v.6 (ROZAS *et al*., 2017). Reconstruction of the haplotype network for *cox1* was inferred by means of a Median Joining Network (BANDELT *et al*., 1999) in POPART (LEIGH & BRYANT, 2015). Direct GenBank submissions of *Channa* sequences from India that were identified as *C. kelaartii* in the present study were also incorporated in the analyses, to map the distribution of haplotypes of *C. kelaartii* between Sri Lanka and India.

A Principal Component Analysis (PCA) in a covariance matrix was carried out to discriminate between the shape of *Channa kelaartii* and *C. gachua* using the size-corrected measurements in the software PAST (HAMMER *et al*., 2001). Size correction was carried out using the equation

$$M_s = M_o \left(\frac{L_s}{L_o}\right)^b$$

where $M_S$ and $M_O$ are the standardized measurement and the measured character length, respectively, $L_S$ is the overall (arithmetic) mean standard length for all individuals from all populations of all putative species, and $L_O$ is the standard length of each specimen. The allometric-growth equation $M=aL^b$ was used to estimate the value of $b$ for each character from the observed data, where $b$ is the gradient of regression of log $M_O$ on $L_O$ (ELLIOTT *et al*., 1995).

## Results

**Molecular analysis.** The GenBank sequence MF496733 (an aquarium specimen from Sri Lanka), MF462268 (from Yercaud, 11.783 N 78.209 E), MK303762 (from Nagalapuram, 13.417 N 79.742 E), MK303761, MK303765 (from Kolathur, 11.826 N 77.780 E) in southern peninsular India and MF496762 (an aquarium specimen of unknown provenance) possess a percentage identity in BLAST of > 99% with the 11 newly generated sequences of Sri Lankan *Channa kelaartii*. The 17 *cox1* sequences

**Table 1.** Samples of *Channa kelaartii* used to generate *cox1* gene sequences in this study, with their localities, voucher references, and GenBank accession numbers.

| Voucher | Location | GPS coordinates | GenBank Accession number |
|---|---|---|---|
| DZ 3222 | Sri Lanka: Deraniyagala, Kelani River basin | 6.898 N 80.353 E | MT299903 |
| WHT 30097 | Sri Lanka: Ekneligoda, Kalu River basin | 6.793 N 80.366 E | MT299904 |
| DZ 3896 | Sri Lanka: Nakiyadeniya, Gin River basin | 6.142 N 80.342 E | MT299905 |
| DZ 4242 | Sri Lanka: Rajwaka, Walawe River basin | 6.608 N 80.793 E | MT299906 |
| DZ 4596 | Sri Lanka: Nakkala, Kumbukkan Oya basin | 6.884 N 81.298 E | MT299907 |
| DZ 4219 | Sri Lanka: Udakiruwa, Lunugala, Kumbukkan Oya basin | 7.073 N 81.223 E | MT299908 |
| DZ 4560 | Sri Lanka: Kotagama, Gal Oya basin | 7.149 N 81.210 E | MT299909 |
| DZ 3171 | Sri Lanka: Polonnaruwa, Mahaweli River basin | 7.935 N 81.011 E | MT299910 |
| DZ 4520 | Sri Lanka: Keppetigala, Deduru Oya basin | 7.435 N 80.546 E | MT299911 |
| DZ 4391 | Sri Lanka: Giriulla, Ma Oya basin | 7.312 N 80.088 E | MT299912 |
| DZ 5127 | Sri Lanka: Medawacchiya, Malwathu Oya basin | 8.509 N 80.422 E | MT299913 |

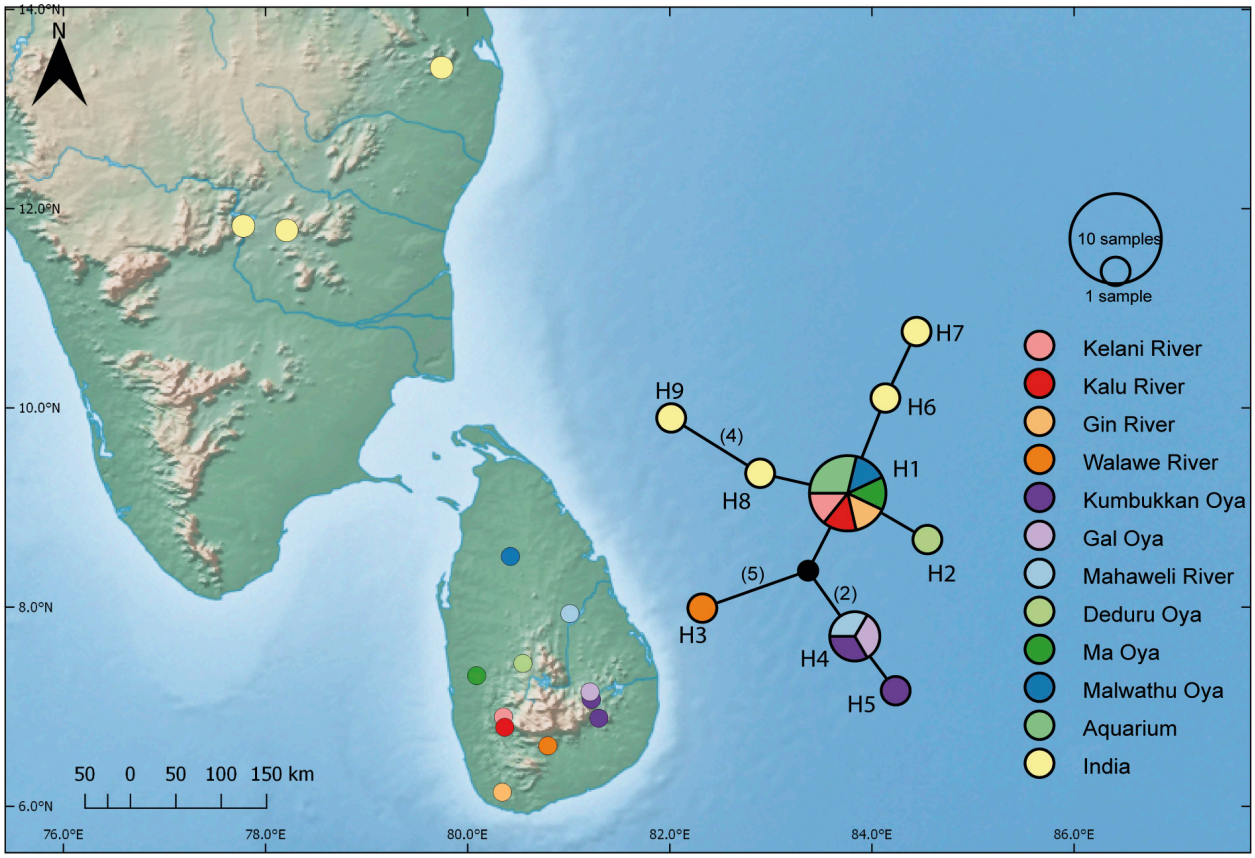


**Fig. 1.** Median-joining haplotype network for *Channa kelaartii* based on the analysis of a 654 bp fragment of the *cox1* gene. The areas of the circles are proportional to the number of individuals sharing a given haplotype. The number of mutational steps > 1 is indicated in parentheses. Black circles are hypothetical nodes. Legend colours correspond to the origin of the samples as illustrated on the map of Sri Lanka and southern peninsular India.

