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# Eight new species of Rainbowfishes (Melanotaeniidae) from the Birds Head Region, West Papua, Indonesia 

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#### Abstract

Eight new species of Rainbowfishes are described from the Birds Head region by combining a cytochrome oxydase I gene (COI) phylogeny, 12 microsatellite loci and diagnostic morphological characters. The new species Melanotaenia klasioensis, M. longispina and M. susii belong to the "Central Ayamaru Plateau" cluster in the COI phylogeny and are genetically allied to M. ajamaruensis, M. boesemani, M. ericrobertsi and M. fasinensis. A Factorial Component Analysis made on the multilocus microsatellite genotypes reveals that these new species are genetically distinct from each other and from other species known from the area. With the same approach, we also describe M. manibuii, a species belonging to the "Northern Birds Head" mitochondrial clade and $M$. sembrae, a species genetically close to $M$. multiradiata. Three additional new species, M. naramasae, M. rumberponensis and M. sikuensis, belong to the "Birds Neck" cluster and are genetically allied to M. angfa and M. parva. The microsatellite markers were also used to distinguish M. angfa from M. parva, two species sharing the same mitochondrial haplotype. For the sake of comparison, the equivalent morphometric


 data are provided in appendix for the 20 valid species already described from the Birds Head area.Résumé. - Huit nouvelles espèces de poissons arc-en-ciel (Melanotaeniidae) de la région de la Tête d'Oiseau en Papouasie occidentale, Indonésie.

## Key words

Melanotaeniidae
Melanotaenia longispina Melanotaenia susii
Melanotaenia klasioensis Melanotaenia sembrae Melanotaenia manibuii Melanotaenia naramasae Melanotaenia sikuensis Melanotaenia
rumberponensis
Australia
New Guinea
New species


#### Abstract

Huit nouvelles espèces de poissons arc-en-ciel sont décrites de la région de la Tête d'Oiseau en combinant une phylogénie du gène cytochrome oxydase I (COI), 12 locus microsatellites et plusieurs caractères morphologiques diagnostiques. Les espèces nouvelles Melanotaenia klasioensis, M. longispina et M. susii appartiennent au cluster "Central Ayamaru Plateau" dans la phylogénie et sont génétiquement proches des espèces M. ajamaruensis, M. boesemani, M. ericrobertsi et M.fasinensis. Une analyse factorielle des correspondances effectuée sur les génotypes microsatellites multilocus montre que ces espèces sont génétiquement différentiées les unes des autres ainsi qu'avec toutes les espèces présentes dans la région. Avec la même approche, nous décrivons également M. manibuii, une espèce appartenant au groupe phylogénétique "Northern Birds Head", ainsi que $M$. sembrae, une espèce génétiquement proche de M. multiradiata. Les 3 dernières espèces nouvelles que nous décrivons, à savoir M. naramasae, M. rumberponensis et $M$. sikuensis, appartiennent au cluster "Birds Neck" et sont phylogénétiquement apparentées à M. angfa et M. parva. Les marqueurs microsatellites ont également permis de différencier génétiquement $M$. angfa et $M$. parva, deux espèces qui possédaient le même haplotype mitochondrial.


Rainbowfishes of the family Melanotaeniidae are one of the most speciose group of freshwater fishes from the Aus-tralia-New Guinea region (Eschmeyer, 2014). They typically possess a compressed body covered by relatively large scales, two separate dorsal fins (the first with 3-7 spines and the second with a single spine and 6-22 segmented rays), a
long-based anal fin, and no lateral line (Allen et al., 2008). The family is characterized by relatively small (usually less than 10 cm ) and often brightly coloured fish. Rainbowfishes are popular ornamental fishes owing to this coloration and their peaceful behaviour and ease of breeding. Sexual dimorphism is often apparent with males generally deeper-bodied

[^0]and more vividly coloured than females (Allen, 1991). They are locally abundant and occupy a large array of freshwater habitats including arid-zone waterholes, swamps, rainforest streams and lakes. They are opportunist omnivores and show little ecological or morphological specialization like many other freshwater species of the Australian region (Roberts, 1978; McDowall, 1981).

Melanotaeniidae occur in tropical and subtropical Australia and one species occupies the southern Murray-Darling system. The family is also found throughout the island of New Guinea below about 1600 m elevation, as well as on most surrounding large islands of the western half of the mainland, including the Raja Ampat and Aru Archipelagos and Yapen Island (Allen, 1991).

According to Eschmeyer (2014) and Allen et al. (2014a, b), seven genera and 86 species have been described so far within Melanotaeniidae: Cairnsichthys Allen, 1980 (1 species), Chilatherina Regan, 1914 (11 species), Glossolepis Weber, 1907 (9 species), Iriatherina Meinken, 1974 (1 species), Melanotaenia Gill, 1862 ( 62 species), Pelangia Allen, 1998 (1 species), and Rhadinocentrus Regan, 1914 (1 spe-
cies). The greater diversity of the family occurs on the island of New Guinea with 71 endemic species, while 13 species are restricted to Australia, and only two species are shared between both biogeographic entities (Allen and Hadiaty, 2013; Unmack et al., 2013).

The tectonic history of the New Guinea region shows that the Birds Head Peninsula is a section of the Australian craton that became separated from the main continental mass during the Early Cretaceous (Pigram and Davies, 1987). At the same period, the main section of New Guinea was expanded by the collision of the northward-moving Indo-Australian plate with the westward-moving Pacific tectonic plate, and a series of smaller plates (Hamilton, 1988; Charlton, 2000; Hill and Hall, 2003). During the Late Miocene (c. 10-12 MYA), a northeast-southwest compression coupled with several subduction processes resulted in the uplift of the rugged Lengguru fold-and-thrust belt, which unified the Birds Head to the greater New Guinea (Bailly et al., 2009). This geologic episode was concomitantly marked by the uplift of the current Central Highlands that extend east west through New Guinea (Hall, 2002). These intense tectonic and orogenic


Figure 1. - Type localities of the 24 valid Melanotaenia species and the eight new species from the Birds Head region

Table I. - Rainbowfish species used in the barcode phylogenetic analysis and in the microsatellite marker genotyping; *, type locality; $N_{\text {COI }}$, sample size for barcode; GenBank \# COI, accession number for barcode sequence; $N_{S S R}$, sample size for microsatellite markers.

| Species | Locality | $N_{\text {COI }}$ | GenBank \# COI | $N_{S S R}$ |
| :---: | :---: | :---: | :---: | :---: |
| M. ajamaruensis Allen \& Cross, 1980 | Kaliwensi R, Birds Head | 3 | KF491175-77 | 30 |
| M. ammeri Allen et al., 2008 | Gusimawa*, Arguni Bay | 3 | KF491184-86 | 20 |
| M. angfa Allen, 1990 | Yakati R*, Birds Neck | 3 | KF491293, 16-17 | 36 |
| M. arfakensis Allen, 1990 | Prafi $\mathrm{R}^{*}$, Birds Head | 3 | KF491225, 27-28 | 45 |
| M. arguni Kadarusman et al., 2012 | Jasu Ck*, Arguni Bay | 3 | KF491452-53, 56 | 22 |
| M. batanta Allen \& Renyaan, 1996 | Warmon Ck*, Batanta Is | 3 | KF491239, 42-43 | 21 |
| M. boesemani Allen \& Cross, 1980 | L Ayamaru*, Birds Head | 3 | KF491250-51, 55 | 28 |
| M. catherinae (de Beaufort, 1919) | Waiwo Ck, Waigeo Is* | 3 | KF491258-60 | 37 |
| M. ericrobertsi Allen et al., 2014 | Suswa*, Birds Head | 2 | KF491410-11 | 2 |
| M. fasinensis Kadarusman et al., 2010 | Fasin Ck*, Birds Head | 2 | KF491265, 68 | 40 |
| M. flavipinnis Allen et al., 2014 | Ifaupan $\mathrm{Ck}^{*}$, Misool Is |  | no sample |  |
| M. fredericki (Fowler, 1939) | Sampson R*, Birds head | 3 | KF491284, 88-89 | 13 |
| M. irianjaya Allen, 1985 | Fruata*, Bomberai | 3 | KF491340, 46-47 | 24 |
| M. kokasensis Allen et al., 2008 | Kokas Ck*, Bomberai |  | no sample |  |
| M. klasioensis sp. nov. | Klasio Ck, Birds Head | 3 | KF491398-99, 03 | 40 |
| M. laticlavia Allen et al., 2014 | Aifuf Ck*, Birds Head |  | no sample |  |
| M. longispina sp. nov. | Klahfot R, Birds Head | 2 | KF491415-16 | 39 |
| M. manibuii sp. nov. | Tisbo R, Birds Head | 3 | KF491440-41,44 | 39 |
| M. misoolensis Allen, 1982 | Wai Tama*, Misool Is | 3 | KF491366-68 | 6 |
| M. multiradiata Allen et al., 2014 | Moswaren*, Birds Head | 3 | KF491422, 26-27 | 40 |
| M. naramasae sp. nov. | Naramasa R, Birds Neck | 3 | KF491213-15 | 29 |
| M. parva Allen, 1990 | L Kurumoi*, Birds Neck | 3 | KF491376-78 | 40 |
| M. rumberponensis sp. nov. | Rumberpon Is. Birds Neck | 3 | KF491207, 09-10 | 17 |
| M. salawati Kadarusman et al., 2011 | Doktor Ck*, Salawati Is | 3 | KF491390, 94-95 | 22 |
| M. sembrae sp. nov. | Sembra R, Birds Head | 3 | KF491435-37 | 15 |
| M. sikuensis sp. nov. | Siku Ck, Birds Neck | 3 | KF491203-05 | 42 |
| M. sneideri Allen \& Hadiaty, 2013 | Small Ck in Kumawa*, Bomberai |  | no sample |  |
| M. susii sp. nov. | Susi Ck, Birds Head | 3 | KF491417, 19, 21 | 31 |
| M. synergos Allen \& Unmack, 2008 | Wai Bin Ck, Batanta Is* | 3 | KF491466-68 | 39 |
| M. urisa Kadarusman et al., 2012 | L Sewiki*, Arguni Bay | 3 | KF491404-06 | 20 |
| M. veoliae Kadarusman et al., 2012 | Gebiasi Ck*, Arguni Bay | 3 | KF491447-49 | 24 |
| M. wanoma Kadarusman et al., 2012 | Wermura Ck*, Arguni Bay | 3 | KF491459-61 | 14 |

events resulted in the isolation of three major aquatic biotic provinces: northern New Guinea, the combined southern New Guinea/Australia, and the Birds Head region including the Lengguru Range (Allen, 1991; Abell et al., 2008).

Kadarusman et al. (2012a) assessed the DNA barcoding diversity of 53 valid species of Melanotaeniidae throughout the Indo-Australian archipelago. This study confirmed the results of McGuigan et al. (2000) showing that Melanotaenia, along with Chilatherina and Glossolepis were subdivided into three main clades whose distribution is tightly matching the three biogeographic regions of New Guinea Kadarusman et al. (2012a) added a fourth clade restricted to Lengguru Range.

In a recent study involving nuclear and mitochondrial DNA sequences, Unmack et al. (2013) confirmed that the
three main clades correlated with the three main biogeographic regions of New Guinea, but failed to evidence the fourth clade restricted to Lengguru due to the lack of genetic samples (i.e. Melanotaenia mairasi Allen \& Hadiaty, 2011).

Kadarusman et al. (2012a) therefore confirmed that the Melanotaenia species from the Birds Head region are monophyletic compared to the other main clades and highlighted the presence of nearly twice as many evolutionary lineages among the 15 valid species sampled in this area than previously described. These results revealed unexpected levels of cryptic diversity, demonstrating that the diversity of the family is still largely underestimated. Kadarusman and colleagues (2012a) concluded for Melanotaeniids that the biogeographic range of the Birds Head region should include the western side of Lengguru Range (i.e. all watersheds
flowing to Arguni Bay), the Bomberai and the Birds Head Peninsulas, the Birds Head Isthmus joining both peninsulas and the four major Raja Ampat islands (i.e. Misool, Batanta, Salawati, Waigeo)

The Birds Head region is a centre for rainbowfish diversity with 24 species currently described (Tab. I, Fig. 1).

A combination of molecular and morphologic approaches was used to determine differences between most of the currently recognised species and eight undetermined taxa that were recently obtained from the Birds Head region. We used partial sequences from the mitochondrial cytochrome oxydase I gene (COI) and 12 nuclear DNA microsatellites markers (Simple Sequence repeats - SSR) (Nugraha et al. 2014) to assess whether morphological similar specimens from distinct locations are conspecifics or whether sufficient genetic variation and reproductive isolation exist to consider these specimens as distinct species.

The samples were collected during three expeditions conducted between 2007 and 2009 in West Papua by Balai Riset Budidaya Ikan Hias in Depok, Indonesia (BRBIHKKP), the Akademi Perikanan Sorong, Indonesia (APSORKKP) and by the Institut de Recherche pour le Développement (Montpellier, France).

## MATERIAL AND METHODS

## DNA barcodes and tree-based species delimitation

Partial, 650-bp sequences from the 5 ' region of the COI were obtained from GenBank for 20 valid species and eight undetermined taxa according to Kadarusman et al. (2012a) Details about samples are given in figure 1 and table I. DNA samples were not available for M. flavipinnis, M. kokasensis, M. laticlavia and M. sneideri.

Phylogenetic analysis of the COI data set was inferred with neighbour joining (NJ) and maximum likelihood (ML) methods in MEGA5 (Tamura et al., 2011). The Kimura 2-parameter (K2P) substitution model was used for the NJ analysis with 1000 bootstrap replicates to infer evolutionary distances. We also performed ML analyses with 500 bootstrap replicates using the Kimura 2-parameter model with a discrete Gamma distribution $(\mathrm{K} 2 \mathrm{P}+\mathrm{G})$, which was the most appropriate nucleotide substitution model for our dataset based on the Bayesian Information Criterion (BIC) in the ML model selection feature of MEGA5.

## Genotyping with nuclear DNA microsatellites

Individuals from the 20 valid species and the eight undetermined taxa described in table I were genotyped with 12 nuclear microsatellite markers that were recently developed (Nugraha et al., 2014). Collected populations include the same localities and the same taxa analyzed at COI DNA barcodes (Tab. I; Fig. 1). Sampling strategy consisted in collect-
ing each species at their type locality. For most of the species between 13 and 48 individuals were captured per site, using landing nets. Because of low population density, five species (i.e. M. ammeri, M. fredericki, M. irianjaya, M. manibuii sp. nov., M. naramasae sp. nov.) were sampled at various localities in the same river drainage (geographic distances varying between 1 and 5 km ) and collected individuals were pooled for subsequent analyses.

DNA was extracted from caudal fin clips preserved in absolute ethanol and stored at $-20^{\circ} \mathrm{C}$ by using the NucleoSpin® $\circledR^{\circledR}$ Tissue kit (Macherey-Nagel). DNA was extracted according to the manufacturer instructions using a Janus automated Workstation (Perkin Elmer). Microsatellite amplifications were performed with fluorescently labelled primers (Eurofins) and each reaction contained $5 \mu \mathrm{l}$ of 2 x Master mix (Roche), $0.1 \mu \mathrm{M}$ of forward primer, $0.4 \mu \mathrm{M}$ of reverse primer and $0.5 \mu \mathrm{l}$ of template DNA. Cycling conditions were as follow: initial denaturation at $95^{\circ} \mathrm{C}$ for 4 min followed by 30 cycles of $95^{\circ} \mathrm{C}$ for $20 \mathrm{~s}, 56^{\circ} \mathrm{C}$ for 20 s and $72^{\circ} \mathrm{C}$ for 30 s , and a final elongation step of 7 min at $72^{\circ} \mathrm{C}$. Amplicon size was analyzed by capillary electrophoresis, in the technical facilities of the labex "Centre Méditerranéen de l'Environnement et de la Biodiversité" (Montpellier). PCR products were diluted 1:50 in $\mathrm{H}_{2} \mathrm{O}$ (or $1: 100$ in the case of fluorescence saturation). One $\mu \mathrm{l}$ of diluted PCR from 4 distinct fluorescent couples of primers were mixed together with $13.8 \mu$ of formamide and $0.2 \mu$ l of GeneScan ${ }^{\mathrm{TM}} 600 \mathrm{LIZ}{ }^{\circledR}$ Size Standard (Applied Biosystems). Capillary electrophoresis was run in an Applied ABI Prism® 3500 XL 24 capillary sequencer Allele sizing and genotyping were achieved with the Peak Scanner v 1.0 and GeneMapper ${ }^{\circledR}$ v5 .0 software (Applied Biosystems).

Allelic diversity and average observed (Ho) heterozygosity were calculated using GENETIX 4.05 (Belkhir et al., 1996). Population gene pools were checked for departure from Hardy-Weinberg equilibrium by estimating the significance of the multilocus inbreeding coefficient (FIS) from sets of 1000 random allelic permutations of the original dataset as implemented by GENETIX 4.05 software. Significance levels of FIS $p$-values were tested using a one-tailed test as the probability of obtaining absolute values higher than or equal to the one observed under the null hypothesis (i.e. the individuals can be considered as the sample from a panmictic population at Hardy-Weinberg equilibrium). As the excess of homozygote can be partly explained by genotyping errors, the presence of null alleles, stuttering or large allele dropout was also tested for each species and locus-bylocus with the Micro-Checker, v. 2.2.3 software (Van Oosterhout et al., 2004).