of *C. kelaartii* included 12 segregating sites and 5 parsimony-informative sites, with a haplotype and nucleotide diversity of 0.824 and 0.00499, respectively. Tajima's D test and Fu and Li's F test statistic were both negative (−1.52768, −2.08533) but not significant ($p > 0.05$, $p > 0.02$). The Sri Lankan and Indian sequences of *C. kelaartii* formed five and four haplotypes, respectively, none of them shared between the two countries (Fig. 1). The Sri Lankan sequences of *C. kelaartii* from the southwestern wet zone (Kelani, Kalu and Gin River basins) and northern dry zone (Malwathu and Ma Oya basins) form a single shared haplotype (H1) along with the two aquarium-based specimen sequences (MF496733 and MF496762). Sequences of *C. kelaartii* from the Mahaweli basin and the eastern dry zone (Gal Oya, Kumbukkan Oya and Walawe basins) are separated from the southwest and northern dry zone sequences of Sri Lankan *C. kelaartii* by a minimum of three mutational steps

(Fig. 1). The Sri Lankan sequences of *C. kelaartii* show an intraspecific genetic diversity of 0.0–1.3 % for *cox1* and differ from Indian sequences of *C. kelaartii* by 0.2–1.1 %. The newly generated *cox1* gene sequences of *C. kelaartii* differ by an uncorrected pairwise genetic distance of 7.9–8.8 %, and 8.0–8.5 % from topotypic *C. gachua* and '*C. marginata*', respectively.

## *Channa kelaartii* (Günther, 1861)

*Ophiocephalus kelaartii* Günther, 1861: 472.
*Ophiocephalus gachua* (not Hamilton, 1822): DAY, 1878: 367 (in part); DAY, 1889: 364 (in part).
*Ophicephalus gachua* (not Hamilton, 1822): DERANIYAGALA, 1929: 93.
*Ophicephalus gachua kelaartii* (GÜNTHER, 1861): DERANIYAGALA, 1952: 128.
*Channa gachua* (not HAMILTON, 1822): PETHIYAGODA, 1991: 277; COURTENAY & WILLIAMS, 2004: 83 (in part); CHAUDHRY, 2010 (in part); JAYARAM, 2010: 508 (in part); KOTTELAT, 2013: 459 (in part).
*Channa orientalis* (not Bloch, *in* Schneider, 1801): TALWAR & JHINGRAN, 1991: 1019 (in part).

**Material examined.** From Sri Lanka: BMNH 1858.10.19.108, *Ophiocephalus kelaartii*, syntypes, 10, 74.5–116 mm SL, Ceylon (=Sri Lanka); DZ 3370, 128 mm SL, Nugegoda, Bolgoda basin; DZ 4596, 1, 92.8 mm SL, Bellan Oya, Kumbukkan Oya basin; DZ 4702, 2, 60.2–102 mm SL, Bellan Oya, Kumbukkan Oya basin; DZ 4262, 1, 93.9 mm SL, Kiri Oya, Lunugala, Kumbukkan Oya basin; DZ 4301, 1, 78.1 mm SL, Angammedilla, Mahaweli basin; DZ 3171, 1, 70.1 mm SL, Polonnaruwa, Mahaweli basin; DZ 4083, 2, 54.2–61.3 mm SL, Polonnaruwa, Mahaweli basin; DZ 3772, 1, 86.1 mm SL, Nilgala, Gal Oya basin; DZ 4560, 1, 77.0 mm SL, Kotagama, Gal Oya basin; DZ 4242, 62.8 mm SL, Rajawaka, Walawe basin; DZ 4270, 54.9 mm SL, Wellawaya, Kirindi Oya basin; DZ 4322, 1, 56.0 mm SL, Kolamunu Oya, Deduru Oya basin; WHT 7726, 3, 87.3–114 mm SL, Kurunegala, Deduru Oya basin; DZ 5127–5128, 2, 68.5–89.7 mm SL, Medawacchiya, Malwathu Oya basin; WHT 30476, 5, 61.1–79.5 mm SL, Mahagodayaya near Buttala, Menik River basin.

Cleared and stained: DZ 4684, 75.5 mm SL, Kotagama, Gal Oya basin; DZ 4701, 67.0 mm SL, Moneragala, Kumbukkan Oya basin; WHT 11020, 63.2 mm SL, Ingiriya, Kalu basin; WHT 11110, 46.8 mm SL, Kottawa, near Galle, Gin basin.

Other material (identified for distribution data, but not measured): DZ 4684, 1, 42.2 mm SL, Kotagama, Gal Oya basin; DZ 4967–4969, 3, 36.2–46.7 mm SL, Hiniduma, Gin River basin; DZ 5015, 1, 45.7 mm SL, Hiniduma, Gin River basin; DZ 3877, 1, 43.6 mm SL, Nakiyadeniya, Gin River basin; WHT 30114, 1, 49.7 mm SL, Kottawa, near Galle, Gin River basin; WHT 30374, 1, 46.0 mm SL, Wakwella, Gin River basin; WHT 30430, 1, 28.9 mm SL, Koralegama, Kanneliya, Gin River basin; WHT 30219, 1, 30.5 mm SL, Kottawa, near Galle, Gin River basin; WHT 7759, 2, 54.1–56.5 mm SL, Akuressa, Nilwala River basin; DZ 4073, 1, 26.7 mm SL, Miyanawita, Deraniyagala, Kelani River basin; WHT 30097, 1, 44.3 mm SL, Ekneligoda, Kuruwita, Kalu River basin; WHT 7870, 1, 22.3 mm SL, Mawanella, Ma Oya basin; DZ 3909, 2, 29.4–36.4 mm SL, Sarasavi Oya, Mahaweli River basin; WHT 1669, 1, 27.7 mm SL, Habarana, Mahaweli River basin; WHT 30427, 1, 40.0 mm SL, Moneragala, Kumbukkan Oya basin; WHT 30161, 1, 40.7 mm SL, Nikapotha, Walawe River basin; DZ 5253, 3, 39.9–53.5 mm SL, Medawacchiya, Malwathu Oya basin.

**Diagnosis.** *Channa kelaartii* is distinguished from the other members of the Gachua group by the following combination of characters: pelvic fin present; lateral head profile pointed anteriorly as in Figure 2A; adults usually possessing 2–4, rarely 5 or 6, brown concentric bands in the pectoral fin; 38–43 lateral-line scales; 5–½5+1+6½ scales in transverse line on body; 24–28 circumpeduncular scales; 31–35 dorsal-fin rays; 19–23 anal-fin rays; 39–42 vertebrae; and live adult coloration as in Figure 3.