Genetic relationships between multilocus genotypes were assessed using factorial correspondence analysis (FCA) in GENETIX 4.05 software. Genetic structure among species was also investigated by calculating pairwise FST
values with 1000 random allelic permutations of the original dataset as implemented by GENETIX 4.05 software. Significance level of $p$-value for FST was defined as described above for FIS.

## Species descriptions and specimen deposition

Specimens have been deposited at the Museum Zoologicum Bogoriense (MZB, Indonesia). The methods of meristic counts and measurements follow Allen and Cross (1980) with some modifications and additions (Kadarusman et al., 2010). Measurements were performed with digital dial callipers under monocular lens ( $\times 2$ ) and counts were made under binocular lens ( $\times 4$ ). Measurements were made on the left side and are expressed to the nearest 0.1 mm . All proportions are expressed as percentage of the standard length.

Counts are as follow. - Lateral scales are the number of scales in horizontal row from the upper corner of the gill cover to the caudal fin base, excluding the small scales posterior to the hypural junction. Transverse scales are the number of scales in vertical row between the base of the first dorsal fin and the base of the anal fin origin. Predorsal scales are the number of scales along the midline of the nape in front of the first dorsal fin. Cheek scale is the total number of scales covering the suborbital and preoperculum. Dorsal rays are the number of spines in the first dorsal fin and the spine and soft rays in second dorsal fin. Anal rays are the single spine and number of soft rays. The last soft ray of the anal and second dorsal fins is divided at the base and counted as a single ray Pectoral rays are the total number of segmented rays. Pelvic rays are the single spine and number of soft rays. Gillrakers are the total number on the first branchial arch.

Measurements are as follow. - Standard length is measured from the anteriormost tip of the upper lip to the posteriormost point of the hypural fold formed when the caudal peduncle is bent. Head length is measured from the tip of the upper lip to the upper rear edge of the gill opening. Snout length is the least distance measured from the tip of the upper lip to the fleshy anterior border of the eye. Interorbital width is the least width between the eyes anteriorly to the suture between frontal and nasal bones. Eye diameter is the maximal horizontal width of the orbital cavity. Body depth is measured from the base of the first dorsal spine to the base of the first anal spine. Body width is the maximal width measured posteriorly just behind the pectoral-fin base. Caudal peduncle depth is the minimum depth. Caudal peduncle length is measured from the base of the last dorsal fin ray to the vertebral-hypural junction at the caudal fin base. Predorsal length is measured from the tip of the upper lip to the base of the spine at the origin of first dorsal fin. Prepelvic length is measured from the tip of the upper lip to the base of the spine at the origin of pelvic fin. Preanal length is measured from the tip of the upper lip to the base of the spine at the origin of anal fin. Pectoral fin length is measured from the
anteriormost part of pectoral fin base to the tip of the longest soft ray. Pelvic fin length is measured from the anteriormost part of pelvic fin base to the tip of the longest soft ray. Spine length of the first dorsal fin is measured from the base to the tip of the first spine on the first dorsal fin. Spine length of the second dorsal fin is measured from the base to the tip of the spine on the second dorsal fin. Spine length of the anal fin is measured from the base to the tip of the single anal spine. Dorsal fin base length is measured from the posterior base of the first spine of first dorsal fin to the posterior base of last soft ray of second dorsal fin. Second dorsal fin base length is measured on the second dorsal fin from the posterior base of the first spine to the posterior base of last soft ray. Anal fin base length is measured from the posterior base of the spine to the posterior base of the last soft ray. Anal fin height is measured from the base to the tip of the second soft ray.

Comparative material included 20 species described from the Birds Head region. This material includes type specimens and additional specimens collected at the type localities during three surveys (2007-2008-2010). These additional specimens were deposited at MZB, RMNH and MNHN. Their geographic locations are shown in figure 1.

Melanotaenia ajamaruensis. - Indonesia, West Papua. RMNH 28068 (holotype), 77.9 mm SL, Ajamaru; RMNH 28069-71 (paratypes), 7 specimens ( $57.0-63.8 \mathrm{~mm} \mathrm{SL}$ ), collected with holotype by Boeseman, 4-6 Mar. 1955; MZB 17692-94, 16 spms ( $62.5-96.5 \mathrm{~mm}$ SL), MNHN 2009-1617, 6 spms ( $55.5-66.5 \mathrm{~mm}$ SL), Kaliwensi River at Soroang village, $1^{\circ} 15.073^{\prime} \mathrm{S}, 132^{\circ} 08.156$ ' E , collected by Kadarusman, Krenak, Paradis \& Pouyaud, 22-23 May 2007.

Melanotaenia ammeri. - Indonesia, West Papua. MZB 16455 (holotype), 82 mm SL; Gusimawa village; MZB 16456 (paratypes), 4 spms ( $55.9-71.0 \mathrm{~mm} \mathrm{SL}$ ), collected with holotype by Allen \& Ammer, 12 Jan. 2008; MZB 17709, 9 spms ( $62.4-101.8 \mathrm{~mm} \mathrm{SL}$ ), collected at type locality, $3^{\circ} 02.438^{\prime} \mathrm{S}, 133^{\circ} 52.844^{\prime} \mathrm{E}$, Lemauk \& Pouyaud, 4 Nov. 2010.

Melanotaenia angfa. - Indonesia, West Papua. MZB 17698 3 spms ( $69.2-86.2 \mathrm{~mm}$ SL), MNHN 2009-1620, 5 spms (62.168.6 mm SL), RMNH.PISC. 35675 , 5 spms ( $59.5-62.6 \mathrm{~mm}$ SL), Pondok Creek, type locality, River Yakati, $2^{\circ} 11.067$ 'S, $134^{\circ} 05.584^{\prime}$ E, Kadarusman, Ajambua, Sumanta \& Pouyaud, 11 Apr. 2008.

Melanotaenia arfakensis. - Indonesia, West Papua. MZB $17702,3 \mathrm{spms}$ ( $68.7-76.9 \mathrm{~mm} \mathrm{SL}$ ), MNHN 2009-1622, 4 spms ( $60.7-70.6 \mathrm{~mm}$ SL), RMNH.PISC. $35677,3 \mathrm{spms}(60.9-71.3 \mathrm{~mm}$ SL), Supsan Creek, $0^{\circ} 58.376^{\prime}$ S, $133^{\circ} 54.964^{\prime}$ E, a tributary of Prafi River (type locality), Kadarusman, Ajambua, Paradis \& Pouyaud, 30 May 2007.

Melanotaenia arguni. - Indonesia, West Papua. MZB 17712 (holotype), male, 54.9 mm SL , Egerwara village, Jasu Creek, $3^{\circ} 05.292^{\prime} \mathrm{S}, 133^{\circ} 37.879^{\prime} \mathrm{E}$; MZB 17713 (paratypes), 6 spms (58.7-67.6 mm SL), MNHN 2010-0029 (paratypes), 4 spms (59.164.3 mm SL), RMNH.PISC. 35876 (paratypes), 4 spms (58.9-
72.6 mm SL ), collected with holotype by Kadarusman, Ruwe \& Wamburie, 1 Nov. 2010.

Melanotaenia batanta. - Indonesia, West Papua. MZB 17705-06, 5 spms (88.299.2 mm SL), MNHN 2009-1625, 5 spms (79.5-107.9 mm SL), RMNH.PISC.35678, 5 spms ( $73.9-110.3 \mathrm{~mm} \mathrm{SL}$ ), type locality, Warmon stream, $0^{\circ} 50.256^{\prime} \mathrm{S}, 130^{\circ} 43.287^{\prime} \mathrm{E}$, Bourhis, Sumanta \& Pouyaud, 30 Apr. 2008.

Melanotaenia boesemani. - Indonesia, West Papua. RMNH 28061 (holotype), 67.2 mm SL, Ajamaru Lakes, Boeseman, 4 Mar. 1955; RMNH 28067 (paratypes), 2 spms ( $63.8-86.9 \mathrm{~mm} \mathrm{SL}$ ), same data as holotype; MZB 17691, 6 spms (54.7-60.7 mm SL) and MNHN 2009-1616, 4 spms (61.866.0 mm SL ), Tiwit Creek, $1^{\circ} 15.463$ 'S, $132^{\circ} 14.939^{\prime}$ E, Kadarusman, Slembrouck \& Pouyaud, 22 May 2007.

Melanotaenia catherinae. - Indonesia, West Papua. MZB 17703, 4 spms (65.4$79.8 \mathrm{~mm} \mathrm{SL})$ and MNHN 2009-1623, 4 spms (58.1-67.1 mm SL), Waiwo Creek on Waigeo Island (type locality), $0^{\circ} 25.060^{\prime} \mathrm{S}$, $130^{\circ} 46.462^{\prime}$ E, Kadarusman \& Pouyaud, 14 May 2007.

Melanotaenia fasinensis. - Indonesia, West Papua. MZB 17700 (holotype), male, 108.5 mm SL, Ween village, Fasin Creek, $1^{\circ} 13.856^{\prime} \mathrm{S}, 131^{\circ} 58.186^{\prime} \mathrm{E}$; MZB 17701 (paratypes), 4 spms ( $91.0-120.2 \mathrm{~mm} \mathrm{SL}$ ), MNHN 2009-1627 (paratypes), 4 spms (77.1-90.8 mm SL), RMNH.PISC.35680, 4 spms ( $69.9-78.5 \mathrm{~mm} \mathrm{SL}$ ), collected with holotype by Sumanta, Krenak, Kadarusman, Paradis \& Pouyaud, 24 May 2007.

Melanotaenia fredericki. - Indonesia, West Papua. MZB 17695, 4 spms (65.071.9 mm SL), RMNH.PISC. $35673,4 \mathrm{spms}$ (65.0-81.5 mm SL), MNHN 2009-1618, 4 spms (55.7-71.7 mm SL), Sampson River (or Warsamson), type locality, $0^{\circ} 49.361$ 'S, $131^{\circ} 24.193$ ' , Kadarusman \& Paradis, 13 Jun. 2007.

Melanotaenia irianjaya. - Indonesia, West Papua. MZB 4952 (holotype), 58.8 mm SL, Fruata; MZB 4953 (paratypes), 3 spms (39.6-57.8 mm SL), same data as holotype; MZB 17708 , 10 spms ( $67.7-102.6 \mathrm{~mm} \mathrm{SL}$ ),


Figure 2. - Maximum likelihood tree for Birds Head region Melanotaenia species based on analysis of partial COI sequences ( 650 bp ). Bootstrap values obtained for ML on 500 replicates and for NJ (within brackets).

Wat Creek, $2^{\circ} 58.576^{\prime} \mathrm{S}, 133^{\circ} 27.971^{\prime} \mathrm{E}$, about 7 km from type locality, Kadarusman, 1 Nov. 2010.

Melanotaenia kokasensis. - Indonesia, West Papua. MZB 16453 (holotype), 57.2 mm SL, Kokas, Allen \& Ammer, 16 Jan. 2008; MZB 16454 (paratypes), 2 spms (49.1-53.7 mm SL), same data as for holotype.

Melanotaenia misoolensis. - Indonesia, West Papua. MZB 17707, 3 spms (59.8-77.4 mm SL), RMNH.PISC. $35679,3 \mathrm{spms}$ (46.1-48.9 mm SL), MNHN 2009-1626, 4 spms (54.0-58.4 mm SL), Wai Tama, type locality, $1^{\circ} 50.978$ 'S, $129^{\circ} 54.654^{\prime} \mathrm{E}$, Ajambua, Slembrouck, Sumanta \& Pouyaud, 28 Apr. 2008.

Melanotaenia multiradiata. - Indonesia, West Papua. MZB 20033, 14 spms (64.1-89.9 mm SL), Waren R. at Moswaren, type locality, $1^{\circ} 29.158^{\prime}$ S, $132^{\circ} 13.596^{\prime}$ E, Sumanta, Ajambua, Kadarusman, Slembrouck \& Pouyaud, 23 Apr. 2008.

Melanotaenia parva. - Indonesia, West Papua. MZB 17699, 2 spms (65.4-67.0 mm SL), MNHN 2009-1621, 3 spms (57.762.0 mm SL), RMNH.PISC. $35676,3 \mathrm{spms}(50.7-58.6 \mathrm{~mm} \mathrm{SL})$, Lake Kurumoi, $2^{\circ} 09.761^{\prime} \mathrm{S}, 134^{\circ} 05.155^{\prime} \mathrm{E}$, collected at type locality by Kadarusman, Paradis, Sumanta, Pouyaud; 7-8 Jun. 2007.

Melanotaenia salawati. - Indonesia, West Papua. MZB 17710 (holotype), male, 88.7 mm SL, Waipule village, Doktor Creek, $1^{\circ} 01.128^{\prime} \mathrm{S}, 130^{\circ} 41.407^{\prime} \mathrm{E}$; MZB 17711 (paratypes), 5 spms (71.4-91.6 mm SL), MNHN 2010-0030 (paratypes), 5 spms (68.083.6 mm SL), RMNH.PISC.35875, 5 spms ( $77.1-82.2 \mathrm{~mm} \mathrm{SL}$ ), collected with holotype by Sumanta, Ajambua, Slembrouck \& Pouyaud, 29 Apr. 2008.

Melanotaenia synergos. - Indonesia, West Papua. MZB 17704, 2 spms (61.8-67.1 mm SL) and MNHN 2009-1624, 3 spms (57.763.5 mm SL ), a small creek on north-eastern Batanta Island, less than 3 km from type locality, $0^{\circ} 50.288^{\prime} \mathrm{S}, 130^{\circ} 47.227^{\prime} \mathrm{E}$, Kadarusman, Sumanta \& Pouyaud, 15 May 2007.

Melanotaenia urisa. - Indonesia, West Papua. MZB 17715 (holotype), male, 71.4 mm SL, Sewiki Lake, $3^{\circ} 15.061$ 'S, $133^{\circ} 47.735^{\prime} \mathrm{E}$; MZB 20025 (paratypes), 6 spms ( $60.6-71.0 \mathrm{~mm}$ SL), MNHN 2010-0031 (paratypes), 5 spms ( $63.7-87.8 \mathrm{~mm} \mathrm{SL}$ ), RMNH.PISC. 35877 (paratypes), 5 spms ( $57.4-62.0 \mathrm{~mm}$ SL), collected with holotype by Ajambua, Lemauk, Legendre \& Pouyaud, 1 Nov. 2010.

Melanotaenia veoliae. - Indonesia, West Papua. MZB 20026 (holotype), male, 92.3 mm SL , Gebiasi Creek, $3^{\circ} 27.607$ 'S, $133^{\circ} 41.071^{\prime} \mathrm{E}$; MZB 20027 (paratypes), 5 spms (62.8-87.2 mm SL), MNHN 2010-0032, $5 \mathrm{spms}(53.9-84.5 \mathrm{~mm} \mathrm{SL})$, RMNH. PISC. $35878,5 \mathrm{spms}$ ( $64.5-65.0 \mathrm{~mm}$ SL), collected with holotype by Segura, Caruso, Setiawibawa, Sauri, Suruwaki, 7 Nov. 2010.

Melanotaenia wanoma. - Indonesia, West Papua. MZB 20028 (holotype), male, 71.9 mm SL , Wermura Creek, $3^{\circ} 28.261^{\prime} \mathrm{S}$, $133^{\circ} 42.770^{\prime}$ E; MZB 20029 (paratypes), 5 spms (62.8-72.8 mm SL), MNHN 2010-0033, $6 \mathrm{spms}(59.6-65.0 \mathrm{~mm} \mathrm{SL})$, RMNH. PISC. $35879,6 \mathrm{spms}$ ( $61.0-71.9 \mathrm{~mm}$ SL), collected with holotype by Segura, Caruso, Setiawibawa, Sauri, Suruwaki, 7 Nov. 2010.

Morphometric data corresponding to these species are given at the end of this paper (in appendix).

## RESULTS

## DNA barcodes and tree-based species delimitation

The ML tree obtained from COI mitochondrial sequences for 81 individuals belonging to 20 valid species and 8 new species (Tab. I) is presented in figure 2. The same topology was obtained for the K2P-NJ tree, thus, only bootstrap values (in brackets) were displayed together with those obtained for the ML tree.

Three major clades are highlighted by the ML tree (Fig. 2). These results are congruent with the topology of the ML tree based on cytochrome b provided in Allen et al. (2014b). The first clade "Northern Birds Head" (bootstrap: ML $96 \%$, NJ 94\%) includes all Melanotaenia species from the Birds Head Peninsula (i.e. M. ajamaruensis, M. arfakensis, M. boesemani, M. ericrobertsi, M. fasinensis, M. fredericki, M. multiradiata) and from the Southern Raja Ampat Islands (i.e. M. batanta, M. misoolensis, M. salawati). It also includes five new species (i.e. M. klasioensis, M. susii, M. longispina, M. sembrae, M. manibuii). The second clade "Southern Birds Head" (bootstrap: ML 98\%, NJ $94 \%$ ) includes all the Melanotaenia species from the Bomberai Peninsula (i.e. M. ammeri, M. arguni, M. irianjaya, M. urisa, M. veoliae, M. wanoma) and from the Birds Neck (i.e. M. angfa, M. parva). It also includes three new species (i.e. M. naramasae, M. rumberponensis, M. sikuensis). The third clade "Waigeo" is supported by high bootstrap values (ML $100 \%$; NJ 99\%) and includes the two species M. catherinae and M. synergos known from the Northern Raja Ampat (Fig. 1).
M. manibuii sp. nov. has a basal position in the first clade (Fig. 2) and displays an important phylogenetic distance with all the species composing this clade (average K2P distance: $0.053 \pm 0.008$ ). M. manibuii and M. irianjaya are morphologically closely related, although, they represent distinct species sorting in two different clades (i.e. first clade for M. manibuii and second clade for M. irianjaya) and are separated by a high phylogenetic distances (K2P distance: $0.069 \pm 0.009$ ).

The new species M. sembrae forms together with M. multiradiata the "Southern Ayamaru Plateau" cluster within the first clade (bootstrap: ML 98\%, NJ 99\%). The two species are separated by a low phylogenetic distance of less than $1 \%$ (K2P distance: $0.007 \pm 0.003$ ).

The new species $M$. klasioensis, M. susii and M. longispina belong to the cluster "Central Ayamaru Plateau" together with M. ajamaruensis, M. boesemani,M. ericrobertsi and M. fasinensis (bootstrap: ML 88\%, NJ 86\%). These species are characterized by low phylogenetic distances (average K2P distance: $0.015 \pm 0.003$ ) and are all distributed in the fragmented river systems of the karstic Ayamaru Plateau. This cluster displays higher phylogenetic distances with M. arfakensis (average K2P distance: $0.030 \pm 0.005$ ) as well
as with the "Southern Ayamaru Plateau" cluster (average K2P distance: $0.029 \pm 0.005$ ).

Finally, the 3 new species $M$. naramasae, M. sikuensis and $M$. rumberponensis are genetically closely related with M. angfa and M. parva. They belong to the cluster "Birds Neck" and are characterised by phylogenetic distances of less than $1 \%$ (average K2P distance: $0.005 \pm 0.002$ ). This cluster, however, displays a higher phylogenetic distance with the remaining species composing the "Southern Birds Head" clade (K2P distance: $0.046 \pm 0.007$ ). Interestingly, the COI failed to differentiate $M$. angfa from M. parva, which display the same DNA barcode. This absence of genetic differentiation among these species was also revealed by Allen et al. (2014) for the cytochrome b gene and by Unmack et al. (2013) on one nuclear gene (S7) and seven mitochondrial markers (ND1, ND2, ND4L, ND4, ATPase6/8, cyt b, and partial COIII).

## Nuclear DNA microsatellites

Twelve microsatellite loci were successfully amplified in 775 specimens including those analyzed by their COI DNA
barcodes (Tab. I; Fig. 1). Characteristics of these loci, including allele size range and number per locus, are presented in table II. All microsatellite loci revealed polymorphism with a number of alleles per-locus ranging between 8 (locus $\mathrm{Mb}_{-}$ tri2) to 53 (Mb_di2). The total number of allele per-species (Tab. III) indicates that $M$. ericrobertsi and $M$. veoliae are the species with the lowest level of polymorphism (13 and 17 alleles, respectively), while M. multiradiata and the new species $M$. longispina are the most polymorphic species (124 and 133 alleles, respectively). Average observed heterozygosity per species ranged between 0.042 and 0.743 (Tab III). Most species were at panmictic equilibrium according to non-significant multilocus FIS values (Tab. III). Only five species (i.e. M.ammeri, M. fredericki, M. irianjaya, M. manibuii, M. naramasae) showed a significant deviation from Hardy-Weinberg equilibrium. No evidence for null alleles, scoring errors due to stuttering and for large allele dropout was revealed on the entire dataset according to Micro-Checker software. The five species presenting significant multilocus FIS values are a mix of individuals sampled at various locations along the same river drainage. These

Table II. - Characteristics of the 12 microsatellite markers used in the present study for 20 valid species and eight new species from the Birds Head region. S: Allele size range (bp) per locus for all species; A: Allele number per locus for all species.

| Locus Name | Gene Bank \# | Primer sequence $5^{\prime}-3{ }^{\prime}$ | Repeat motif | S | A |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Mb_dil | KF856886 | F: TGAGTCAAGGGATGTCCAAA <br> R : GATGTCCCTCCATAGCCTGT | CA | 085-151 | 34 |
|  |  |  |  |  |  |
| Mb_di2 | KF856887 | $\begin{aligned} & \text { F: TCCCACCATGCATTATTAACAC } \\ & \text { R: GAACTGCAGGCTCAACACAT } \end{aligned}$ | GT | 111-227 | 53 |
|  |  |  |  |  |  |
| Mb_di3 | KF856888 | F: TGGAGGATTGTAGGTCTGGG <br> R: CATCAACATAGCAATCAGTGCC | GT | 148-231 | 48 |
|  |  |  |  |  |  |
| Mb_pental | KF856889 | $\begin{aligned} & \text { F: TGTAACGAGTGAATTTCTCCACTG } \\ & \text { R: TCCACAATATTTACTGGAACTGC } \end{aligned}$ | TCTAA | 150-240 | 18 |
|  |  |  |  |  |  |
| Mb_di4 | KF856890 | F: CAAGGCAGCAAAAGAACAAAR: CAGGCCATTCCTGAGTCAAT | AC | 098-172 | 38 |
|  |  |  |  |  |  |
| Mb_tetra1 | KF856891 | $\begin{aligned} & \text { F: TTTACTACACGTGGTCTTCACTTT } \\ & \text { R: CGTTTTAGCCACAAACAGCC } \end{aligned}$ | AATG | 125-217 | 33 |
|  |  |  |  |  |  |
| Mb_tri1 | KF856892 | F: CTGTCAGAGTGCAGGACTGG | GGA | 101-128 | 10 |
|  |  | R: TCTTTTCCAGGCCAAGTGAC |  |  |  |
| Mb_tri2 | KF856893 | F: CGTGTCTATTCCTATCGTGCC | GAG | 132-153 | 8 |
|  |  | R: TGGATTCACATCCTCTTGAGTG |  |  |  |
| Mb_di5 | KF856894 | F: TCCTTGAATACATTCCTGCCA | AC | 077-129 | 23 |
|  |  | R: CAATAATTTCAAGGAAGAGCCTTT |  |  |  |
| Mb_tetra2 | KF856895 | F: GAAGAGTATGAAGAAGCCTTAGTCTGA | CATC | 136-324 | 39 |
|  |  | R: CGTCCTGCAATCTACTGTGA |  |  |  |
| Mb_tri3 | KF856896 | F: TGACAGTAACAGGGACGATGA | ATG | 111-163 | 16 |
|  |  | R: AAGGCAACCTAATGTGCTGT |  |  |  |
| Mb_tri4 | KF856897 | F: AACAACAGGCAGGGAGTCAC | ATG | 098-132 | 13 |
|  |  | R: CCAAGAGGTTGTGGTGTTCC |  |  |  |

results therefore suggest the possible occurrence of genetically differentiated subpopulations patchily distributed in the same river.

Several factorial correspondence analyses (FCA) were conducted using microsatellite genotypes in order to assess the genetic differentiation between the new species and all other closely related valid species according to the COI phylogeny. The results are presented herein after:
(1) The three new species, M. klasioensis, M. longispina and $M$. susii, are genetically differentiated from each other as well as from M. arfakensis and all the remaining species that constitute the "Central Ayamaru Plateau" cluster (Fig. 3). All pairwise FST values show highly significant genetic divergence ( $\mathrm{p}<0.001$ ) among these species (Tab. IV). Pairwise

FST values between the three new species (i.e.M. klasioensis, M. longispina, M. susii) are comprised between 0.254 and 0.418 . The new species $M$. klasioensis showed a low genetic distance with M. fasinensis on the COI (Fig. 2). The microsatellite data indicates that these two species constitute distinct genetic entities (Fig. 3) characterised by a significant FST value of 0.633 (Tab. IV). The same results were observed between M. susii and M. ericrobertsi and between M. longispina and all other species belonging to the "Central Ayamaru Plateau" cluster.
(2) The FCA presented in figure 4 shows that the new species M. sembrae is genetically differentiated from its sister species M. multiradiata (cluster "Southern Ayamaru Plateau"; Fig. 2). This new species is also genetically differ-

Table III. - Allele diversity (per species and per locus), average observed heterozygosity per species across loci, and per-species multilocus Fis values. Nall.: number of alleles per-species; Hobs.: average observed heterozygosity; Fis values significance: * p $<0.01$; ** p $<0.001$.

|  | $\begin{aligned} & \bar{z} \\ & \sum \end{aligned}$ | $\begin{aligned} & \mathbb{Z} \\ & y_{1} \\ & \sum \end{aligned}$ | $\begin{aligned} & \mathfrak{Z} \\ & \dot{n} \\ & n_{1} \end{aligned}$ |  | $\begin{aligned} & : \frac{7}{1} \\ & i \end{aligned}$ | $\begin{aligned} & \text { ت} \\ & \text { E } \\ & \text { n } \end{aligned}$ | $\begin{aligned} & \Xi_{1} \\ & \dot{\sum} \end{aligned}$ | $\begin{aligned} & \tilde{E}_{1} \\ & \sum_{1}^{0} \end{aligned}$ |  |  | $\begin{aligned} & \tilde{E} \\ & \tilde{\sum} \end{aligned}$ | $\begin{aligned} & \pm \\ & E \\ & i \end{aligned}$ | $\dot{\overline{\widetilde{z}}}$ |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| M.ajamaruensis | 9 | 12 | 8 | 7 | 10 | 6 | 3 | 5 | 5 | 11 | 3 | 3 | 82 | 0.670 | -0.037 |
| M. ammeri | 2 | 2 | 2 | 3 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 18 | 0.105 | 0.351** |
| M. angfa | 1 | 2 | 2 | 2 | 1 | 3 | 1 | 1 | 3 | 2 | 1 | 1 | 20 | 0.245 | -0.032 |
| M. arfakensis | 6 | 3 | 12 | 9 | 1 | 5 | 2 | 1 | 2 | 11 | 6 | 1 | 59 | 0.404 | -0.004 |
| M. arguni | 8 | 7 | 11 | 7 | 5 | 10 | 5 | 4 | 5 | 10 | 5 | 3 | 80 | 0.677 | 0.048 |
| M. batanta | 1 | 8 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 9 | 1 | 1 | 28 | 0.158 | -0.104 |
| M. boesemani | 14 | 14 | 8 | 8 | 15 | 7 | 4 | 4 | 8 | 18 | 3 | 4 | 105 | 0.681 | 0.013 |
| M. catherinae | 2 | 1 | 1 | 3 | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 3 | 19 | 0.146 | -0.006 |
| M. ericrobertsi | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 13 | 0.042 | - |
| M. fasinensis | 4 | 5 | 9 | 3 | 4 | 6 | 1 | 1 | 2 | 8 | 1 | 1 | 45 | 0.364 | -0.027 |
| M. fredericki | 7 | 19 | 17 | 10 | 3 | 12 | 3 | 6 | 12 | 9 | 4 | 4 | 106 | 0.657 | 0.118** |
| M. irianjaya | 13 | 14 | 17 | 9 | 6 | 14 | 8 | 5 | 10 | 12 | 7 | 5 | 120 | 0.708 | 0.084* |
| M. klasioensis | 1 | 15 | 6 | 2 | 3 | 4 | 2 | 1 | 2 | 3 | 1 | 1 | 41 | 0.310 | -0.006 |
| M. longispina | 18 | 9 | 16 | 9 | 15 | 17 | 3 | 6 | 13 | 14 | 7 | 6 | 133 | 0.743 | -0.003 |
| M. manibuii | 4 | 19 | 19 | 8 | 2 | 9 | 5 | 2 | 5 | 3 | 6 | 2 | 84 | 0.565 | 0.084** |
| M. misoolensis | 4 | 5 | 3 | 5 | 4 | 5 | 2 | 1 | 4 | 4 | 2 | 1 | 40 | 0.561 | 0.009 |
| M. multiradiata | 13 | 10 | 23 | 9 | 19 | 13 | 3 | 3 | 4 | 18 | 7 | 2 | 124 | 0.608 | 0.020 |
| M. naramasae | 15 | 15 | 18 | 10 | 12 | 8 | 4 | 6 | 6 | 9 | 6 | 1 | 110 | 0.638 | $0.100^{* *}$ |
| M. parva | 5 | 5 | 8 | 6 | 1 | 5 | 2 | 2 | 3 | 4 | 2 | 1 | 44 | 0.386 | -0.005 |
| M. rumberponensis | 2 | 2 | 2 | 3 | 1 | 4 | 1 | 2 | 3 | 1 | 2 | 1 | 24 | 0.216 | 0.001 |
| M. salawati | 1 | 5 | 6 | 5 | 8 | 4 | 2 | 2 | 3 | 6 | 2 | 1 | 45 | 0.315 | -0.061 |
| M. sembrae | 2 | 15 | 7 | 5 | 2 | 5 | 4 | 2 | 3 | 13 | 2 | 6 | 66 | 0.537 | -0.015 |
| M. sikuensis | 2 | 3 | 2 | 2 | 1 | 3 | 2 | 2 | 1 | 1 | 2 | 1 | 22 | 0.149 | 0.068 |
| M. susii | 1 | 13 | 14 | 5 | 6 | 11 | 3 | 1 | 1 | 5 | 3 | 1 | 64 | 0.432 | 0.024 |
| M. synergos | 2 | 1 | 1 | 3 | 1 | 3 | 1 | 1 | 2 | 3 | 2 | 1 | 21 | 0.191 | -0.010 |
| M. urisa | 1 | 3 | 2 | 5 | 2 | 5 | 1 | 3 | 1 | 4 | 2 | 4 | 33 | 0.376 | 0.080 |
| M. veoliae | 1 | 1 | 1 | 2 | 1 | 1 | 3 | 1 | 3 | 1 | 1 | 1 | 17 | 0.127 | -0.048 |
| M. wanoma | 1 | 2 | 4 | 4 | 3 | 5 | 3 | 3 | 2 | 3 | 1 | 2 | 33 | 0.387 | -0.012 |



Figure 3. - Factorial correspondence analysis of genotypes (255 individuals; 12 loci) from all the species belonging to the phylogenetic cluster "Central Ayamaru Plateau" and to M. arfakensis. Projection on axis 2 and axis 4 segregating the new species M. klasioensis, M. longispina and M. susii with other species.


Figure 4. - Factorial correspondence analysis of genotypes (200 individuals; 12 loci) from all valid species belonging to cluster "Southern Ayamaru Plateau", to cluster "Central Ayamaru Plateau" and to $M$. arfakensis. Projection on axis 1 and axis 3 segregating M. sembrae sp. nov. with other species.

Table IV. - Pairwise FST values between species that form the cluster "Central Ayamaru Plateau" and M. arfakensis.

| FST | M. klasioensis | M.ajamaruensis | M.fasinensis | M.susii | M. arfakensis | M. boesemani | M. ericrobertsi |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| M. longispina | 0.407 | 0.191 | 0.354 | 0.254 | 0.374 | 0.171 | 0.338 |
| M. klasioensis | - | 0.398 | 0.633 | 0.418 | 0.597 | 0.361 | 0.707 |
| M.ajamaruensis | - | - | 0.415 | 0.348 | 0.427 | 0.072 | 0.418 |
| M.fasinensis | - | - | - | 0.587 | 0.595 | 0.412 | 0.231 |
| M.susii | - | - | - | - | 0.512 | 0.322 | 0.601 |
| M.arfakensis | - | - | - | - | 0.432 | 0.647 |  |
| M.boesemani | - | - | - | - | 0.393 |  |  |

Table V. - Pairwise FST values between species composing the cluster "Southern Ayamaru Plateau", all valid species from "Central Ayamaru Plateau" cluster, and M. arfakensis.

| FST | M.ajamaruensis | M.arfakensis | M.boesemani | M. sembrae | M.fasinensis | M.ericrobertsi |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| M. multiradiata | 0.238 | 0.415 | 0.198 | 0.355 | 0.498 | 0.488 |
| M. ajamaruensis | - | 0.427 | 0.072 | 0.288 | 0.415 | 0.418 |
| M. arfakensis | - | - | 0.432 | 0.484 | 0.596 | 0.647 |
| M.boesemani | - | - | - | 0.262 | 0.412 | 0.393 |
| M. sembrae | - | - | - | 0.517 | 0.524 |  |
| M.fasinensis | - | - | - | - | 0.231 |  |

entiated from M. arfakensis and from all other species (i.e. M. ajamaruensis, M. boesemani, M. ericrobertsi, M. fasinensis) belonging to the cluster "Central Ayamaru Plateau". All pairwise FST values computed between these species were highly significant ( $\mathrm{p}<0.001$ ) and are given in table V .
(3) The FCA in figure 5 shows that the new species M. manibuii is genetically separated from M. arfakensis, M. multiradiata, M. fredericki and from all the species distributed in the Raja Ampat islands (i.e. M. batanta, M. misoolensis, M. salawati). In addition, the FCA presented in figure 6 indicates that $M$. manibuii is genetically separated from all the species composing the cluster "Central Ayamaru Plateau".
(4) The FCA obtained from the genotypes of the five new species (Fig. 7) confirms that M. klasioensis, M. longispina, M. manibuii, M. sembrae and M. susii are genetically differentiated from each other and therefore constitute reproductively isolated entities.
(5) The three new species $M$. naramasae, $M$. rumberponensis and M. sikuensis are genetically differentiated from each other, as well as from the remaining species M. angfa and M. parva that compose the "Birds Neck" cluster (Fig. 8). All pairwise FST values show highly significant genetic divergence ( $\mathrm{p}<0.001$ ) among these species (Tab. VI). Pairwise FST values between the three new species are comprised between 0.356 and 0.714 . Interestingly, M. angfa and


Figure 5. - Factorial correspondence analysis of genotypes (186 individuals; 12 loci) from M. manibuii, M. arfakensis, M. multiradiata, M. fredericki, M. batanta, M. misoolensis, M. salawati. Projection on axis 3 and axis 4 segregating M. manibuii sp. nov. with other species.