**Description.** General appearance as in Figures 3–4. Morphometric data are provided in Table 2. Body elongate, slender, cross-section almost circular in anterior half, its depth greatest at pelvic-fin base, its width greatest at pectoral-fin origin, posteriorly compressed. Head pointed anteriorly (Fig. 2A), its length about 0.3–0.4 times SL. Eye positioned at anterior ⅓ of head. Lips prominent, fleshy, upper lip extending further forward than lower. Mouth large, posterior angle of gape reaching beyond vertical through posterior margin of orbit.

Pectoral-fin with 13 (1), 14 (14), or 15 (8) rays, when adpressed reaching vertical through 10th or 11th branched dorsal-fin ray. Pelvic-fin with 6 rays, short, reaching to about 5 scale-widths in front of anus, its origin at about vertical through third branched dorsal-fin ray. Caudal fin rounded, with 6+6 (10), or 6+7 (7) principal rays and 3 dorsal and 2 ventral procurrent rays. Dorsal fin with 31 (1), 32 (5), 33 (10), 34 (5), or 35 (1) rays; anal fin with 19 (1), 20 (3), 21 (9), 22 (8), or 23 (2) rays. Lateral-line scales 38 (1), 39 (4), 40 (9), 41 (7), 42 (1), or 43 (1) in total, 10 (5), 11 (10), 12 (5), or 13 (3) in pre-drop, single scale forming drop, 26 (3), 27 (5), 28 (7), 29 (6), 30 (1), or 31 (1) in post-drop. Scales above pre-drop 3½ (6), 4 (13), or 4½ (4), above post-drop 5 (2), or 5½ (21); below post-drop 6½. Predorsal scales 5 (4), 6 (17), or 7 (2). Circumpeduncular scales 24 (2), 26 (16), or 28 (5). Cheek scales 7 (4), 8 (17), or 9 (2), with 5 (21), or 6 (2) scales in front of opercle, 2 (4), or 3 (19) scales on opercle. Single scale on ventral surface of lower jaw.

Based on WHT 11020 and WHT 11110: palatine with band of small teeth; dentary with 4–5 tooth-rows on anterior third, converging to a single row at angle of gape. Branchiostegal rays 5. Ceratobranchial 5 with ca 50 pointed, curved teeth, 8 posterolateral teeth relatively larger than others. Based on WHT 11020, WHT 11110, DZ 4684, DZ 4701, DZ 3370 and DZ 4560: total vertebrae 39 (2), 40 (2), 41 (1) or 42 (1).

**Coloration in preservative.** Juveniles of about 20–30 mm SL (Fig. 4A) with head and body light brown dorso-laterally, becoming lighter laterally, off-white ventrally. A series of black spots on head and anterior half of body. One or two black ocelli on posterior part of dorsal fin. Caudal fin with 3–4 alternating brown and hyaline concentric bands. Dorsal and anal fins hyaline with scattered black pigmentation. Basal blotch at pectoral fin brown, not distinct. Pectoral fin with 1 or 2 greyish-brown concentric bands, not apparent in some examples.

Subadults of about 30–50 mm SL (Fig. 4B) similar to juveniles, except as follows. Black spots on head and body and black ocelli on posterior part of dorsal fin

**Table 2.** Morphometric data of *Channa kelaartii* (n=23; DZ 3171, DZ 3370, DZ 3772, DZ 4083, DZ 4301, DZ 4242, DZ 4262, DZ 4560, DZ 4596, DZ 4701, DZ 5127, DZ 5128, WHT 7726, WHT 30476) and *C. gachua* (n=17; WHT 2179, WHT 2183, WHT 2184, WHT 2186, WHT 7919B).

| | ***Channa kelaartii*** | | | | ***C. gachua*** | | | |
|---|---|---|---|---|---|---|---|---|
| | Min | Max | Mean | s.d. | Min | Max | Mean | s.d. |
| Standard length (mm) | 54.2 | 128 | | | 59.2 | 128 | | |
| **In percentage of standard length** | | | | | | | | |
| Predorsal length | 33.3 | 38.9 | 36.9 | 1.5 | 32.3 | 36.5 | 34.4 | 1.1 |
| Preanal length | 45.7 | 61.3 | 54.9 | 2.9 | 50.9 | 58.2 | 54.3 | 1.9 |
| Prepelvic length | 37.5 | 44.9 | 39.6 | 2.1 | 36.6 | 40.6 | 38.5 | 1.3 |
| Prepectoral length | 32.0 | 39.4 | 35.1 | 1.7 | 30.9 | 36.8 | 33.8 | 1.5 |
| Dorsal-fin length | 54.2 | 62.3 | 58.2 | 2.0 | 58.9 | 64.8 | 62.2 | 2.0 |
| Anal-fin length | 32.5 | 37.8 | 36.4 | 1.5 | 36.0 | 42.0 | 39.0 | 1.9 |
| Pectoral-fin length | 17.0 | 24.2 | 20.7 | 1.7 | 18.6 | 21.5 | 20.3 | 1.0 |
| Pelvic-fin length | 8.2 | 11.5 | 9.7 | 1.0 | 8.2 | 10.1 | 9.1 | 0.5 |
| Body depth | 15.6 | 19.7 | 17.9 | 1.0 | 17.2 | 21.9 | 19.0 | 1.3 |
| Body width | 11.8 | 14.8 | 13.1 | 0.7 | 11.9 | 15.9 | 13.2 | 1.3 |
| Caudal peduncle length | 10.0 | 14.0 | 11.3 | 1.1 | 7.9 | 11.8 | 10.1 | 1.0 |
| Caudal peduncle depth | 10.4 | 12.0 | 11.3 | 0.4 | 10.3 | 12.6 | 11.5 | 0.7 |
| Head length | 30.9 | 36.2 | 33.5 | 1.5 | 29.9 | 35.3 | 32.8 | 1.4 |
| Head depth | 14.8 | 18.9 | 16.9 | 1.0 | 15.9 | 19.5 | 17.8 | 0.9 |
| Head width | 19.2 | 23.6 | 21.3 | 1.1 | 19.2 | 22.8 | 21.1 | 1.0 |
| **In percentage of head length** | | | | | | | | |
| Snout length | 20.9 | 25.2 | 23.0 | 1.4 | 20.6 | 24.5 | 22.3 | 1.1 |
| Eye diameter | 13.9 | 18.6 | 16.2 | 1.3 | 13.4 | 18.9 | 16.2 | 1.3 |
| Preorbital depth | 22.9 | 30.8 | 25.7 | 2.2 | 25.0 | 31.6 | 28.4 | 2.0 |
| Postorbital depth | 31.5 | 40.8 | 35.4 | 2.1 | 37.4 | 43.3 | 40.4 | 1.8 |
| Interorbital width | 27.0 | 31.6 | 28.8 | 1.2 | 27.6 | 32.7 | 30.4 | 1.4 |
| Upper jaw length | 32.4 | 39.4 | 35.2 | 1.9 | 31.1 | 38.4 | 35.8 | 2.0 |