Figure 7. - Factorial correspondence analysis of genotypes (164 individuals; 12 loci) from the five new species belonging to COI "Northern Birds Head" clade. Projection on axis 1 and axis 2 segregating the five new species $M$. klasioensis, M. longispina, M. manibuii, M. sembrae and M. susii.


Figure 6. - Factorial correspondence analysis of genotypes (139 individuals; 12 loci) from M. manibuii and all valid species belonging to the cluster "Central Ayamaru Plateau". Projection on axis 1 and axis 2 segregating $M$. manibuii sp. nov. with other species.


Figure 8. - Factorial correspondence analysis of genotypes (164 individuals; 12 loci) from all the species belonging to cluster "Birds Neck". Projection on axis 1 and axis 2 segregating the three new species M. naramasae, M. rumberponensis and M. sikuensis with other species composing this cluster.

Table VI. - Pairwise FST values between species composing the cluster "Birds Neck"

| FST | M.parva | M.angfa | M. rumberponensis | M.naramasae |
| :--- | :---: | :---: | :---: | :---: |
| M. sikuensis | 0.630 | 0.739 | 0.714 | 0.485 |
| M. parva | - | 0.460 | 0.545 | 0.245 |
| M.angfa | - | - | 0.707 | 0.401 |
| M. rumberponensis | - | - | - | 0.356 |

M. parva, the two species that share the same COI haplotype, displayed a significant pairwise FST value of 0.460. The locus Mb_tri1 revealed diagnostic for these two species, with a fixed allele (104) for M. angfa and two alleles [110 (75\%) and 113 (25\%)] for M. parva.

The microsatellite data therefore demonstrate that the
eight new species represent distinct genetic entities, since they differ from each other and also from closely related valid species. Because no intermediate genotypes and no overlap were observed between these taxonomic entities, we therefore consider that these species represent new species whose morphological descriptions are given below.

## SYSTEMATICS

## Melanotaenia klasioensis, sp. nov. Kadarusman, Hadiaty \& Pouyaud

 (Figs 9, 10; Tab. VII)
## Type material

Holotype. - MZB 20034, male, $83.9 \mathrm{~mm} \mathrm{SL}, 1^{\circ} 09.005$ 'S, $131^{\circ} 51.927^{\prime}$ E, a bridge on Klasio Creek near Malabolo village and on the road from Sorong to Ajamaru (Km 110), at the frontier post between Sorong and Sorong Selatan Regencies, Papua Barat Province, Indonesia. Sumanta, Ajambua, Kadarusman, Slembrouck \& Pouyaud, 24 Apr. 2008.

Paratypes. - MZB 22151, 4 specimens (77.4-91.5 mm SL), same data as for holotype

## Diagnosis

Melanotaenia klasioensis is distinguished from all its congeners in the Birds Head region by the following combination of characters: dorsal rays V to $\mathrm{VI}+\mathrm{I}, 14$ to 15 ; anal rays $I, 22$ to 24 ; lateral scales 36 to 37 ; transverse scales 10 ; predorsal scales 17 to 18 ; cheek scales 16 to 17 ; total gillrakers on first arch 18 to 20; a large interorbital width, 8.6-9.2\% of SL; a large body width, 14.2-15.8\% of SL; a short preanal length, 47.7-49.4\% of SL; a long pectoral fin length, 20.1$20.7 \%$ of SL; a long pelvic fin length, 19.4-22.6\% of SL; $11.1 \%$ of SL; a prominent red margin stripe on dorsal fins;

Table VII. - Measurements taken on the holotype and four paratypes of Melanotaenia klasioensis sp. nov.

|  | Holotype | Paratypes |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\mathrm{SL}(\mathrm{mm})$ | 83.9 |  |  | 77.2-9 |  |  |
| in \% standard length |  | n | Min | Max | Mean | SD |
| Head length | 25.9 | 4 | 24.5 | 25.3 | 24.8 | 0.3 |
| Snout length | 9.1 | 4 | 8.6 | 9.1 | 8.9 | 0.2 |
| Interorbital width | 9.2 | 4 | 8.6 | 8.9 | 8.7 | 0.1 |
| Eye diameter | 6.9 | 4 | 6.5 | 7.4 | 6.9 | 0.4 |
| Body depth | 37.7 | 4 | 30.4 | 35.2 | 33.1 | 2.1 |
| Body width | 14.5 | 4 | 14.2 | 15.8 | 14.9 | 0.7 |
| Caudal peduncle depth | 11.4 | 4 | 10.2 | 10.7 | 10.5 | 0.2 |
| Caudal peduncle length | 14.9 | 4 | 14.7 | 15.8 | 15.2 | 0.5 |
| Predorsal length | 49.4 | 4 | 49.6 | 50.2 | 49.9 | 0.3 |
| Prepelvic length | 39.3 | 4 | 37.2 | 37.6 | 37.4 | 0.2 |
| Preanal length | 49.4 | 4 | 47.7 | 48.4 | 48.2 | 0.3 |
| Pectoral fin length | 20.2 | 4 | 20.1 | 20.7 | 20.3 | 0.3 |
| Pelvic fin length | 22.6 | 4 | 19.4 | 19.8 | 19.6 | 0.2 |
| Spine length of first dorsal fin | 10.4 | 4 | 10.4 | 10.9 | 10.7 | 0.2 |
| Spine length of second dorsal fin | 9.1 | 4 | 9.8 | 11.1 | 10.5 | 0.6 |
| Spine length of anal fin | 7.1 | 4 | 7.5 | 7.9 | 7.7 | 0.2 |
| Dorsal fin base length | 39.5 | 4 | 38.7 | 40.3 | 39.4 | 0.8 |
| Second dorsal fin base length | 26.2 | 4 | 24.5 | 26.1 | 25.3 | 0.8 |
| Anal fin base length | 45.0 | 4 | 39.1 | 40.7 | 39.9 | 0.7 |

dorsal fin origin vertically projected behind anal fin origin between $1^{\text {st }}$ and $3^{\text {rd }}$ anal soft ray.

## Description

Counts and proportions that appear in parentheses refer to the range for paratypes (based on 4 specimens, 77.2 91.5 mm SL ) if different from the holotype. Morphometric data are given in table VII.

Dorsal rays V + I,14 (V-VI + I,14-15); anal rays I,24 (I,22-24); pectoral rays 14 (13-15); pelvic rays I,5; lateral scales 37 (36-37); transverse scales 10 ; predorsal scales 17 (17-18); cheek scales 17 (16-17); total gillrakers on first arch 18 (18-20); jaws equal, oblique, premaxilla with an abrupt bend between the anterior horizontal portion and lateral part; maxilla ends below anterior edge of eye; lips thin; teeth conical with slightly curved tips; teeth at front of upper jaw in about 5-6 irregular rows, reduced to 1-2 rows posteriorly; teeth at front of lower jaws in about 7-8 irregular rows, reduced to $1-2$ rows posteriorly; small conical teeth on vomer and palatines

Scale of body large, cycloid, crenulated, arranged in regular horizontal rows; predorsal scales extending to posterior margin of interorbital; 3 rows of preopercle scales. First dorsal fin origin projected behind anal fin origin, between $1^{\text {st }}$ and $3^{\text {rd }}$ anal soft ray; tip of first dorsal fin reaching base of spine to $2^{\text {nd }}$ soft ray of second dorsal fin; tip of second dorsal fin reaching half to $3 / 4$ of caudal peduncle in females and $3 / 4$ to hypural junction in males; tip of anal fin reaching $1 / 3$ to half of caudal peduncle in females and half to $3 / 4$ of caudal peduncle in males; pelvic fin tips reaching base of $3^{\text {rd }}$ to $6^{\text {th }}$ anal soft ray in males and $2^{\text {nd }}$ to $4^{\text {th }}$ in females; caudal fin moderately forked

Colour of freshly collected male specimens: overal body dark mauve; brown dorsally; lateral flanks mauve on upper half and yellowish on lower half; belly whitish; a continuous dark green midlateral stripe of 1 scale wide ( 2 scales on caudal peduncle) and sometimes interrupted on anterior part by 1-3 vertical bars (never exceeding 5 scales in length); pectoral fin translucent with black rays; pelvic fin yellow; anal fin overall dark with black rays separated by red hues; dorsal fins black with a marked white or red margin. Colour pattern of females is less vivid: overall body yellowish; a faint dark green midlateral stripe of 1 scale wide; no vertical bars; anal fin overall brown with green rays; dorsal fins grey with a narrow pink margin stripe.

Sexual dimorphism: Males are deeper bodied than females ( $35.2-37.7$ vs 30.4-34.2\% SL) and have second dorsal and anal fins more elongated posteriorly.

## Comparisons

The new species M. klasioensis is part of the phylogenetic "Northern Birds Head" group and belongs
to the cluster "Central Ayamaru Plateau", together with the valid species M.fasinensis, M. ericrobertsi, M. boesemani and M. ajamaruensis (Fig. 2). Melanotaenia klasioensis is genetically close to M.fasinensis on the COI phylogeny but is easily distinguishable from the latter by the variability of analysed microsatellite loci (Figs 3, 7).

Melanotaenia klasioensis differs from M. fasinensis by more transverse scales ( $10 v s 9$ ), fewer anal soft rays (22-24 vs 24-27), a greater interorbital width (8.6-9.2 vs 7.6-8.2\% SL), a greater body width (14.2-15.8 vs 12.1-14.2\% SL), a longer pectoral fin length (20.1-20.7 vs 17.4-19.9\% SL) and fewer lateral scales (36-37 vs 37-39.

Following Allen et al. (2014b), Melanotaenia klasioensis can be distinguished from M. ericrobertsi by fewer lateral scales ( $36-37$ vs 37-39), more cheek scales (16-17 vs 12-16), the position of the first dorsal fin origin compared to the anal fin origin (dorsal fin origin behind anal origin, between $1^{\text {st }}$ and $3^{\text {rd }}$ anal soft ray $v s$ dorsal fin origin about equal with anal fin origin).

Melanotaenia klasioensis differs from M. ajamaruensis and $M$. boesemani by more transverse scales ( 10 vs 7-8), more predorsal scales (17-18 vs 15-16), a shorter preanal length (47.7-49.4 vs 49.4-57.6\% SL), a longer pectoral fin length (20.1-20.7 vs 16.9-19.9\% SL), a longer pelvic fin length (19.4-22.6 vs 13.8-18.2\% SL).

Melanotaenia klasioensis differs from M. laticlavia by fewer soft anal rays (22-24 vs 24-26), more gillrakers (1820 vs 16-17), the position of the first dorsal fin origin compared to the anal fin origin (dorsal fin origin behind anal origin, between $1^{\text {st }}$ and $3^{\text {rd }}$ anal soft ray $v s$ dorsal fin origin about level with anal fin origin). Melanotaenia laticlavia belongs to the "Southern Birds Head" phylogenetic group following Allen et al. (2014b) and is genetically distant from the species belonging to the "Northern Birds Head" group. Nevertheless, this species is geographically close to the species inhabiting the Central Ayamaru Plateau, as it is distributed in the upper reaches of the Kamundan River system lying just on the eastern side of the Ayamaru Plateau (Fig. 1).

## Distribution and habitat

The new species is currently known only from Klasio Creek, a karst resurgence of less than 5 m width with a course of a few kilometres before disappearing in a subterranean outlet probably connected to the underground course of the Fasin River (Fig. 1). The habitat in the vicinity of Malabolo village (Fig. 11) consists of a crystalline stream, relatively shallow (up to about 1 m ), and flowing over white sand and limestone boulders in secondary forest.

## Etymology

The species is named klasioensis, with reference to the creek name at the type locality.

## Melanotaenia longispina, sp. nov. Kadarusman, Avarre \& Pouyaud

(Figs 12, 13; Tab. VIII)

## Type material

Holotype. - MZB 22152, female, 78.7 mm SL, $1^{\circ} 04.160$ 'S, $131^{\circ} 45.595$ ' E , a bridge on Klahfot R., near Saluk village, Km 92 on road from Sorong to Teminabuan Sorong Regency, Papua Barat Province, Indonesia. Sumanta, Krenak, Kadarusman, Paradis \& Pouyaud, 24 Apr. 2008.

Paratypes. - MZB 22153, 3 specimens ( $61.3-73.3 \mathrm{~mm}$ SL), same data as for holotype; MZB 22154, 5 specimens ( $71.1-86.9 \mathrm{~mm}$ SL), collected at type locality by Sumanta, Kadarusman, Ajambua, Slembrouck \& Pouyaud, 19 May 2007.

## Diagnosis

Melanotaenia longispina is distinguished from all of its congeners in the Birds Head region by the following combination of characters: dorsal rays IV to VI + I, 13 to 14 ; anal rays I,23 to 26; lateral scales 37 to 40 ; transverse scales 10 ; predorsal scales 19 to 21 ; cheek scales 17 to 18 ; total gill-

Table VIII. - Measurements taken on the holotype and eight paratypes of Melanotaenia longispina sp. nov.

|  | Holotype | Paratypes |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| SL (mm) | 78.7 | 61.3-86.9 |  |  |  |  |
| in \% standard length |  | n | Min | Max | Mean | SD |
| Head length | 24.7 | 8 | 24.1 | 25.2 | 24.5 | 0.4 |
| Snout length | 9.1 | 7 | 8.6 | 9.0 | 8.8 | 0.1 |
| Interorbital width | 7.9 | 8 | 7.8 | 8.2 | 8.0 | 0.2 |
| Eye diameter | 7.8 | 7 | 7.5 | 8.8 | 8.0 | 0.5 |
| Body depth | 30.4 | 8 | 26.2 | 33.9 | 31.2 | 2.7 |
| Body width | 11.5 | 8 | 11.7 | 13.2 | 12.2 | 0.6 |
| Caudal peduncle depth | 10.0 | 8 | 9.2 | 10.7 | 10.0 | 0.5 |
| Caudal peduncle length | 16.2 | 7 | 15.4 | 16.7 | 16.1 | 0.5 |
| Predorsal length | 51.7 | 8 | 50.2 | 51.8 | 51.1 | 0.6 |
| Prepelvic length | 36.7 | 8 | 35.5 | 36.7 | 36.2 | 0.5 |
| Preanal length | 48.3 | 8 | 46.0 | 48.2 | 47.3 | 0.8 |
| Pectoral fin length | 20.5 | 3 | 18.3 | 18.5 | 18.4 | 0.1 |
| Pelvic fin length | 19.9 | 3 | 19.6 | 20.4 | 20.1 | 0.4 |
| Spine length of first dorsal fin | 15.3 | 6 | 13.1 | 14.8 | 13.6 | 0.6 |
| Spine length of second dorsal fin | 15.7 | 7 | 12.4 | 15.5 | 13.7 | 1.4 |
| Spine length of anal fin | 11.3 | 5 | 10.1 | 10.4 | 10.3 | 0.1 |
| Dorsal fin base length | 33.4 | 8 | 34.1 | 36.5 | 35.5 | 1.0 |
| Second dorsal fin base length | 20.2 | 8 | 20.5 | 22.6 | 21.9 | 0.8 |
| Anal fin base length | 39.8 | 8 | 38.8 | 43.2 | 41.1 | 1.6 |



Figure 9. - Melanotaenia klasioensis, a male, 79 mm SL, Malabolo, Sorong Selatan, West Papua, Indonesia. Figure 10. - Melanotaenia klasioensis, a female, 71 mm SL, Malabolo, Sorong Selatan, West Papua, Indonesia
Figure 11. - Type locality of Melanotaenia klasioensis, Klasio Creek, near Malabolo, Sorong Selatan, West Papua, Indonesia.
Figure 12. - Melanotaenia longispina, MZB 22152 (holotype), female, 78.7 mm SL, near Saluk, Sorong Regency, West Papua, Indonesia.
Figure 13. - Melanotaenia longispina, MZB 22153 (paratype), male, 73.3 mm SL, same data as for holotype.
Figure 14. - Type locality of Melanotaenia longispina, Klahfot River, near Saluk, Sorong Regency, West Papua, Indonesia.
Figure 15. - Melanotaenia susii, MZB 22155 (holotype), male, 114.1 mm SL, Susi Creek, Sorong Selatan, West Papua, Indonesia.
Figure 16. - Melanotaenia susii, MZB 22156 (paratype), female, 111.7 mm SL, same data as for holotype.
rakers on first arch 19; a short head length, 24.1-25.2\% of SL; a thin interorbital width, 7.8-8.2\% of SL; a long predorsal length, 50.2-51.8\% of SL; a long pelvic fin length, 19.6$20.4 \%$ of SL; a long spine length on first dorsal fin, 13.1$15.3 \%$ of SL; relatively elongate second dorsal fin spine, 12.4-15.7\% of SL; elongate anal fin spine, 10.1-11.3\% of SL; a short dorsal fin base, 33.4-36.5\% of SL; a short second dorsal fin base, 20.2-22.6\% of SL; no stripe on margin of dorsal fins; dorsal fin origin vertically projected behind anal origin, between $1^{\text {st }}$ and $3^{\text {rd }}$ anal soft ray.

## Description

Counts and proportions that appear in parentheses refer to the range for paratypes (based on 8 specimens, 61.386.9 mm SL ) if different from the holotype. Morphometric data are given in table VIII.

Dorsal rays V + I, 13 (IV-VI + I,13-14); anal rays I,23 (I,23-26); pectoral rays 15 ; pelvic rays I,5; lateral scales 38 (37-40); transverse scales 10 ; predorsal scales 20 (19-21); cheek scales 18 (17-18); total gillrakers on first arch 19; snout pointed and rounded dorsally; jaws equal, oblique, premaxilla with an abrupt bend between the anterior horizontal portion and lateral part; maxilla ends below anterior edge of eye; lips thin; teeth conical with slightly curved tips; teeth at front of upper jaw in about 4-5 irregular rows, reduced to 1-2 rows posteriorly; teeth at front of lower jaws in about 7-9 irregular rows, reduced to $1-2$ rows posteriorly; small conical teeth on vomer and palatines.