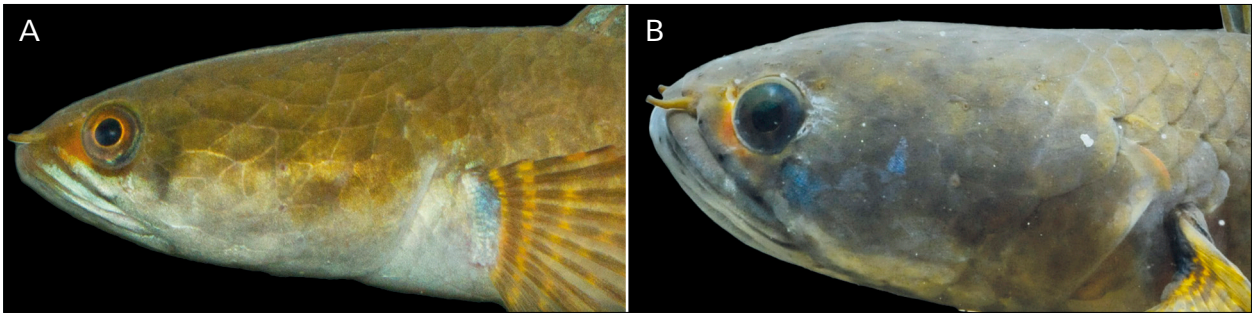


**Fig. 2.** Left-lateral profile of head in adults of **A**, *Channa kelaartii*, ~ 90 mm SL; and **B**, *C. gachua*, ~ 130 mm SL.

absent in some examples. Pectoral fin with black basal blotch and 1–3 concentric dark-brown bands, not apparent in some examples. Interradial membrane of dorsal, anal and caudal fins brown with melanophores. Pelvic fin hyaline. Light-cream diagonal bands on side of body, appearing as chevrons. Hazy black vertically-elongate blotch posterior to eye.

Adults > 50 mm SL (Fig. 4C–E) with variable overall coloration from dark brown to bluish grey. Dorsal surface of body dark brown or grey, becoming lighter laterally, off-white ventrally. Some individuals with 6–8 diagonal dark-brown bands on dorso-lateral body, beneath base of dorsal fin (Fig. 4C–D). Interradial membrane of dorsal, anal and caudal fins grey. Margins of dorsal, anal, pelvic and caudal fins white. Pelvic fin hyaline. Pectoral fin with black basal blotch, usually with 2–4 dark-brown concentric bands separated by hyaline bands, some individuals with up to 6 such bands (Fig. 4D). Indistinct black vertically-elongate blotch posterior to eye.

**Coloration in life.** Juveniles of about 20–30 mm SL (Fig. 3A) with head and body light brown dorso-laterally, becoming lighter laterally and off-white ventrally. A series of black spots on head and anterior half of body. One or two black ocelli on posterior region of dorsal fin. Fin membranes mostly translucent. Caudal fin with concentric light- and dark-brown bands. Dorsal and anal fins with vague irregular line-pattern of light and dark brown pigmentation. Pectoral fin with basal blotch and 1 or 2 dark-brown concentric bands, not apparent in some individuals. Pupil outlined by yellowish orange rim; iris reddish-orange.

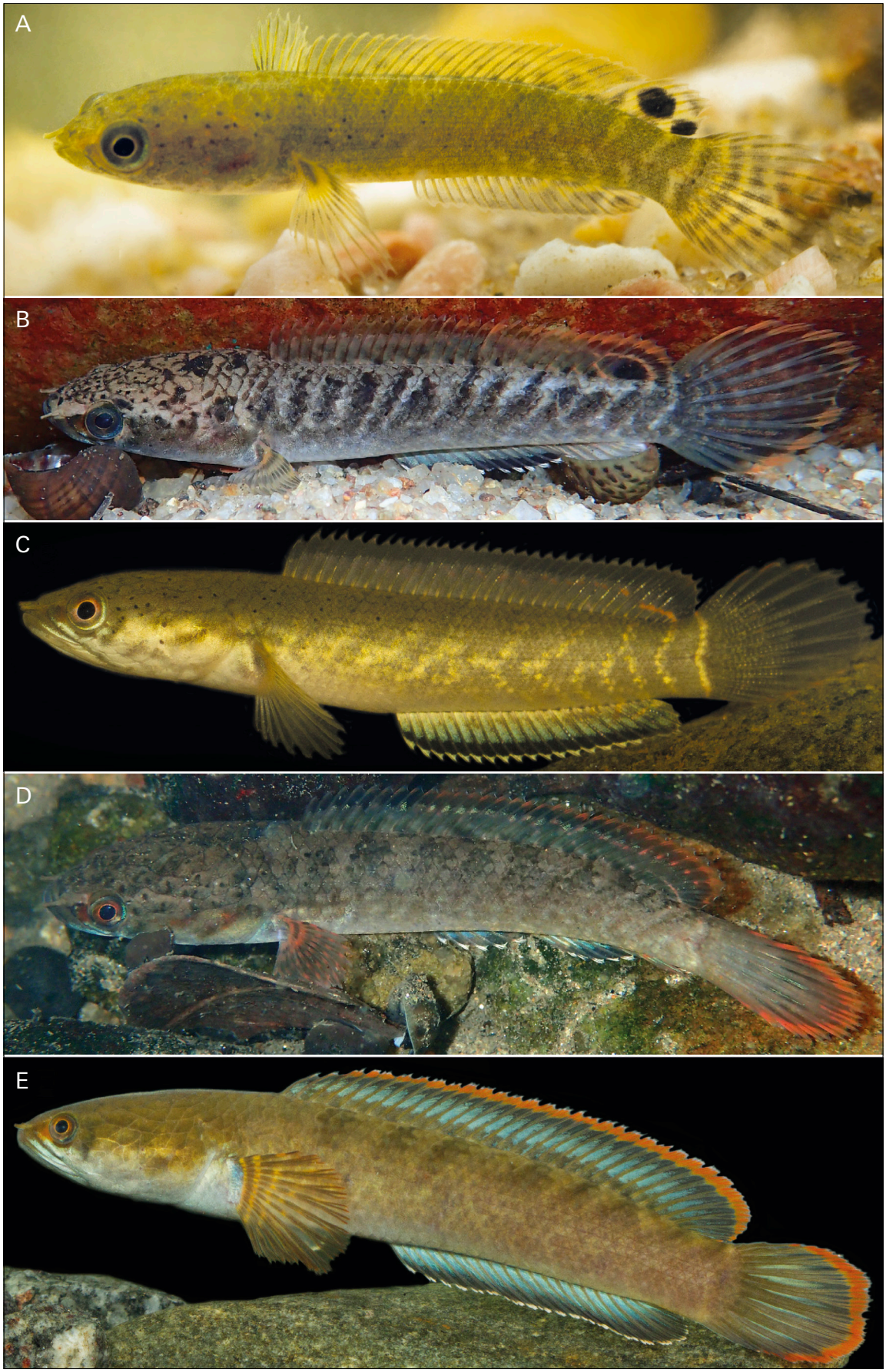


**Fig. 3.** Coloration of *Channa kelaartii* in life. All from Sri Lanka. **A**, juvenile, DZ 4073, 26.7 mm SL, Deraniyagala, Kelani River; **B**, subadult, ~ 40 mm SL, Wellawaya, Kirindi Oya; **C**, subadult, ~45 mm SL, Peradeniya, Mahaweli River; **D**, adult, ~ 70 mm SL, Gurulupotha, Mahaweli River; **E**, adult, ~ 90 mm SL, southwestern Sri Lanka.