Scale of body cycloid, large, with crenulated margin and arranged in regular horizontal rows; predorsal scales extending to posterior half of interorbital; preopercle scales arranged in 3 rows. First dorsal fin origin vertically projected behind anal fin origin, between the $1^{\text {st }}$ and $3^{\text {rd }}$ anal soft ray; tip of first spine of first dorsal fin reaching base of first spine of second dorsal fin; tip of second dorsal fin reaching half of caudal peduncle; pelvic fin tips reaching base of $1^{\text {st }}$ to $5^{\text {th }}$ anal soft ray; soft dorsal and anal fins triangular in outline; caudal fin moderately forked.

Colour of freshly collected male specimens: Overall body pale with pinkish and greenish reflections; series of 7-8 narrow and discrete yellowish stripes between each horizontal scale row; pale gray to bluish dorsally and whitish to pale pink ventrally; a midlateral stripe faint or absent in middle part of the body and sometimes only visible directly behind pectoral fin base and at the extremity of the caudal peduncle; pectoral fin translucent; remaining fins pink in males and whitish to translucent in females. No margin stripe on dorsal and anal fins. Overall colour of females is paler than males with darker narrower stripes between each horizontal scale row.

Sexual dimorphism: although some overlap is apparent, males are usually deeper bodied than females (28.7-33.9 vs $26.2-30.4 \% \mathrm{SL}$ ).

## Comparisons

Melanotaenia longispina belongs to the "Central Ayamaru Plateau" group of species together with M. fasinensis, M. ericrobertsi, M. boesemani and M. ajamaruensis and the new species $M$. klasioensis. (Fig. 2). The new species differs from all of these species by the genetic polymorphism assessed from the 12 microsatellite loci (Figs 3, 7).

Melanotaenia longispina is easily distinguishable from all of these species by its lack of markings on the dorsal fin (present in other species).

In addition, the new species differs from M.ajamaruensis, M. boesemani and M. fasinensis by more transverse scales (10 vs 7-9) , a longer pelvic fin length (19.6-20.4 vs 13.8-19.5\% SL), a longer spine length on first dorsal fin (13.1-15.3 vs 8.6-12.7\% SL), a longer spine length on second dorsal fin (12.4-15.7 vs 7-11.6\% SL), a longer spine length on anal fin (10.1-11.3 vs 6.6-9.7\% SL). The new species differs from M. ajamaruensis and M.fasinensis by a longer predorsal length (50.2-51.8 vs 45.3-50.0\% SL), a shorter dorsal fin base length ( $33.4-36.5 \mathrm{vs} 38.6-43.5 \% \mathrm{SL}$ ), and a shorter second dorsal fin base length (20.2-22.6 vs 24.1-29.5\% SL). The new species differs from $M$. boesemani by a shorter head length (24.1-25.2 vs $25.5-28.5 \% \mathrm{SL}$ ), a narrow interorbital width (7.8-8.2 vs 8.3-9.5\% SL), and a slender body depth (26.2-33.9 vs 34.0-44.7\% SL).

Following Allen et al. (2014b), Melanotaenia longispina is distinguishable from M. ericrobertsi and M. laticlavia by more predorsal scales (19-21 vs 16-19), by the position of the first dorsal fin origin compared to the anal fin origin (dorsal fin origin behind anal origin, between $1^{\text {st }}$ and $3^{\text {rd }}$ anal soft ray $v s$ dorsal fin origin about equal with anal fin origin). The new species differs from $M$. laticlavia by fewer soft dorsal rays ( $13-14$ vs 14-17), more lateral scales ( $37-40$ vs 36-37) and more gillrakers ( 19 vs 16-17). It differs from M. ericrobertsi by more cheek scales (17-18 vs 12-16).

Melanotaenia longispina differs from M. klasioensis sp. nov. by a greater eye diameter (7.5-8.8 vs 6.5-7.4\% SL), a shorter dorsal fin base length (33.4-36.5 vs 38.7-40.3\% SL), a shorter second dorsal fin base length (20.2-22.6 vs 24.5$26.2 \%$ SL), and by longer spines respectively on first dorsal fin (13.1-15.3 vs 10.4-10.9\% SL), on second dorsal fin (12.415.7 vs $9.1-11.1 \% \mathrm{SL}$ ), on anal fin (10.1-11.3 vs 7.1-7.9\% SL).

## Distribution and habitat

The new species is currently known from the Klahfot River. This river ranged from about 10 to 15 m in width at the type locality (Fig. 14) and was flowing through secondary rainforest habitat over gravel and sand substrate with no aquatic vegetation and turbid water. The river is part of the middle course of the Kladuk River system by underground connection.

Physical water parameters at the type locality on May 2007 were: water temperature $28.0^{\circ} \mathrm{C}$; pH 7.35 ; conductivity $368 \mu \mathrm{~S}$. Chemical parameters (in mg/L): K: 0.1; Ca: 32.62; Mg: 2.55; Na: 0.29; Mn: 0.0; PO4: 0.1; SO4: 0.61; HCO3: 138; CO3: 0.0; Cl: 2.07; Cd: 0.0; Ni: 0.0.

## Etymology

The species is named longispina, with reference from the Latin longus and spinus: named for the long spines on dorsal and anal fins.

## Melanotaenia susii, sp. nov. Kadarusman, Hubert \& Pouyaud

(Figs 15, 16; Tab. IX)

## Type material

Holotype. - MZB 22155, male, 114.1 mm SL, $1^{\circ} 09.114^{\prime} \mathrm{S}, 131^{\circ} 57.665^{\prime} \mathrm{E}$, a bridge on Susi Creek, on the road from Sorong to Ajamaru, 12 km after the frontier post between Sorong and Sorong Selatan Regencies, Papua Barat Province, Indonesia. Sumanta, Ajambua, Kadarusman Slembrouck \& Pouyaud, 24 Apr. 2008

Paratypes. - MZB 22156, 4 specimens ( $94.5-111.7 \mathrm{~mm}$ SL), same data as for holotype; MZB 22157, 11 specimens (74.1-122.7 mm SL), collected at type locality by Kadarusman, Sudarto, Paradis \& Pouyaud, 24 May 2007.

Table IX. - Measurements taken on the holotype and 15 paratypes of Melanotaenia susii sp. nov.

|  | Holotype | Paratypes |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\mathrm{SL}(\mathrm{mm})$ | 114.1 |  |  | 4.1-1 | 2.7 |  |
| in \% standard length |  | n | Min | Max | Mean | SD |
| Head length | 25.3 | 15 | 23.7 | 25.5 | 24.6 | 0.6 |
| Snout length | 10.2 | 15 | 9.2 | 9.9 | 9.4 | 0.2 |
| Interorbital width | 8.4 | 15 | 8.0 | 8.4 | 8.2 | 0.2 |
| Eye diameter | 6.6 | 15 | 6.4 | 7.3 | 6.8 | 0.3 |
| Body depth | 39.9 | 13 | 30.7 | 39.1 | 34.2 | 2.7 |
| Body width | 13.8 | 13 | 12.7 | 14.1 | 13.2 | 0.4 |
| Caudal peduncle depth | 10.8 | 15 | 9.8 | 10.8 | 10.4 | 0.4 |
| Caudal peduncle length | 14.8 | 14 | 13.9 | 15.3 | 14.6 | 0.5 |
| Predorsal length | 50.9 | 15 | 50.4 | 52.2 | 51.3 | 0.6 |
| Prepelvic length | 38.5 | 15 | 36.3 | 38.3 | 37.2 | 0.7 |
| Preanal length | 49.0 | 15 | 47.4 | 49.3 | 48.3 | 0.6 |
| Pectoral fin length | 18.3 | 15 | 17.6 | 19.0 | 18.3 | 0.5 |
| Pelvic fin length | 21.3 | 12 | 19.8 | 24.4 | 21.3 | 1.4 |
| Spine length of first dorsal fin | 12.4 | 13 | 11.4 | 12.4 | 11.8 | 0.4 |
| Spine length of second dorsal fin |  | 14 | 8.2 | 11.6 | 9.4 | 1.0 |
| Spine length of anal fin | 8.8 | 13 | 7.6 | 9.7 | 8.5 | 0.7 |
| Dorsal fin base length | 38.6 | 15 | 37.2 | 39.0 | 38.1 | 0.6 |
| Second dorsal fin base length | 25.7 | 15 | 23.9 | 26.6 | 25.3 | 0.9 |
| Anal fin base length | 44.6 | 15 | 41.1 | 45.6 | 43.1 | 1.4 |

## Diagnosis

Melanotaenia susii is distinguished from all of its congeners in the Birds Head region by: dorsal rays IV to VI + I, 13 to 16 ; anal rays I, 23 to 27 ; lateral scales 38 to 39 ; transverse scales 10 to 11 ; predorsal scales 17 to 20 ; cheek scales 16 to 20; total gillrakers on first arch 19; a compressed body with a long snout length, 9.2-10.2\% of SL; a thin interorbital width, 8.0-8.4\% of SL; a long predorsal length, $50.4-52.2 \%$ of SL; a short pectoral fin length, 17.6-19.0\% of SL; a long pelvic fin length, 19.8-24.4\% of SL; a long spine length on first dorsal fin, 11.4-12.4\% of SL; a moderately long dorsal fin base length, 37.2-39.0\% of SL; a long anal fin base length, 41.1$45.6 \%$ of SL; a marked red margin stripe on dorsal fins; 2-5 vertical bars extending across the entire body depth; dorsal fin origin vertically projected behind anal origin, between $3^{\text {rd }}$ and $5^{\text {th }}$ anal soft ray.

## Description

Counts and proportions that appear in parentheses refer to the range for paratypes (based on 15 specimens, 74.1122.7 mm SL ) if different from the holotype. Morphometric data are given in table IX

Dorsal rays V + I,15 (IV-VI + I,13-16); anal rays I,27 (I,23-27); pectoral rays 14 (13-15); pelvic rays I,5; lateral scales 39 (38-39); transverse scales 10 (10-11); predorsal scales 19 (17-20); cheek scales 16 (16-20); total gillrakers on first arch 19; jaws equal, oblique, premaxilla with an abrupt bend between the anterior horizontal portion and lateral part; maxilla ends below anterior edge of eye; lips thin; teeth conical with slightly curved tips; teeth at front of upper jaw in about 6-7 irregular rows, reduced to 2 rows posteriorly; teeth at front of lower jaws in about 9-11 irregular rows, reduced to 2 rows posteriorly; small conical teeth on vomer and palatines.

Scale of body large, cycloid, crenulated, arranged in regular horizontal rows; predorsal scales extending to posterior margin of interorbital; 3 rows of preopercle scales. First dorsal fin origin projected behind anal origin, between $3^{\text {rd }}$ and $5^{\text {th }}$ anal soft ray; tip of first dorsal fin reaching base of $3^{\text {rd }}$ to $5^{\text {th }}$ soft ray of second dorsal fin; tip of second dorsal fin reaching $3 / 4$ of caudal peduncle in females and $3 / 4$ to hypural junction in males; tip of anal fin reaching ${ }^{1 / 3}$ to half of caudal peduncle in females and half to $3 / 4$ of caudal peduncle in males; pelvic fin tips reaching base of $3^{\text {rd }}$ to $7^{\text {th }}$ anal soft ray; caudal fin moderately forked.

Colour of freshly collected male specimens: variable from green olive to intense black dorsally; lateral flanks with mauve reflections on upper half and reddish on lower half; a discontinuous midlateral dark green olive stripe with 1 scale row in middle part of body and 2 scale rows on caudal peduncle; 2-5 dark olive green vertical bars on anterior body region with


Figure 17. - Type locality of Melanotaenia susii, Susi Creek, Sorong Selatan, West Papua, Indonesia.
Figure 18. - Melanotaenia sembrae, MZB 22158 (holotype), male, 87.3 mm SL, Sembra River near Teminabuan, Sorong Selatan, West Papua, Indonesia.
Figure 19. - Melanotaenia sembrae, a female, 85 mm SL, same data as for holotype.
Figure 20. - Melanotaenia manibuii, MZB 22166 (holotype), male, 103.7 mm SL, Tisbo River near Bintuni, West Papua, Indonesia.
Figure 21. - Melanotaenia naramasae, MZB 22160 (holotype), male, 99.1 mm SL, Naramasa River, Birds Neck Isthmus
Figure 22. - Melanotaenia naramasae, MZB 22161 (paratype), female, 75.9 mm SL, same data as for holotype.
Figure 23. - Type locality of Melanotaenia naramasae, Naramasa River, Birds Neck, West Papua, Indonesia.

1-6 scales width and extending from dorsal to ventral edges; pectoral fin translucent with black rays; pelvic fin reddish black; anal fin overall dark with blue rays and with a reddish
posterior tip; dorsal fins black with a marked red margin.
Colour pattern of females similar, but less vivid than males.
Sexual dimorphism: males are slightly deeper bodied
than females (33.6-39.9 vs 31.0-37.0\% SL) and have second dorsal and anal fins more elongated posteriorly.

## Comparisons

Melanotaenia susii belongs to the "Central Ayamaru Plateau" group of species, together with M. fasinensis, M. ericrobertsi, M. boesemani, M. ajamaruensis, M. klasioensis sp. nov. and M. longispina sp. nov. (Fig. 2). The new species differs from all of these species by the genetic polymorphism assessed from the 12 microsatellite loci (Figs 3, 7).

Melanotaenia susii differs from M. fasinensis by the coloration pattern (presence of 2-5 vertical bars on anterior body region $v s$ absent), more transversal scales (10-11 vs 9), a longer predorsal length (50.4-52.2 vs 48.1-49.8\% SL), a longer pelvic fin length (19.8-24.4 vs 17.0-19.5\% SL) and a shorter dorsal fin base length (37.2-39.0 vs 39.0-42.2\% SL).

The new species differs from M. ajamaruensis and M. boesemani by a longer snout length (9.2-10.2 vs 7.2-8.7\% SL), a longer pelvic fin length (19.8-24.4 vs 13.8-18.2\% SL), a longer anal fin base length (41.1-45.6 vs 32.2-40.4\% SL), more transverse scales (10-11 vs 7-8), more lateral scales (38-39 vs 33-37) and more predorsal scales (17-20 vs 15-16).

Following Allen et al. (2014b), Melanotaenia susii can be distinguished from M. ericrobertsi and M. laticlavia by the position of the first dorsal fin origin compared to the anal fin origin (dorsal fin origin behind anal origin, between $3^{\text {rd }}$ and $5^{\text {th }}$ anal soft ray $v s$ dorsal fin origin about equal with anal fin origin), and the pattern of body coloration (presence of vertical bars on anterior body region vs absent). Melanotaenia susii differs from $M$. laticlavia by more lateral scales (38-39 vs 36-37) and more gillrakers (19 vs 16-17). It differs from M. ericrobertsi by more cheek scales (16-20 vs 12-16).

Melanotaenia susii differs from M. longispina sp. nov. by the presence of a dorsal margin stripe ( $v s$ absent), shorter spines on first dorsal, second dorsal and anal fins (11.4-12.4 vs 13.1-15.3, 8.2-11.6 vs 12.4-15.7, 7.6-9.7 vs 10.1-11.3\% SL, respectively), a longer dorsal fin base length (37.2-39.0 vs $33.4-36.5 \% \mathrm{SL}$ ), and a longer second dorsal fin base length (23.9-26.6 vs 20.2-22.6\% SL).

Melanotaenia susii differs from M. klasioensis sp. nov. by more lateral scales (38-39 vs 36-37), a longer snout length (9.2-10.2 vs 8.6-9.1\% SL), a narrower interorbital width (8.0-8.4 vs 8.6-9.2\% SL), a narrower body width (12.7-14.1 vs $14.2-15.8 \% \mathrm{SL}$ ), a longer predorsal length (50.4-52.2 vs 49.4-50.2\% SL), a shorter pectoral fin length (17.6-19.0 vs 20.1-20.7\% SL), and a longer spine length on first dorsal fin (11.4-12.4 vs 10.4-10.9\% SL).

## Distribution and habitat

The new species is currently known from Susi Creek, a karst resurgence of less than 3 m width with a course of a few kilometres before disappearing in a subterranean outlet
(Fig. 1). The habitat at the type locality (Fig. 17) consists of clear, shallow and slow flowing water. The creek flows over limestone boulder and muddy bottom with many dead tree branches and is bordered by dense forest.

Physical water parameters at the type locality on May 2007 were: water temperature $26.0^{\circ} \mathrm{C} ; \mathrm{pH} 7.7$; conductivity $330 \mu \mathrm{~S}$. Chemical parameters (in mg/L): K: 0.01; Ca: 45.70; Mg: 2.17; Na: 0.27; Mn: 0.00; PO4: 0.09; SO4: 0.49; HCO3: 181; CO3: 0.0; Cl: 2.07; Cd: 0.0; Ni: 0.03 .

## Etymology

The species is named susii, with reference to the creek name at the type locality.

## Melanotaenia sembrae, sp. nov. Kadarusman, Carman \& Pouyaud

 (Figs 18, 19; Tab. X)
## Type material

Holotype. - MZB 22158, male, $87.3 \mathrm{~mm} \mathrm{SL}, 1^{\circ} 24.667$ 'S, $131^{\circ} 59.231$ 'E, Sembra River near Teminabuan, Sorong Selatan Regency, Papua Barat Province, Indonesia. Sumanta, Ajambua, Kadarusman, Slembrouck \& Pouyaud, 23 Apr. 2008.