**Fig. 4.** Coloration of *Channa kelaartii* in preservation. All from Sri Lanka. **A**, juvenile, DZ 4073, 26.7 mm SL, Deraniyagala, Kelani River; **B**, subadult, DZ 3909, 36.4 mm SL, Peradeniya, Mahaweli River; **C**, adult, DZ 4322, 56.0 mm SL, Kolamunu Oya, Deduru Oya; **D**, adult, DZ 3722, 86.1 mm SL, Nilgala, Gal Oya; **E**, large adult, DZ 3370, 128 mm SL, Nugegoda, Bolgoda River.

Subadults of about 30–50 mm SL (Fig. 3B–C), with head and body light brown dorso-laterally, becoming lighter laterally and off-white ventrally. Series of black spots on head and anterior half of body, not conspicuous, disappearing with age. One or two black ocelli on dorsal fin posteriorly, disappearing with age. Pectoral fin with black basal blotch and 1–3 dark brown concentric bands, not apparent in some individuals. Interradial membrane of anal fin iridescent blue proximally, dark-bluish black distally. Margins of anal fin white. Dorsal and caudal fins

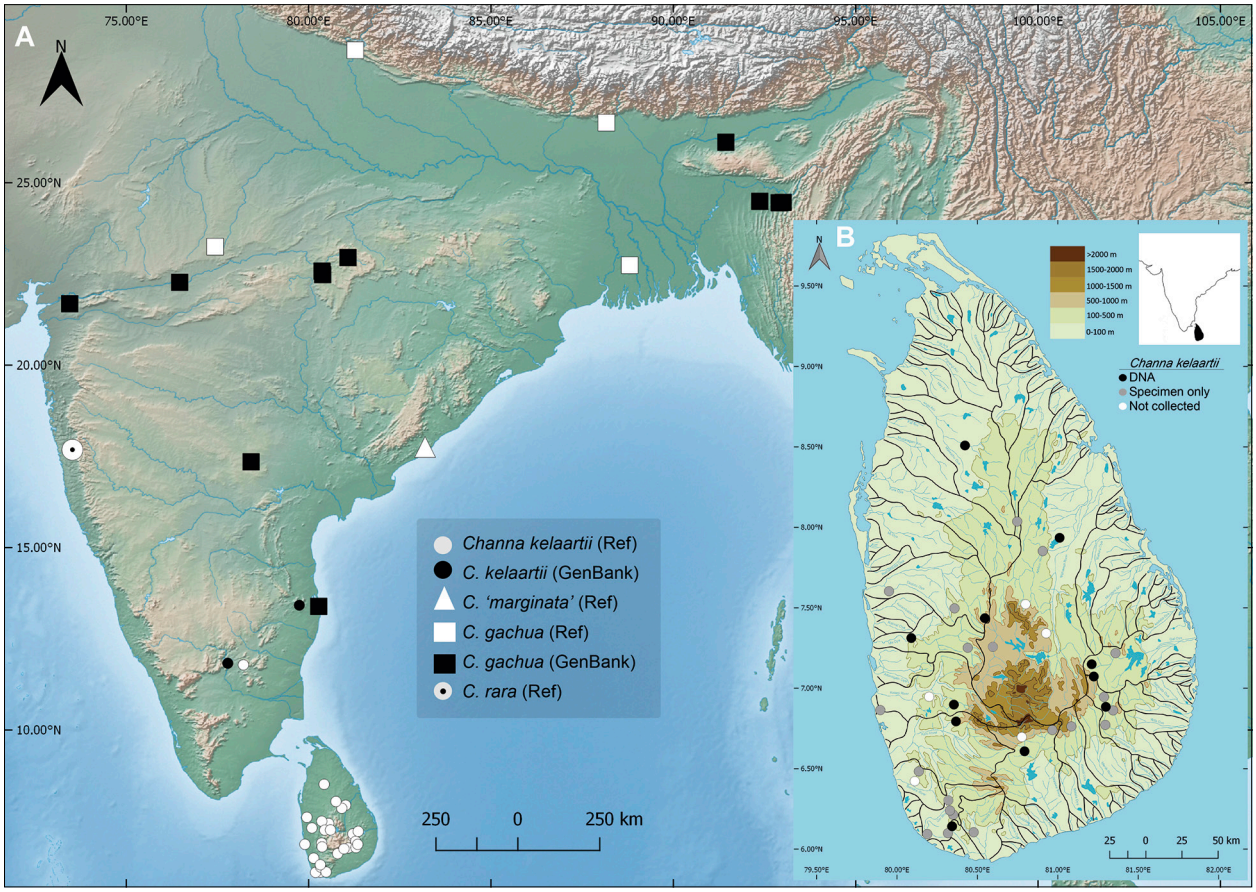


**Fig. 5. A**, Map of the Indian subcontinent, showing the geographic distribution of *Channa gachua*, C. *kelaartii* and *C. rara*; **B**, Map of Sri Lanka, showing the geographical distribution of *Channa kelaartii*. Specimens referred to as 'not collected' were observed in the wild but not included in the molecular or morphological analyses. The black lines represent drainage margins.

mostly translucent, with orange and bluish markings beginning to appear as in adults. In most individuals, 5–7 dark-brown diagonal bands on dorso-lateral body, beneath base of dorsal fin, not apparent in some examples. Orange stripe extending from snout tip to anterior margin of eye. Pupil outlined by yellowish orange rim, iris reddish-orange.

Adults > 50 mm SL (Fig. 3D–E) with variable overall coloration. Usually dark brown, but breeding pairs with darker bluish-grey-brown hue. Lateral body coloration lighter than dorsum. Interradial membrane of dorsal fin iridescent blue medially, dark bluish-black proximally and distally. Interradial membrane of anal and caudal fins iridescent blue proximally, dark bluish-black distally. Reddish-orange distal band above dark blue band on dorsal and caudal fins. Margins of dorsal, anal, pelvic and caudal fin rays white, more prominent on anal fin. Pectoral fin usually with 2–4 dark brown concentric bands separated by light yellow to orange bands, some individuals with up to 6 such bands. Most individuals with 5–7 diagonal dark-brown bands on dorso-lateral body, beneath base of dorsal fin, not apparent in some specimens. Orange stripe extending from snout tip to anterior margin of eye. A yellowish-orange ring on sclera, outlining pupil. Ventrum of body off-white. Gular region turning bluish in breeding pairs. Black vertically-elongate blotch posterior to eye; 1–3 orange blotches apparent on preopercle and opercle in most individuals.