Paratypes. - MZB 22159, 9 specimens ( $69.5-101.7 \mathrm{~mm}$ SL), same data.

## Diagnosis

Melanotaenia sembrae is distinguished from all of its congeners in the Birds Head region by the following combination of characters: dorsal rays IV to $\mathrm{V}+\mathrm{I}, 12$ to 14 ; anal rays I, 22 to 24 ; lateral scales 36 to 37 ; transverse scales 10 ; predorsal scales 17 to 19 ; cheek scales 12 to 15 ; total gillrakers on first arch 17 to 18 ; a pointed head with a long snout length, $9.1-9.7 \%$ of SL; an intermediate interorbital width, $8.4-8.8 \%$ of SL; a compressed body with a long predorsal length, $51.1-53.2 \%$ of SL; a great caudal peduncle depth, 10.7-11.6\% of SL; a long pectoral fin length, 20.2-21.9\% of SL; a moderately short dorsal fin base length, 32.9-38.5; a marked red margin stripe on second dorsal fin; dorsal fin origin vertically projected behind anal origin, between $3^{\text {rd }}$ and $5^{\text {th }}$ anal soft ray.

## Description

Counts and proportions that appear in parentheses refer to the range for paratypes (based on 9 specimens, 69.5101.7 mm SL ) if different from the holotype. Morphometric data are given in table X .

Dorsal rays V + I,13 (IV-V + I,12-14); anal rays I,23 (I,22-24); pectoral rays 16 (14-16); pelvic rays I,5; lateral scales 36 (36-37); transverse scales 10; predorsal scales 19 (17-19); cheek scales 15 (12-14); total gillrakers on first
arch 18 (17-18); jaws equal, oblique, premaxilla with an abrupt bend between the anterior horizontal portion and lateral part; maxilla ends behind anterior edge of eye; lips thin; teeth conical with slightly curved tips; teeth at front of upper jaw in about 4-6 irregular rows, reduced to 1-2 rows posteriorly; teeth at front of lower jaws in about 6-8 irregular rows, reduced to $1-2$ rows posteriorly; small conical teeth on vomer and palatines.

Scale of body large, cycloid, crenulated, arranged in regular horizontal rows; predorsal scales extending to posterior margin of interorbital; 3 rows of preopercle scales. First dorsal fin origin projected behind anal origin, between $3^{\text {rd }}$ and $5^{\text {th }}$ anal soft ray; tip of first dorsal fin reaching base of $2^{\text {nd }}$ to $4^{\text {th }}$ soft ray of second dorsal fin in males and spine to $1^{\text {st }}$ soft ray in females; tip of second dorsal fin reaching half of caudal peduncle in females and $3 / 4$ in males; tip of anal fin reaching $1 / 3$ to half of caudal peduncle in females and half to $3 / 4$ of caudal peduncle in males; pelvic fin tips reaching base of $1^{\text {st }}$ to $4^{\text {th }}$ anal soft ray; caudal fin forked.

Colour of freshly collected male specimens: overall body green olive; posterior part of lateral flanks with 6-7 narrow orange-red stripes alternating with horizontal scale rows; a discontinuous midlateral stripe of 3-4 scales wide, varying from intense black to blue steel and marked on caudal peduncle and just behind pectoral fins; pectoral fin translucent; anal fin green olive with orange-red hues; remaining fins green olive with marked orange-red margin on second

Table X. - Measurements taken on the holotype and nine paratypes of Melanotaenia sembrae sp. nov.

|  | Holotype |  |  |  |  |  |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: |
| SL (mm) | Paratypes |  |  |  |  |  |
|  | 87.3 | $69.5-101.7$ |  |  |  |  |
| in \% standard length | 25.4 | 9 | 24.6 | 26.6 | 25.4 | 0.8 |
| Head length | 9.4 | 9 | 9.1 | 9.7 | 9.3 | 0.3 |
| Snout length | 8.4 | 9 | 8.5 | 8.8 | 8.6 | 0.1 |
| Interorbital width | 7.2 | 9 | 6.9 | 7.9 | 7.5 | 0.4 |
| Eye diameter | 34.6 | 9 | 31.2 | 37.2 | 33.7 | 2.2 |
| Body depth | 14.0 | 9 | 12.9 | 14.3 | 13.5 | 0.5 |
| Body width | 10.8 | 9 | 10.7 | 11.6 | 11.0 | 0.3 |
| Caudal peduncle depth | 14.8 | 9 | 14.0 | 16.2 | 14.8 | 0.8 |
| Caudal peduncle length | 52.0 | 9 | 51.1 | 53.2 | 52.0 | 0.7 |
| Predorsal length | 37.3 | 9 | 37.3 | 39.4 | 38.5 | 0.7 |
| Prepelvic length | 48.6 | 9 | 48.5 | 52.7 | 50.8 | 1.3 |
| Preanal length | 20.4 | 9 | 20.2 | 21.9 | 20.9 | 0.6 |
| Pectoral fin length | 17.2 | 9 | 15.9 | 21.3 | 19.1 | 1.9 |
| Pelvic fin length | 9.7 | 9 | 9.7 | 11.1 | 10.5 | 0.6 |
| Spine length of first dorsal fin | 8.3 | 9 | 7.7 | 9.3 | 8.6 | 0.5 |
| Spine length of second dorsal fin | 8.2 | 9 | 7.4 | 9.8 | 8.5 | 0.8 |
| Spine length of anal fin | 37.1 | 9 | 32.9 | 38.5 | 36.5 | 2.1 |
| Dorsal fin base length | 23.7 | 9 | 20.5 | 24.8 | 23.2 | 1.4 |
| Second dorsal fin base length | 43.6 | 9 | 35.3 | 43.1 | 39.8 | 2.3 |
| Anal fin base length |  |  |  |  |  |  |

dorsal fin. Overall colour of female paler, with absence of orange hues on the anal fin and between horizontal scales rows.

Sexual dimorphism: males are deeper bodied than females ( $31.5-37.2$ vs $31.2 \% \mathrm{SL}$ ) and have the two dorsals and anal fins more elongated posteriorly.

## Comparisons

Melanotaenia sembrae is genetically allied to M. multiradiata in the COI phylogeny (Fig. 2). Both species belong to the "Southern Ayamaru" species cluster which is the sister group of the "Central Ayamaru Plateau" cluster and of the monospecific cluster represented by M. arfakensis. The new species is easily distinguishable from all these species based on its microsatellite genotype diversity (Figs 4, 7).

Melanotaenia sembrae differs from M. multiradiata by the overall body form with a greater interorbital width (8.48.8 vs 7.7-8.3\% SL), a greater body depth (31.2-37.2 vs 27.1$30.5 \% \mathrm{SL}$ ), a greater body width (12.9-14.3 vs $11.2-12.6 \%$ SL), a greater caudal peduncle depth (10.7-11.6 vs 9.3-10.0\% SL), a longer predorsal length (51.1-53.2 vs 49.5-50.9\% SL), a longer pectoral fin length (20.2-21.9 vs 16.9-19.2\% SL), a shorter spine length of second dorsal fin (7.7-9.3 vs 10.0$13.6 \%$ SL), fewer anal fin rays ( $22-24$ vs 24-27), and fewer total gillrakers on first arch (17-18 vs 18-19)

Melanotaenia sembrae differs from M. arfakensis by a longer snout length (9.1-9.7 vs 7.6-8.2\% SL), a slender interorbital width (8.4-8.8 vs 8.8-9.3\% SL), a shorter and slender caudal peduncle (its length $14.0-16.2 \mathrm{vs} 16.5-$ 18.3 and depth 10.7-11.6 vs 12.0-13.2\% SL), a longer predorsal length (51.1-53.2 vs 47.1-49.6\% SL), more lateral scales ( $36-37$ vs 34-36), and more gillrakers (17-18 vs 15-16).

The new species differs from M. ajamaruensis and $M$. boesemani by more transverse scales ( 10 vs $7-8$ ), more predorsal scales (17-19 vs 15-16), a longer snout length (9.1-9.7 vs 7.2-8.7\% SL) and a longer pectoral fin length (20.2-21.9 vs 16.9-19.9\% SL).

Melanotaenia sembrae is distinguishable from M. fasinensis by more transverse scales (10-12 vs 9), fewer dorsal soft rays (12-14 vs 14-17), fewer anal rays (22-24 vs 24-27), fewer lateral scales ( $36-37$ vs 37-39) , a greater interorbital width (8.4-8.8 vs 7.6-8.2\% SL) , a longer predorsal length (51.1-53.2 vs 48.1-49.8\% SL), and several other characters (see morphometric data related to $M$. fasinensis in appendix).

Melanotaenia sembrae differs from M. ericrobertsi and M. laticlavia (see Allen et al., 2014b) by the position of the first dorsal fin origin compared to the anal fin origin (dorsal fin origin behind anal origin, between $3^{\text {rd }}$ and $5^{\text {th }}$ anal soft ray $v s$ dorsal fin origin about equal with anal fin origin). It also differs from M. ericrobertsi by fewer lateral scales ( 36.37 vs

37-39) and from M. laticlavia by fewer dorsal rays (12-14 vs 14-17), fewer anal rays (22-24 vs 24-26), more gillrakers (17-18 vs 16-17)

Melanotaenia sembrae differs from M. klasioensis sp. nov. by a longer predorsal length (51.1-53.2 vs 49.4-50.2\% SL), a shorter dorsal fin base length (32.9-38.5 vs 38.7$40.3 \% \mathrm{SL}$ ), fewer dorsal soft rays ( $12-14$ vs 14-15), fewer cheek scales (12-15 vs 16-17) and fewer gillrakers (1718 vs 18-20). It differs from M. longispina sp. nov. by the general pattern of coloration, the presence of a dorsal margin stripe (vs absent), fewer lateral scales (36-37 vs 37-40), fewer predorsal scales (17-19 vs 19-21), fewer cheek scales (12-15 vs 17-18), fewer gillrakers (17-18 vs 19) and several other morphological characters (see Tab. VIII for comparisons). Melanotaenia sembrae differs from M. susii sp. nov by fewer lateral scales ( $36-37$ vs 38-39), fewer cheek scales (12-15 vs 16-20), fewer gillrakers (17-18 vs 19), a greater interorbital width (8.4-8.8 vs 8.0-8.4\% SL), a longer pectoral fin length (20.2-21.9 vs 17.6-19.0\% SL), a shorter spine length on first dorsal fin (9.7-11.1 vs $11.4-12.4 \% \mathrm{SL}$ ), and the coloration pattern (no vertical bars vs presence of 3-5 vertical bars on anterior body region).

## Distribution and habitat

The new species is currently known from the Sembra River, a karst resurgence emerging from the southern side of the Ayamaru Plateau, west of Teminabuan town and flowing into Teminabuan Bay (Fig. 1). The type locality consists of a $20-25 \mathrm{~m}$ wide stream with depths to about 4 m and moderate to fast flow through second growth forest. The specimens were collected over a limestone rock bottom in clear water.

## Etymology

The species is named sembrae, with reference to the river name at the type locality.

## Melanotaenia manibuii, sp. nov. Kadarusman, Slembrouck \& Pouyaud

(Fig. 20; Tab. XI)

## Type material

Holotype. - MZB 22166, male, 103.7 mm SL, $1^{\circ} 56.330^{\prime}$ S, $133^{\circ} 31.036^{\prime}$ E, Tisbo R. near Bintuni, Papua Barat Province, Indonesia. Sumanta, Ajambua, Kadarusman, 4 Jun. 2007.

Paratypes. - MZB 22167, 14 specimens (66.4-106.7 mm SL), same data

## Diagnosis

Melanotaenia manibuii is distinguished from all of its congeners in the Birds Head region by the following combination of characters: dorsal rays IV to $\mathrm{V}+\mathrm{I}, 13$ to 16 ; anal
rays I, 22 to 25 ; lateral scales 35 to 37 ; transverse scales 10 predorsal scales 15 to 18 ; cheek scales 13 to 19 ; gillrakers 18 to 19 ; a short head length, $24.0-25.1 \%$ of SL; a long snout length, 8.6-9.3\% of SL; a broad interorbital width, 8.8-9.2\% of SL; a broad caudal peduncle depth, 11.7-13.3\% of SL; a short caudal peduncle length, 13.6-15.4\% of SL; a short predorsal length, 47.5-49.9\% of SL; a moderately short spine length on first dorsal fin, 9.7-12.0\% of SL; an intermediate spine length on second dorsal fin, $7.8-12.2 \%$ of SL, and on the anal fin, 7.2-9.8\% of SL; moderately long dorsal fin base length, 37.2-41.8\% of SL, and second dorsal fin base length, 24.0-28.7\% of SL; a moderately long anal fin base length, 40.0-43.9\% of SL; no stripe on the margin of the dorsal and anal fins; dorsal fin origin vertically projected behind anal origin, between $1^{\text {st }}$ and $3^{\text {rd }}$ anal soft ray; absence of sexual dimorphism in contrast to most members of the genus.

## Description

Counts and proportions that appear in parentheses refer to the range for paratypes (based on 14 specimens, $66.4-$ 106.7 mm SL ) if different from the holotype. Morphometric data are given in table XI.

Dorsal rays V + I, 14 (IV-V + I,13-16); anal rays I,24 (I,22-25); pectoral rays 14 (14-15); pelvic rays I,5; lateral scales 37 (35-37); transverse scales 10; predorsal scales 16 (15-18); cheek scales 19 (13-19); total gillrakers on first arch 18 (18-19); jaws equal, oblique, premaxilla with an abrupt bend between the anterior horizontal portion and lateral part; maxilla ends below anterior edge of eye; lips thin; teeth conical with slightly curved tips; teeth at front of upper jaw in about 5-7 irregular rows, reduced to 1-2 rows posteriorly; teeth at front of lower jaws in about 6-10 irregular rows, reduced to $1-2$ rows posteriorly; small conical teeth on vomer and palatines.

Scale of body large, cycloid, crenulated, arranged in regular horizontal rows; predorsal scales extending to posterior margin of interorbital; 3 rows of preopercle scales. First dorsal fin origin projected behind anal origin, between $1^{\text {st }}$ and $3^{\text {rd }}$ anal soft ray; tip of first dorsal fin reaching base of spine or $1^{\text {st }}$ to $4^{\text {th }}$ soft ray of second dorsal fin; tip of second dorsal fin reaching middle of caudal peduncle; pelvic fin tips reaching base of $4^{\text {th }}$ to $5^{\text {th }}$ anal soft ray; caudal fin forked.

Colour of freshly collected male specimens: upper half of the body, nape and dorsal region brown with olive green reflections; lower half of the body and belly whitish; an intense and continuous black (sometimes with blue hues) midlateral stripe of 1 scale wide on pectoral region and 2-3 scales wide on caudal peduncle; pectoral fin translucent; anal and dorsal fins uniformly pale red; a brownish caudal fin with green hues at its base and extending to caudal peduncle; pelvic fins yellowish; a diffuse blue blotch on side of abdomen. Colour pattern of females similar, but paler than males No sexual dimorphism.

## Comparisons

Melanotaenia manibuii and M. irianjaya are geographically close (approx. 90 km between both type localities separated by the Bintuni Bay) and possess similar meristic features (see appendix). Nevertheless, both species belong to distinct phylogenetic groups with important genetic divergence (Fig. 2). Melanotaenia manibuii belongs to the "Northern Birds Head" group, while M. irianjaya belongs to the "Southern Birds Head" group. Melanotaenia manibuii is easily distinguishable from $M$. irianjaya by a shorter head length (24.0-25.1 vs 25.3-27.0\% SL), a greater caudal peduncle depth (11.7-13.3 vs 9.7-11.1\% SL), a shorter predorsal length (47.5-49.9 vs 50.0-52.5\% SL), shorter spine length of first and second dorsal fin (respectively 9.7-12.0 $v s$ 12.3-13.6 and 7.8-12.2 vs 12.3-14.1\% SL), a shorter spine length of anal fin (7.2-9.8 vs 9.8-11.6\% SL), a longer second dorsal fin base length (24.0-28.7 vs 21.1-23.7\% SL), fewer gillrakers (18-19 vs 19-21), and by the absence of a stripe on the dorsal fin margin.

The new species is easily distinguishable from all of the species belonging to the "Northern Birds Head" group by the genetic polymorphism assessed from the 12 microsatellite loci (Figs 5, 6,7) and by the morphological characters given below.

Melanotaenia manibuii differs from M. misoolensis by a shorter head length (24.0-25.1 vs $25.4-26.6 \% \mathrm{SL})$, a smaller

Table XI. - Measurements taken on the holotype and 14 paratypes of Melanotaenia manibuii sp. nov.

|  | Holotype | Paratypes |  |  |  |  |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: |
| SL (mm) | 103.7 | $66.4-106.7$ |  |  |  |  |
|  |  | 25.0 | 14 | 24.0 | 25.1 | 24.8 |

eye diameter (6.8-8.0 vs 8.4-9.9\% SL), a deeper and shorter caudal peduncle (its depth 11.7-13.3 vs 10.7-11.3 and length 13.6-15.4 vs $15.6-16.5 \% \mathrm{SL}$ ). It differs from M. flavipinnis by the position of the first dorsal fin origin compared to the anal fin origin (dorsal fin origin behind anal origin, between $1^{\text {st }}$ and $3^{\text {rd }}$ anal soft ray $v s$ dorsal fin origin between $5^{\text {th }}$ and $6^{\text {th }}$ anal fin origin) and by the general pattern of coloration (see Allen et al., 2014a for more details). The new species differs from M. batanta and M. salawati by a shorter predorsal length (47.5-49.9 vs 50.8-54.8\% SL) and a shorter anal fin base length (40.0-43.9 vs 44.0-50.5\% SL). Compared to M. fredericki, the new species displays a longer snout length (8.6-9.3 vs 7.7-8.4\% SL), a greater interorbital width (8.8 $9.2 v s 8.0-8.4 \% \mathrm{SL}$ ) and a greater caudal peduncle depth (11.7-13.3 vs 9.3-11.0\% SL). The new species differs from M. arfakensis by a longer snout length (8.6-9.3 vs 7.6-8.2\% SL) and a shorter caudal peduncle length (13.6-15.4 vs 16.5 $18.3 \% \mathrm{SL}$ ).

Many characters enable M. manibuii to be distinguished from M. longispina sp. nov, such as a greater interorbital width (8.8-9.2 vs 7.8-8.2\% SL), a broader caudal peduncle (its depth 11.7-13.3 vs 9.2-10.7 and length 13.6-15.4 vs 15.4 $16.7 \% \mathrm{SL})$, a shorter predorsal length (47.5-49.9 vs 50.2$51.8 \% \mathrm{SL}$ ), shorter spine length on first dorsal (9.7-12.0 vs 13.1-15.3) and second dorsal fins (7.8-12.2 vs 12.4-15.7\% SL), a shorter spine length of anal fin (7.2-9.8 vs 10.1-11.3\% SL), a longer total dorsal fin base (37.2-41.8 vs 33.4-36.5) and second dorsal fin base lengths (24.028.7 vs 20.2-22.6\% SL).

Following Allen et al. (2014b), M. manibuii differs from $M$. laticlavia and M. ericrobertsi by the pattern of coloration of the dorsal fin (absence of margin stripe $v s$ present) and the position of the first dorsal fin origin compared to the anal fin origin (dorsal fin origin behind anal origin, between $1^{\text {st }}$ and $3^{\text {rd }}$ anal soft ray $v s$ dorsal fin origin about level). The new species also displays more gillrakers than M. laticlavia (18-19 vs 16-17) and fewer lateral scales than M. ericrobertsi (35-37 vs 37-39).

Melanotaenia manibuii differs from the remaining members of the "Central Ayamaru Plateau" and the "Southern Ayamaru Plateau" species clusters by the pattern of coloration of the dorsal fin (absence of margin stripe $v s$ present) and several other morphological characters (see Tabs VII, IX, X and Appendix for more details).

## Distribution and habitat

The new species is currently known from the Tisbo River in the southern foothills of the Arfak Mountains at an elevation of about 87 m , approximately 20 km north of Bintuni town. The Tisbo River is part of the Tembuni River system, which
flows into Bintuni Bay on the south coast of the Birds Head Peninsula. The stream, which ranged between 5 and 10 m in width at the type locality, was flowing through secondary forest habitat over gravel and sand substrate.

## Etymology

The species is named manibuii, in honour of Alfons Manibui, Bupati from Bintuni.

## Melanotaenia naramasae, sp. nov. Kadarusman, Nugraha \& Pouyaud

(Figs 21, 22; Tab. XII)

## Type material

Holotype. - MZB 22160, male, 99.1 mm SL, $2^{\circ} 48.440^{\prime} \mathrm{S}$, $134^{\circ} 19.965^{\prime}$ E, Naramasa R., Birds Neck Isthmus, Papua Barat province, Indonesia. Kadarusman, Ogistira, Sumanta \& Pouyaud, 21 Apr. 2009.

Paratypes. - MZB 22161, 7 specimens (75.9-97.3 mm SL), same data

## Diagnosis

Melanotaenia naramasae is distinguished from all of its congeners in the Birds Head region by the following combination of characters: dorsal rays IV to $\mathrm{V}+\mathrm{I}, 13$ to 15 ; anal rays I, 21 to 24 ; lateral scales 33 to 35 ; transverse scales 10; predorsal scales 16 to 17 ; cheek scales 13 to 16 ; gillrakers 15 ; a large body depth, 33.3-37.8, with a moderately short prepelvic length 36.3-38.3\% of SL; a moderately short caudal peduncle length, 12.9-16.3, with a large depth, 11.8-12.4\% of SL; a moderately long pectoral fin length, 18.7-21.7, and a long pelvic fin length $19.4-23.5 \%$ of SL; a long dorsal fin base length, 38.4-41.4\% of SL; a moderately long anal fin base length, 39.8-46.0; no stripe on the anal and dorsal fin margins; dorsal origin behind anal origin between $1^{\text {st }}$ and $2^{\text {nd }}$ anal soft ray.

## Description

Counts and proportions that appear in parentheses refer to the range for paratypes (based on 7 specimens, $75.9-97.3 \mathrm{~mm} \mathrm{SL}$ ) if different from the holotype. Morphometric data are given in table XII.

Dorsal rays V + I, 15 (IV-VI + I,13-15); anal rays I,24 (I,21-24); pectoral rays 14 (13-14); pelvic rays I,5; lateral scales 34 (34-35); transverse scales 10 ; predorsal scales 16 (16-17); cheek scales 16 (13-16); total gillrakers on first arch 15; head rounded; jaws about equal, oblique, premaxilla with an abrupt bend between the anterior horizontal portion and lateral part; maxilla ends below anterior edge of eye; lips thin; teeth conical with slightly curved tips extend-
ing to outer surface of lips; teeth of upper jaws in about 6-7 irregular rows, reduced to 1-2 rows posteriorly; lower jaws in about 5-8 irregular rows anteriorly, reduced to 1-2 rows posteriorly; vomer and palatines edentate.

Scale of body cycloid, relatively large, and arranged in regular horizontal rows; scale margin slightly crenulate; predorsal scales extending to middle portion of interorbital; preopercle scales from posterior angle to edge of eye arranged in 3 rows.

First dorsal fin origin behind anal fin origin, between $1^{\text {st }}$ to $2^{\text {nd }}$ anal soft rays; tip of first dorsal fin reaching $2^{\text {nd }}$ to $3^{\text {rd }}$ soft ray of second dorsal fin; tip of second dorsal fin reaching hypural junction for the males and half length of caudal peduncle for the females; pelvic fin tips when depressed reaching base of $2^{\text {nd }}$ to $3^{\text {rd }}$ soft anal fin ray for females and $3^{\text {rd }}$ to $6^{\text {th }}$ for males; caudal fin moderately forked.

Colour of freshly collected male specimens: overall yellow; nape and dorsal part of head brown, belly yellowish; a dark blue midlateral stripe of 1-2 scale wide and not continuous, intense with 2 scales wide just behind pectoral fin base, interrupted on middle of side and faint on caudal peduncle; pectoral fin translucent; remaining fins yellow; no margin stripe on dorsal and anal fins; colour pattern of females similar but less vivid on fins and on lower part of the body with presence of a large blue blotch extending from pectoral fin base to middle of anal fin.

Table XII. - Measurements taken on the holotype and seven paratypes of Melanotaenia naramasae sp. nov.

|  | Holotype | Paratypes |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| SL (mm) | 99.1 |  |  | 75.9-9 |  |  |
| in \% standard length |  | n | Min | Max | Mean | SD |
| Head length | 24.7 | 7 | 24.9 | 26.2 | 25.5 | 0.4 |
| Snout length | 8.8 | 7 | 8.6 | 9.5 | 9.0 | 0.3 |
| Interorbital width | 8.4 | 7 | 8.4 | 9.0 | 8.7 | 0.2 |
| Eye diameter | 7.5 | 7 | 7.1 | 8.1 | 7.6 | 0.3 |
| Body depth | 36.4 | 7 | 33.3 | 37.8 | 35.1 | 1.6 |
| Body width | 13.7 | 7 | 12.5 | 14.4 | 13.7 | 0.6 |
| Caudal peduncle depth | 11.8 | 7 | 11.9 | 12.4 | 12.1 | 0.2 |
| Caudal peduncle length | 14.3 | 7 | 12.9 | 16.3 | 15.3 | 1.2 |
| Predorsal length | 48.9 | 7 | 48.4 | 51.4 | 49.5 | 1.0 |
| Prepelvic length | 37.0 | 7 | 36.3 | 38.3 | 37.4 | 0.7 |
| Preanal length | 49.2 | 7 | 46.8 | 51.4 | 49.1 | 1.6 |
| Pectoral fin length | 19.3 | 6 | 18.7 | 21.7 | 20.1 | 1.0 |
| Pelvic fin length | 20.0 | 6 | 19.4 | 23.5 | 21.3 | 1.5 |
| Spine length of first dorsal fin | 9.1 | 7 | 9.0 | 11.0 | 10.3 | 0.7 |
| Spine length of second dorsal fin | 7.9 | 7 | 7.3 | 10.9 | 9.2 | 1.3 |
| Spine length of anal fin | 6.8 | 7 | 7.4 | 9.2 | 8.7 | 0.6 |
| Dorsal fin base length | 40.5 | 7 | 38.4 | 41.4 | 39.5 | 1.1 |
| Second dorsal fin base length | 26.8 | 7 | 24.0 | 26.4 | 25.5 | 0.9 |
| Anal fin base length | 44.2 | 7 | 39.8 | 46.0 | 42.0 | 2.4 |
| Anal fin height |  | 3 | 13.0 | 16.5 | 14.6 | 1.7 |

Sexual dimorphism: Males are deeper bodied than females (body depth 35.4-37.8 vs 33.3-35.3\% SL) and have a longer second dorsal fin base (25.9-26.8 vs 24.0-26.0\% SL).

## Comparisons

Melanotaenia naramasae is part of the "Southern Birds Head" group of species and belongs to the "Birds Neck" species cluster together with M. angfa and M. parva (see Fig. 2), The new species is also easily distinguishable from these species on the basis of the polymorphism of the 12 analyzed microsatellite loci (Fig. 8).

Melanotaenia naramasae differs from M. angfa by a greater body depth (33.3-37.8 vs 28.8-32.3\% SL), a greater caudal peduncle depth (11.8-12.4 vs 10.2-11.4\% SL), a longer pectoral fin length (18.7-21.7 vs 16.2-18.5\% SL), fewer lateral scales (33-35 vs 35-36), fewer gillrakers ( $15 v s$ 16-20), and the position of the first dorsal fin origin compared to the anal fin origin (dorsal fin origin behind anal origin, between $1^{\text {st }}$ and $2^{\text {nd }}$ anal soft ray $v s$ dorsal fin origin before anal fin origin). It differs from M. parva by a shorter caudal peduncle length (12.9-16.3 vs 16.8-19.4\% SL), a shorter prepelvic length (36.3-38.3 vs 38.3-41.0\% SL), a longer pelvic fin length (19.4-23.5 vs 15.1-17.3\% SL), a longer dorsal fin base length ( $38.4-41.4 v s ~ 33.8-37.4 \% ~ S L$ ), a longer anal fin base length ( $39.8-46.0$ vs $33.1-38.2 \% \mathrm{SL}$ ), more dorsal soft rays (13-15 vs 11-13), more cheek scales (13-16 vs 10-13), and

Table XIII. - Measurements taken on the holotype and 11 paratypes of Melanotaenia rumberponensis sp. nov.

|  | Holotype | Paratypes |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| SL (mm) | 65.2 | 50.2-70.0 |  |  |  |  |
| in \% standard length |  | n | Min | Max | Mean | SD |
| Head length | 26.3 | 11 | 26.2 | 27.4 | 26.8 | 0.3 |
| Snout length | 8.4 | 11 | 8.2 | 8.7 | 8.4 | 0.2 |
| Interorbital width | 9.2 | 11 | 9.1 | 9.5 | 9.3 | 0.2 |
| Eye diameter | 8.9 | 11 | 8.7 | 9.3 | 9.0 | 0.2 |
| Body depth | 31.6 | 11 | 29.9 | 33.2 | 31.6 | 1.1 |
| Body width | 13.3 | 11 | 12.7 | 14.5 | 13.7 | 0.6 |
| Caudal peduncle depth | 11.0 | 11 | 10.3 | 11.1 | 10.7 | 0.3 |
| Caudal peduncle length | 13.1 | 11 | 12.6 | 14.4 | 13.7 | 0.6 |
| Predorsal length | 50.3 | 11 | 48.4 | 50.3 | 49.4 | 0.6 |
| Prepelvic length | 39.2 | 11 | 39.0 | 40.4 | 39.8 | 0.5 |
| Preanal length | 50.1 | 11 | 49.7 | 52.5 | 50.9 | 0.9 |
| Pectoral fin length | 19.6 | 11 | 17.5 | 19.6 | 18.7 | 0.7 |
| Pelvic fin length | 17.1 | 11 | 15.1 | 17.9 | 16.8 | 0.8 |
| Spine length of first dorsal fin | 11.5 | 11 | 10.7 | 12.7 | 11.8 | 0.7 |
| Spine length of second dorsal fin | 10.4 | 11 | 8.1 | 12.8 | 10.2 | 1.3 |
| Spine length of anal fin | 8.7 | 11 | 7.7 | 9.0 | 8.3 | 0.4 |
| Dorsal fin base length | 41.6 | 11 | 37.5 | 42.7 | 40.2 | 1.8 |
| Second dorsal fin base length | 25.6 | 11 | 22.2 | 26.8 | 24.7 | 1.6 |
| Anal fin base length | 43.7 | 11 | 36.3 | 43.0 | 39.7 | 2.3 |
| Anal fin height | 14.0 | 3 | 11.7 | 13.6 | 12.7 | 0.9 |

position of first dorsal fin origin relatively to anal fin origin (behind $v s$ before).

## Distribution and habitat

The new species is currently known only from the upstream part of the Naramasa River system flowing westward to Bintuni Bay. The stream, which ranged between 20 and 30 m in width at the type locality, was flowing through primary forest habitat over gravel and sand substrate. Rainbowfishes were mainly concentrated along the riverbank around $\log$ debris.

## Etymology

The species is named naramasae, in reference to the river name at the type locality.

## Melanotaenia rumberponensis, sp. nov. Kadarusman, Ogistira \& Pouyaud

(Fig. 24; Tab. XIII)

## Type material

Holotype. - MZB 22162, male, $65.2 \mathrm{~mm} \mathrm{SL}, 1^{\circ} 51.238$ 'S, $134^{\circ} 09.489^{\prime}$ E, Rumberpon Island, Cendrawasih Bay, Birds Neck Isthmus, Papua Barat Province, Indonesia. Kadarusman, Ogistira, Ajambua, Sumanta \& Pouyaud, 5 Apr. 2008.

Paratypes. - MZB 22163, 11 specimens (50.270.0 mm SL ), same data as holotype.

## Diagnosis

Melanotaenia rumberponensis is distinguished from all of its congeners in the Birds Head region by: dorsal rays IV to $\mathrm{V}+\mathrm{I}, 13$ to 14 ; anal rays I, 21 to 23 ; lateral scales 34 to 35 ; transverse scales 10-11; predorsal scales 16 to 18 ; cheek scales 14 to 16 ; gillrakers 18; a short snout length, 8.2-8.7\% of SL; a broad interorbital width, 9.1-9.5\% of SL; a large eye diameter, 8.7-9.3\% of SL; an elongate body, its depth 29.9-33.2; a long prepelvic length, $39.0-$ $40.4 \%$ of SL; a moderately short predorsal length 48.4-50.3\% of SL; a caudal peduncle short and slender, its length 12.6-14.4 and its depth 10.3-11.1\% of SL; a short pelvic fin length, 15.1-17.9\% of SL; a moderately long dorsal fin base length, 37.5-42.7\% of SL; no stripe on the margin of the anal and dorsal fins; a continuous black midlateral stripe, covering 3 scales wide from upper edge of preopercle to caudal fin base; dorsal origin aligned with anal origin or behind it, until the $3^{\text {rd }}$ anal soft ray.

## Description

Counts and proportions that appear in parentheses refer to the range for paratypes (based on 11


Figure 24. - Melanotaenia rumberponensis, MZB 22162 (holotype), male, 65.2 mm SL, Rumberpon Island, Cendrawasih Bay, Birds Neck, West Papua, Indonesia.
Figure 25. - Melanotaenia sikuensis, MZB 22164 (holotype), male, 91.0 mm SL, Siku Creek, Birds Neck, West Papua, Indonesia.
Figure 26. - Melanotaenia sikuensis, MZB 22165 (paratype), female, 77.6 mm SL, same data as for holotype.
specimens, $50.2-70.0 \mathrm{~mm} \mathrm{SL})$ if different from the holotype. Morphometric data are given in table XIII.

Dorsal rays $\mathrm{V}+\mathrm{I}, 14$ (IV-V $+\mathrm{I}, 13-14$ ); anal rays I, 22 (I,21-23); pectoral rays 14 (13-14); pelvic rays I,5; lateral scales 35 (34-35); transverse scales 11 (10-11); predorsal scales 17 (16-18); cheek scales 14 (14-16); total gillrakers on first arch 18; body elongated with head and eyes well developed; jaws about equal, oblique, premaxilla with an abrupt bend between the anterior horizontal portion and lateral part; maxilla ends below anterior edge of eye; lips thin; teeth conical with slightly curved tips extending to outer surface of lips; teeth of upper jaws in about 3-5 irregular rows, reduced to 1-2 rows posteriorly; lower jaws in about 4-5 irregular rows anteriorly, reduced to 1-2 rows posteriorly; several small conical teeth on vomer and palatines.

Scale of body cycloid, relatively large, and arranged in regular horizontal rows; scale margin slightly crenulate; predorsal scales extending to posterior portion of interorbital; preopercle scales from posterior angle to edge of eye arranged in 3 rows.