**Habitat, distribution and natural history.** *Channa kelaartii* is a widely distributed fish in Sri Lanka (Fig. 5B), occurring mostly in lotic waters such as streams and rivers but also in lentic habitats such as pools and ditches in the lowlands. It is usually associated with submerged roots, leaf debris and marginal vegetation during daytime, with adults being solitary or occurring as pairs. During the night, individuals can be more easily observed in open waters. *Channa kelaartii* and *C. orientalis* do occur in close proximity in south-western Sri Lanka, where their ranges overlap; they are occasionally encountered in syntopy. *Channa kelaartii* occurs even in highly modified habitats such as concretized drains and canals in urban areas. The highest elevation at which we recorded *C. kelaartii* in Sri Lanka was ca 700 m asl at Lunugala, but DERANIYAGALA (1929) reported it from Diyatalawa, ca 1200 m asl. *Channa kelaartii* is not endemic to Sri Lanka and is reported in this study also from east-flowing drainages of southern peninsular India (Fig. 5A).

**Statistical analysis.** In the size-corrected PCA for *Channa kelaartii* and *C. gachua* (Table 3, Fig. 6), PC1 and PC2 explain 37.40 % and 27.57 % of the total variance,

**Table 3.** Component loadings in the principal component analysis of the size-adjusted morphometric measurements of *Channa kelaartii* (n=20) and *C. gachua* (n=16).

| | PC1 | PC2 | PC3 |
|---|---|---|---|
| Eigen value | 8.303 | 6.119 | 1.837 |
| Variance explained % | 37.40 | 27.57 | 8.28 |
| Predorsal length | 0.4132 | 0.0081 | 0.1383 |
| Preanal length | 0.2908 | 0.3166 | −0.5714 |
| Prepelvic length | 0.1753 | 0.3149 | −0.2213 |
| Prepectoral length | 0.1964 | 0.2847 | 0.0414 |
| Dorsal-fin length | −0.6484 | 0.3185 | −0.1087 |
| Anal-fin length | −0.3554 | 0.0709 | 0.2212 |
| Pectoral-fin length | 0.1261 | 0.1360 | 0.5641 |
| Pelvic-fin length | 0.0889 | −0.0041 | 0.2307 |
| Body depth | −0.0679 | 0.3188 | 0.1773 |
| Body width | 0.0026 | 0.0092 | 0.1443 |
| Caudal peduncle length | 0.1497 | −0.1806 | −0.0036 |
| Caudal peduncle depth | 0.0359 | 0.0862 | 0.0989 |
| Head length | 0.2066 | 0.3331 | 0.1947 |
| Head depth | −0.0428 | 0.3004 | 0.1270 |
| Head width | 0.0693 | 0.2687 | −0.0344 |
| Snout length | 0.0777 | 0.0160 | 0.1367 |
| Eye diameter | 0.0265 | 0.0441 | 0.0581 |
| Preorbital depth | −0.0545 | 0.2206 | −0.0234 |
| Postorbital depth | −0.0828 | 0.3177 | −0.0263 |
| Interorbital width | 0.0178 | 0.0947 | 0.0884 |
| Upper jaw length | 0.1001 | 0.1354 | 0.1509 |

respectively. The two species show a slight overlap in morphological space, which is explained mostly by predorsal length and anal-fin length along PC1; and body depth, head depth, and postorbital depth along PC2.

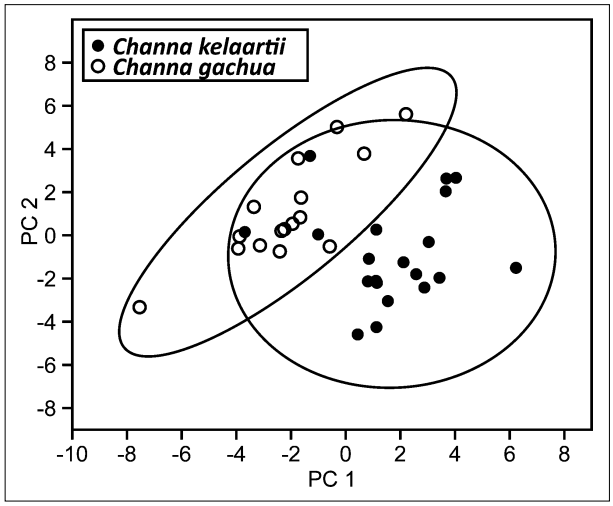


**Fig. 6.** Plot of scores from the principal component analysis of size corrected measurements from *Channa kelaartii* and *C. gachua*. The ellipses indicate 95% confidence intervals.

## Discussion

***Channa orientalis.*** Although Bloch (in Schneider, 1801; hereafter Bloch, 1801) gave the type locality of *Channa orientalis* only as "India orientali", he noted the absence of pelvic fins, confirmed also in the illustration on which he based his description (Bloch, 1801: pl. 90, based on Gronovius, 1763: 135, no. 408, pl. 9: Fig. 1; See Kottelat, 2013). The illustration depicts also the barred coloration of the pectoral fin, making it clear that this was a member of the Gachua group. These characters enabled Günther (1861) to identify a series of *Channa* he had from Sri Lanka as *C. orientalis*; it was at the time, apart from *C. asiatica* (of which Günther lacked material), the only *Channa* known to lack pelvic fins.

While the name *Channa orientalis* has, since Günther (1861), been assigned to the endemic pelvic-fin-less Sri Lankan snakehead, several authors (e.g. Jayaram, 1981; Talwar & Jhingran, 1991; Menon, 1999) followed Hora & Mukerji (1934) in treating *C. gachua* as a synonym of *C. orientalis* because they regarded the absence of pelvic fins in the latter as an aberration. Deraniyagala (1932, 1963), however, validated *C. orientalis* on the basis that broods of Sri Lankan '*C. gachua*' (i.e., *C. kelaartii*) consistently possess pelvic fins while those of *C. orientalis* consistently lack them; and because specimens lacking pelvic fins (i.e., *C. orientalis*) are confined to Sri Lanka's perhumid south-western 'wet zone' (rainfall > 2500 mm/y), whereas those with pelvic fins (*C. kelaartii*) were widely distributed also throughout the island's lowlands and dry zone. Pelvic fins are consistently absent in several species of the Gachua group (*C. andrao* Britz, 2013, *C. bleheri* Vierke, 1991, *C. brunnea* Praveenraj, Uma, Moulitharan & Kannan, 2019, and *C. burmanica* Chaudhuri, 1919), and this character serves immediately to distinguish *C. kelaartii* from *C. orientalis* (see also Raghavan & Dahanukar, 2015; Britz *et al*., 2019). Rüber *et al*. (2020) showed additionally that a sister-group relationship exists between *C. orientalis* and *C. kelaartii*, confirming also the finding by Li *et al*. (2006) and Conte-Grand *et al*. (2017) that pelvic fins have been lost multiple times in the course of channid evolution.

***Channa gachua.*** The type locality of *Channa gachua* was given by Hamilton (1822) simply as 'ponds and ditches in Bengal', a vast area that includes Bangladesh and much of the Indian state of West Bengal (the illustration that accompanied the original description is reproduced in colour in Britz, 2019). In differentiating *C. kelaartii* from *C. gachua* only by the longer caudal fin of the former, however, Günther (1861) was handicapped by having no specimens of *C. gachua* from the type locality, Bengal. The fishes he identified as *C. gachua* were from Dukhun (the Deccan, the vast plateau that encompasses most of central peninsular India), Afghanistan and the East Indies. The East Indies, as used elsewhere in Günther (1861), clearly referred to India in addition to at least Sumatra and Java, so his reference to the 'Types of the species', is puzzling given that Hamilton did not preserve specimens of the fishes he described (Britz, 2019).


**Fig. 7.** *Channa gachua*. In life, **A**, ~130 mm SL, Calcutta, West Bengal, India; **B**, ~125 mm SL, West Bengal, India. In preservation, **C**, WHT 2179A, 128 mm SL, Calcutta, West Bengal, India; **D**, WHT 2183A, 59.6 mm SL, Nadia, West Bengal, India.

While *Channa gachua* sensu stricto (Fig. 7) from West Bengal resembles *C. kelaartii*, the latter species can be distinguished from the former by possessing a pointed (vs rounded) lateral head profile (Fig. 2); 24–28 (vs 22–24) circumpeduncular scales; 12½–13 (vs 11–12) total transverse scales; 5–5½ (vs 4½–5) scales between lateral line at postdrop to origin of dorsal fin; and by the relative distribution of dorsal and anal-fin rays (Table 4). In addition, these two species differ genetically by an uncorrected pairwise *cox1* genetic distance of 7.9–8.8 %.

*Ophicephalus fuscus* Cuvier, *in* Cuvier & Valenciennes, 1831 (type locality Bengal; see Fig. 8) too, is distinguished from *C. kelaartii* by the shape of its head and the scale counts mentioned for *C. gachua*, above; we retain it as a synonym of *C. gachua*.


**Fig. 8.** Syntypes of *Ophicephalus fuscus*, **A**, MNHN A0398, 144 mm SL; **B**, MNHN A0623, 108 mm SL; India: Bengal, courtesy of Claude Ferrara.

**Table 4.** Frequency distribution of selected meristic data in *Channa kelaartii* (DZ3171, DZ3370, DZ3772, DZ4083, DZ4242, DZ4262, DZ4301, DZ4560, DZ4596, DZ4701, DZ5127, DZ5128, WHT7726, WHT7726) and *C. gachua* (WHT 2179, WHT 2183, WHT 2184, WHT 2186, WHT 7919B).

| | Dorsal-fin rays | | | | | | |
|---|---|---|---|---|---|---|---|
| | 31 | 32 | 33 | 34 | 35 | 36 | 37 |
| *Channa kelaartii* | 1 | 5 | 10 | 5 | 1 | | |
| *C. gachua* | | | 1 | 3 | 5 | 5 | 4 |
| | Anal-fin rays | | | | | | |
| | 19 | 20 | 21 | 22 | 23 | 24 | 25 |
| *C. kelaartii* | 1 | 3 | 9 | 8 | 2 | | |
| *C. gachua* | | | 6 | 7 | 3 | 1 | 1 |
| | Circumpeduncular scales | | | | | | |
| | 20 | 22 | 24 | 26 | 28 | 30 | |
| *C. kelaartii* | | | 2 | 16 | 5 | | |
| *C. gachua* | | 14 | 3 | | | | |
| | Scales from dorsal-fin origin to lateral line at post-drop | | | | | | |
| | 4 | 4½ | 5 | 5½ | 6 | | |
| *C. kelaartii* | | | 2 | 21 | | | |
| *C. gachua* | | 17 | 1 | | | | |
| | Scales from lateral line to origin of anal fin at post-drop | | | | | | |
| | 5 | 5½ | 6 | 6½ | 7 | | |
| *C. kelaartii* | | | | 23 | | | |
| *C. gachua* | | 5 | 10 | 3 | | | |
| | Total transverse scales at post-drop | | | | | | |
| | 11 | 11½ | 12 | 12½ | 13 | 13½ | |
| *C. kelaartii* | | | | 2 | 21 | | |
| *C. gachua* | 5 | 9 | 4 | | | | |

**The Gachua group in peninsular India.** In addition to *Channa kelaartii*, the Gachua group presently includes *C. andrao**; *C. aurantimaculata**; *C. aurantipectoralis**; *C. barca**; *C. bipuli* Praveenraj, Uma, Moulitharan & Bleher, 2018*; *C. bleheri**; *C. brunnea**; *C. burmanica**; *C. gachua*; *C. harcourtbutleri* (Annandale, 1918)*; *C. limbata* (Cuvier *in* Cuvier & Valenciennes, 1831)*, *C. lipor* Praveenraj, Uma, Moulitharan & Singh, 2019*; *C. melanostigma* Geetakumari & Vishwanath, 2011*; *C. orientalis*; *C. ornatipinnis* Britz, 2008*; *C. pardalis* Knight, 2016*; *C. rara* Britz, Dahanukar, Anoop & Ali, 2019; *C. stewartii* (Playfair, 1867)*; *C. stiktos* Lalramliana, Knight, Lalhlimpuia & Singh, 2018*; and *C. quinquefasciata* Praveenraj, Uma, Knight, Moulitharan, Balasubramanian, Bineesh & Bleher, 2018*. Species confined to the Ganges basin or locations further east are indicated by an asterisk; in view of the > 2000 km span that separates Sri Lanka from Ganges basin, we do not compare these species individually with *C. kelaartii* here.

Among the remaining members of the Gachua group, *Channa kelaartii* differs from *C. rara* by lacking (vs possessing) one or more ocelli in the posterior part of the dorsal fin in adults, possessing 5–5½ (vs 3½) scales above lateral line at postdrop and 24–28 (vs. 22) circumpeduncular scales (Britz *et al*., 2019). Further, *C. kelaartii* differs from *C. rara* by an uncorrected pairwise genetic distance of 8.0–8.6%.

With regard to other putative members of this group, Britz *et al*. (2019) showed that *C. shingon* Endruweit, 2017, is insufficiently well diagnosed from its congeners, especially *C. harcourtbutleri; C. royi* Praveenraj & Knight, 2018, is a junior synonym of *C. harcourtbutleri; C. torsaensis* Dey, Nur, Chowdhury, Sarkar, Kosygin & Barat, 2019, is a junior synonym of *C. quinquefasciata;* and *C. amari* Dey, Chowdhury, Nur, Sarkar, Kosygin & Barat, 2019, is not an available name for purposes of zoological nomenclature (see also Praveenraj *et al*., 2019).

***Channa marginata* and *C. coramota***. Of the many nomina placed in the synonymy of *Channa gachua*, only two have a type locality in southern peninsular India: *Ophicephalus marginatus* Cuvier, 1829 and *O. coramota* Cuvier, *in* Cuvier & Valenciennes, 1831. The former

name appears in a footnote on p. 230 of Régne animal, "*O. marginatus*, N., ou *O. gachua*, Buch. ? pl. xxi, f. 21, ou Cora motta, Russel, II, pl. 164". As pointed out by KOTTELAT (2000), this original use of *O. marginatus* makes the name available (as *C. marginata*) by indication to RUSSELL (1803: pl. 164). Unfortunately, plate 164 of RUSSELL (1803) was not published, and this species can be characterized only by its description, of which the following portion is relevant to its identification: "The Ophicephalus with a lanceolate, purplish body; a pectoral fin of twelve rays, striated transversely. Called by the Natives Kora Motta. B. v. D. 36. P. 12. V. 5. A. 23. G. 14. This fish has only twelve rays in the pectoral fin, and five in the ventral. In most of the other characters it agrees better with the Muttah, No. CLXII [i.e. *Channa striata*] than with the one last described. In colour it differed from both. The back a cast of dusky purple, the breast bluish, the abdomen dark gray. The dorsal and part of the anal fin of the same colour as the body; the hinder portion of the dorsal a dark orange; the pectoral streaked transversely black and yellow; the points of the caudal rays distinctly separate, and tipped yellow. The length of the subject, six inches. I found them in the lakes of Ankapilly and Casern Cottah, as also in a tank close to Vizagapatam."

The description of *O. coramota* by CUVIER (1831) repeats the description of the Kora Motta of RUSSELL (1803), making it clear that the former was based entirely on the latter. Reference to the transversely-striated pectoral fin makes it clear that the fish RUSSELL (1803) had before him was a member of the Gachua group. Of Russell's fish specimens, which he left with the Madras Museum when he departed India in 1791, there is no trace: only his snake skins survive in BMNH (HAWGOOD, 1994). RUSSELL (1803, vol. 2: 49) implied he had before him only a single specimen of his *O. coramota*: "The length of the subject, 6 inches." Of this too, along with Russell's other fish types, there has been no trace. In any event, it is this specimen that is the holotype of both *Ophicephalus marginatus* Cuvier, 1829 and of *O. coramota* Cuvier, *in* Cuvier & Valenciennes, 1831. The latter name is thus an objective synonym of the former.

BRITZ *et al*. (2019) found topotypical specimens of *C. marginata* to have a very similar coloration to topotypes of *C. gachua*, with an uncorrected pairwise *cox1* genetic distance of only 2.4% between them. We follow these authors in treating *C. marginata* as a synonym of *C. gachua*. The uncorrected pairwise *cox1* genetic distance between *C. kelaartii* and topotypical *C. marginata* is 8.0–8.5 %, which is a similar interspecific genetic distance to those observed between other species-pairs in the Gachua group (CONTE-GRAND *et al*., 2017; BRITZ *et al*., 2019).

**Biogeography.** The shared distribution of *Channa kelaartii* between Sri Lanka and the east-flowing drainages of southern peninsular India is unsurprising. The ichthyofauna of drainages such as the Cauvery, Tamiraparani and Vaigai shows a close relationship to that of the northern dry zone of Sri Lanka (SILAS 1952a,b; DERANIYAGALA, 1955; PETHIYAGODA, 1991; SUDASINGHE *et al*., 2018a, 2019a, 2020), albeit with a few exceptions (SUDASINGHE *et al*., 2019b). The Palk Strait, which separates Sri Lanka from India, is only ~20 km wide: a shallow-shelf sea less than 5 m deep (ANONYMOUS, 1977). Sea levels were more than 30 m below present for much of the last 1.5 Ma of the Pleistocene, and ~120 m below present as recently as the last glacial maximum, *ca* 22 ka (MILLER *et al*., 2005). Based on present-day bathymetry (ANONYMOUS, 1977), this created a ~190 km wide isthmus ('Adam's Bridge') between India and Sri Lanka at a sea level of -100 m, and consequently, hydrological connectivity via shared palaeodrainages (RAMASAMY & SARAVANAVEL, 2019). Given that *C. kelaartii* inhabits small, unshaded, ephemeral pools even in the driest parts of Sri Lanka, there appears to have been no barrier to dispersal between the mainland and Sri Lanka until the last vestiges of the terrestrial connection was lost, owing to rising sea levels, ~ 6 ka.

While *cox1* haplotypes are not shared between the Sri Lankan and Indian populations of *Channa kelaartii*, haplotype and nucleotide diversities are nevertheless low. Within Sri Lanka, *C. kelaartii* shows only modest geographic structure: [southwest + northern dry zone] and [Mahaweli + eastern dry zone]. However, the non-significant results in the neutrality tests offer no support for demographic changes in recent evolutionary time. A GenBank sequence, MF496762 (LR02310), of unknown provenance, shares the same haplotype (H1) as southwest and northern dry zone samples of *C. kelaartii*. This sequence likely originated from southwestern Sri Lanka, where freshwater fishes continue to constitute part of the ornamental fish export industry.

**Conservation.** Stable taxonomy is the starting point for conservation prioritization, and management mechanisms such as the IUCN Red List process (IUCN, 2019), Key Biodiversity Areas (EKEN *et al*., 2004) and national conservation legislation. The present study paves the way for *Channa kelaartii* and *C. gachua* to be assessed separately. *Channa kelaartii* is widely distributed in Sri Lanka, occurring in the lowlands of both the dry and the wet zones of the island, as well as parts of southern peninsular India. Based on the criteria for geographic range (IUCN, 2012), this species should be assessed as Least Concern (LC). Snakeheads remain popular among aquarists in Sri Lanka, and while awareness and appreciation of these fishes is to be welcomed, we express concern that this could raise demand for wild-caught specimens and also increase the risk of unintended release of both native and exotic channids (SUDASINGHE, 2016; SUDASINGHE *et al*., 2018b).

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## Comparative material and data

*Channa gachua*: WHT 7919B, 1, 114 mm SL, India, West Bengal, Hourah; WHT 2186, 6, 85.3–104 mm SL, India, West Bengal; WHT 2179, 4, 84.7–128 mm SL, India, West Bengal, Calcutta; WHT 2184, 3, 75.4–93.9 mm SL, India, West Bengal; WHT 2183, 6, 57.8–61.8 mm SL, India, West Bengal, Nadia.

Cleared and stained: WHT 11019, 93.5 mm SL, India, West Bengal, Boncron; WHT 11090, 85.3 mm SL, India, West Bengal, Boncron.

*C. orientalis*: WHT30727, 1, 71.3 mm SL, Sri Lanka, Gin basin, MKTS estate; WHT30343, 1, 52.2 mm SL, Sri Lanka, Gin basin, Homadola; WHT 30671, 2, 23.7–50.3 mm SL, Sri Lanka, Gin basin, Udugama.

*C. rara* and *C. marginata:* from BRITZ *et al*. (2019).

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