First dorsal fin origin vertically aligned with anal origin or behind it, until the $3^{\text {rd }}$ anal soft ray; tip of first dorsal fin reaching $2^{\text {nd }}$ to $3^{\text {rd }}$ soft ray of second dorsal fin for males and reaching spine of second dorsal fin for females; tip of second dorsal fin reaching $2 / 3$ length of caudal peduncle for the males and half length for the females; pelvic fin tips when depressed reaching base of $1^{\text {st }}$ to $2^{\text {nd }}$ soft anal fin ray for females and $2^{\text {nd }}$ to $3^{\text {rd }}$ for males; caudal fin forked.

Colour of freshly collected male specimens: overall yellow; dorsal part of head and body brownish, belly yellowish; a continuous black midlateral stripe, covering 3 scales wide from upper edge of preopercle to caudal fin base; pectoral fin translucent; remaining fins yellow; no margin stripe on dor-
sal and anal fins; a faint blue blotch extending from pectoral fin base to middle of anal fin; colour of females with equal intensity.

Sexual dimorphism: Males have longer fins than females, are generally deeper bodied (31.6-33.2 vs 29.9-32.1\% SL) and have a deeper caudal peduncle (10.7-11.1 vs 10.3-10.9\% SL).

## Comparisons

Melanotaenia rumberponensis is part of the "Southern Birds Head" group of species and belongs to the "Birds Neck" species cluster together with M. angfa, M. parva and M. naramasae sp. nov. (Fig. 2). The new species is distinguishable from all of these species on the basis of the polymorphism of the 12 analyzed microsatellite loci (Fig. 8).

Melanotaenia rumberponensis is distinguished from M. angfa and M. parva by a greater eye diameter (8.7-9.3 vs 7.3-8.4), a shorter caudal peduncle length (12.6-14.4 vs $14.6-19.4 \% \mathrm{SL}$ ) and by the thickness of the midlateral stripe on the caudal peduncle region (3 scales wide $v s$ faint or absent). In addition, the new species differs from M. angfa by a shorter snout length (8.2-8.7 vs 9.0-9.5\% SL), fewer lateral scales (34-35 vs 35-36), and fewer soft dorsal rays (1314 vs 14-16). The new species differs from M. parva by a slender caudal peduncle depth (10.3-11.1 vs 11.6-12.5\% SL), a shorter predorsal length (48.4-50.3 vs 50.8-52.8\% SL), a longer dorsal fin base length ( $37.5-42.7$ vs $33.8-37.4 \% \mathrm{SL}$ ), more cheek scales (14-16 vs 10-13) and more gillrakers (18 vs 13-16).

Melanotaenia rumberponensis differs from M. naramasae sp. nov. by a greater interorbital width (9.1-9.5 vs 8.4$9.0 \% \mathrm{SL}$ ), a greater eye diameter (8.7-9.3 vs 7.1-8.1\% SL), a slender body depth (29.9-33.2 vs 33.3-37.8) and caudal
peduncle depth (10.3-11.1 vs 11.8-12.4\% SL), a longer prepelvic length (39.0-40.4 vs 36.3-38.3\% SL), a shorter pelvic fin length (15.1-17.9 vs 19.4-23.5\% SL) and more gillrakers (18 vs 15).

## Distribution and habitat

The new species is currently known from the type locality, a swamp drained by a small creek of 5 m in width flowing in the central part of the island. The stream was flowing through primary forest habitat over muddy substrate with abundant aquatic vegetation.

## Etymology

The species is named rumberponensis, in reference to the type locality, the Rumberpon Island.

## Melanotaenia sikuensis, sp. nov. Kadarusman, Sudarto \& Pouyaud

(Figs 25, 26; Tab. XIV)

## Type material

Holotype. - MZB 22164, male, $91.0 \mathrm{~mm} \mathrm{SL}, 1^{\circ} 46.784^{\prime} \mathrm{S}$, $134^{\circ} 04.790^{\prime}$ E, Siku Creek, Birds Neck Isthmus, Papua Barat Province, Indonesia. Kadarusman, Paradis, Ajambua, Sumanta \& Pouyaud, 2 Jun. 2007.

Table XIV. - Measurements taken on the holotype and 10 paratypes of Mela notaenia sikuensis sp. nov.

|  | Holotype | Paratypes |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| SL (mm) | 91.0 |  |  | 3.9-81 |  |  |
| in \% standard length |  | n | Min | Max | Mean | SD |
| Head length | 24.7 | 10 | 25.3 | 26.1 | 25.8 | 0.2 |
| Snout length | 8.2 | 10 | 8.1 | 8.9 | 8.6 | 0.3 |
| Interorbital width | 8.2 | 10 | 8.3 | 8.7 | 8.6 | 0.2 |
| Eye diameter | 7.1 | 10 | 7.3 | 8.0 | 7.7 | 0.2 |
| Body depth | 34.8 | 10 | 30.1 | 35.6 | 33.2 | 1.7 |
| Body width | 13.7 | 10 | 12.6 | 15.0 | 13.4 | 0.9 |
| Caudal peduncle depth | 11.2 | 10 | 10.1 | 11.5 | 11.0 | 0.4 |
| Caudal peduncle length | 13.9 | 10 | 12.9 | 14.3 | 13.8 | 0.6 |
| Predorsal length | 48.6 | 10 | 47.7 | 49.5 | 48.8 | 0.6 |
| Prepelvic length | 37.3 | 10 | 36.7 | 39.0 | 38.0 | 0.7 |
| Preanal length | 48.4 | 10 | 47.2 | 50.6 | 49.3 | 1.0 |
| Pectoral fin length |  | 10 | 18.6 | 20.7 | 19.4 | 0.6 |
| Pelvic fin length | 18.1 | 10 | 15.5 | 19.3 | 17.6 | 1.1 |
| Spine length of first dorsal fin | 8.8 | 10 | 9.9 | 11.5 | 10.4 | 0.6 |
| Spine length of second dorsal fin | 6.5 | 10 | 7.6 | 8.7 | 8.1 | 0.5 |
| Spine length of anal fin | 6.3 | 10 | 6.2 | 9.5 | 7.2 | 1.0 |
| Dorsal fin base length | 41.9 | 10 | 38.5 | 42.1 | 39.6 | 1.2 |
| Second dorsal fin base length | 28.4 | 10 | 24.7 | 28.0 | 26.3 | 1.1 |
| Anal fin base length | 42.8 | 10 | 39.5 | 43.1 | 41.0 | 1.4 |
| Anal fin height |  | 3 | 14.4 | 15.7 | 15.1 | 0.6 |

Paratypes. - MZB 22165, 10 specimens (63.9-81.7 mm SL), same data as holotype.

## Diagnosis

Melanotaenia sikuensis is distinguished from all of its congeners in the Birds Head region by: dorsal rays IV to V + I, 14 to 15 ; anal rays I, 20 to 23 ; lateral scales 34 to 36 ; transverse scales $10-11$; predorsal scales 15 to 18 ; cheek scales 12 to 17; gillrakers 13-15; head length, 24.7-26.1\% of SL; a moderately short snout length, 8.1-8.9\% of SL; interorbital width, 8.2-8.7\% of SL; eye diameter, 7.1-8.0\% of SL; prepelvic length, 36.7-39.0\% of SL; a short predorsal length, 47.7-49.5\% of SL; a short caudal peduncle length, 12.9-14.3; a moderately slender caudal peduncle depth, 10.1-11.5\% of SL; a moderately short pelvic fin length, 15.5-19.3\% of SL; a long dorsal fin base length, $38.5-42.1 \%$ of SL; a long second dorsal fin base length, 24.7-28.4\% of SL; an intermediate anal fin base length 39.5-43.1, with a tall anal fin height $14.4-15.7 \%$ of SL; no stripe on the margin of the anal and dorsal fins; a continuous blue midlateral stripe, covering 2-3 scales wide from pectoral to middle sections and 3-4 scales rows on caudal section; dorsal origin behind anal origin, between $2^{\text {nd }}$ to $3^{\text {rd }}$ anal soft ray.

## Description

Counts and proportions that appear in parentheses refer to the range for paratypes (based on 10 specimens, $63.9-81.7 \mathrm{~mm} \mathrm{SL}$ ) if different from the holotype Morphometric data are given in table XIV.

Dorsal rays V + I, 14 (IV-V + I,14-15); anal rays I, 22 (I,20-23); pectoral rays 14 (13-15); pelvic rays I,5; lateral scales 34 (34-36); transverse scales 10 (10-11); predorsal scales 15 (16-18); cheek scales 14 (12-17); total gillrakers on first arch 15 (1315); jaws about equal, oblique, premaxilla with an abrupt bend between the anterior horizontal portion and lateral part; maxilla ends below anterior edge of eye; lips thin; teeth conical with slightly curved tips extending to outer surface of lips; teeth of upper jaws in about 5-7 irregular rows, reduced to 1-2 rows posteriorly; lower jaws in about 6-7 irregular rows anteriorly, reduced to 1-2 rows posteriorly; several small conical teeth on vomer and palatines.

Scale of body cycloid, relatively large, and arranged in regular horizontal rows; scale margin slightly crenulate; predorsal scales extending to posterior portion of interorbital; preopercle scales from posterior angle to edge of eye arranged in 3 rows.

First dorsal fin origin behind anal fin origin, between $2^{\text {nd }}$ to $3^{\text {rd }}$ anal soft rays; tip of first dorsal fin reaching $2^{\text {nd }}$ to $3^{\text {rd }}$ soft ray of second dorsal fin; tip of second dorsal fin reaching $2 / 3$ length of caudal peduncle for the males and half length for the
females; pelvic fin tips when depressed reaching base of $1^{\text {st }}$ to $3^{\text {rd }}$ soft anal fin ray for females and $3^{\text {rd }}$ to $4^{\text {th }}$ for males; caudal fin forked.

Colour of freshly collected male specimens: overall yellow; dorsal part of head and body yellow, belly yellowish; a continuous blue violet midlateral stripe of 2-3 scale wide from pectoral to middle sections and 3-4 scale rows on caudal section; pectoral fin translucent; remaining fins yellow dark; no margin stripe on dorsal and anal fins; a faint blue blotch extending from pectoral fin base to middle of anal fin; colour of females with equal intensity

Sexual dimorphism: males have longer dorsal and pelvic fins but are not deeper bodied than females.

## Comparisons

Melanotaenia sikuensis is part of the phylogenetic group "Southern Birds Head" species group and belongs to the "Birds Neck" species cluster. The new species is genetically allied to M. angfa, M. parva, M. naramasae sp. nov and M. rumberponensis sp. nov. (Fig. 2). It is distinguishable from all of these species on the basis of the polymorphism of the 12 analyzed microsatellite loci (Fig. 8)

Melanotaenia sikuensis is distinguished from M. angfa and $M$. parva by the position of the dorsal fin origin in relation to the anal fin origin (dorsal behind anal origin $v s$ dorsal before anal origin), by a shorter caudal peduncle length (12.9-14.3 vs 14.6-19.4\% SL), and by the thickness of the midlateral stripe on the caudal peduncle ( $3-4$ scales wide $v s$ faint or absent). The new species differs from M. angfa by a shorter snout length (8.1-8.9 vs 9.0-9.5\% SL) and by fewer gillrakers ( $13-15$ vs 16-20). The new species differs from M. parva by a shorter predorsal length (47.0-49.5 vs 50.8-52.8\% SL), a longer dorsal fin base length (38.5-42.1 vs 33.8-37.4\% SL), a longer second dorsal fin base length (24.7-28.4 vs 20.7-24.7\% SL), a longer anal fin base length (39.5-43.1 vs 33.1-38.2\% SL) and by more dorsal soft rays (14-15 vs 11-13).

Melanotaenia sikuensis is distinguished from M. naramasae sp. nov. by a slender caudal peduncle depth (10.1-11.5 vs 11.8-12.4\% SL), a shorter pelvic fin length (15.5-19.3 vs $19.4-23.5 \% \mathrm{SL}$ ) and by the dorsal origin which is vertically aligned between the $2^{\text {nd }}$ and the $3^{\text {rd }}$ anal soft ray for the former and between the $1^{\text {st }}$ and the $2^{\text {nd }}$ for the latter.

Melanotaenia sikuensis differs from M. rumberponensis sp. nov. by a shorter head length (24.7-26.1 vs 26.2-27.4\% SL), a slender interorbital width (8.2-8.7 vs 9.1-9.5\% SL), a smaller eye diameter (7.1-8.0 vs 8.7-9.3\% SL), a shorter prepelvic length (36.7-39.0 vs 39.0-40.4\% SL), a deeper anal fin height (14.4-15.7 vs 11.7-14.0\% SL), and fewer gillrakers (13-15 vs 18).

## Distribution and habitat

The new species is currently known only from the type
locality, a small creek 5 m in width, and flowing eastward to Cendrawasih Bay. The habitat consists of a typical aquatic system in karstic environment.

## Etymology

The species is named sikuensis, in reference to the river name at the type locality.

## DISCUSSION

The mitochondrial phylogenetic tree combined with the microsatellite genotyping reveals previously undetected diversity among West Papuan rainbowfishes. Prior to this work, 24 valid species had been described from the region. Seven of the newly discovered species are confined to a single river system localized in fragmented karstic environments such as in the limestone karst formations from Ayamaru Plateau or in the northern extension of Lengguru Range. Melanotaenia manibuii, which was discovered on the southern foothills of the Arfak Mountains, is the only species distributed outside of a karstic formation.

Due to the intense tectonic movements of uplift or subsidence and the important erosion activity that happened during more than 10 million years, karst systems are characterized by endorheic drainages consisting of isolated lakes or fragmented rivers with aerial course which length varies from only several hundred metres to a few kilometres. These unique geological formations have therefore promoted an intense diversification and numerous speciation events in the Rainbowfishes from Western Papua (Kadarusman et al., 2010, 2012b; Allen and Hadiaty, 2013; Allen et al., 2014a, b). The total area covered during our field expeditions since 2007 represents approximately $20,000 \mathrm{~km}^{2}$, which corresponds to less than $10 \%$ of the global terrestrial surface of Western Papua and to less than $20 \%$ of karst landscapes Therefore, there are still many unexplored areas that remain to be studied, with a particular mention to the Central Birds Head lowlands eastward of Ayamaru Plateau between southern Tambrauw and Arfak Mountains and along the Northern foothills of Kumawa on Bomberai Peninsula.

The Lengguru fold-and-thrust Belt (LFTB) combined with the Central Dividing Range proved to have played a key role in the diversification of Melanotaeniidae at the regional scale (Kadarusman et al., 2012a; Unmack et al., 2013). Rapid tectonic uplift and subsidence raised in the MidMiocene the radiation of four distinct monophyletic clades, each restricted to a specific biogeographic province. The fact that all the species from Western Papua belonged to the same phylogenetic clade demonstrates their genetic relatedness and proves that dispersal with adjacent biogeographic provinces (i.e. Northern or Southern New Guinea) was disrupted since the geological formation of the LFTB. All the species
of melanotaeniids from Western New Guinea are endemic to the area. Because they are all obligate freshwater fish, further investigations on the diversity of other obligate freshwater taxa of this region appear very promising.

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## Appendix. - Morphometric data for 20 Melanotaenia species from West Papua.

Refer to Allen and Hadiaty (2013) and Allen et al. (2014a, b) for morphometric data corresponding to M. sneideri, M. flavipinnis, M. ericrobertsi and M. laticlavia.

|  | Melanotaenia ajamaruensis |  |  |  |  | Melanotaenia ammeri |  |  |  |  | Melanotaenia angfa |  |  |  |  | Melanotaenia arfakensis |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Material examined |  |  |  |  | Material examined |  |  |  |  | Material examined |  |  |  |  | Material examined |  |  |  |  |
| SL (mm) | 55.5-96.5 |  |  |  |  | 55.9-101.8 |  |  |  |  | 59.5-86.2 |  |  |  |  | 60.7-76.9 |  |  |  |  |
| in \% standard length | n | min | max | mean | SD | n | min | max | mean | SD | n | min | max | mean | SD | n | min | max | mean | SD |
| Head length | 30 | 23.1 | 25.1 | 24.4 | 0.6 | 14 | 24.6 | 27.8 | 25.8 | 0.9 | 13 | 25.2 | 26.5 | 25.7 | 0.4 | 10 | 23.9 | 25.3 | 24.6 | 0.5 |
| Snout length | 30 | 7.2 | 8.1 | 7.8 | 0.3 | 14 | 8.5 | 9.9 | 9.1 | 0.4 | 13 | 9.0 | 9.5 | 9.3 | 0.2 | 10 | 7.6 | 8.2 | 7.9 | 0.2 |
| Interorbital width | 30 | 7.4 | 8.5 | 8.1 | 0.3 | 14 | 8.2 | 8.8 | 8.5 | 0.2 | 13 | 8.6 | 9.4 | 8.9 | 0.2 | 10 | 8.8 | 9.3 | 9.0 | 0.2 |
| Eye diameter | 30 | 7.2 | 8.2 | 7.8 | 0.3 | 13 | 7.3 | 7.8 | 7.6 | 0.2 | 13 | 7.3 | 8.1 | 7.9 | 0.3 | 10 | 7.4 | 8.2 | 7.9 | 0.2 |
| Body depth | 30 | 29.6 | 40.0 | 35.3 | 2.7 | 14 | 29.7 | 38.7 | 33.3 | 2.8 | 13 | 28.8 | 32.3 | 31.0 | 1.0 | 10 | 30.1 | 36.6 | 33.0 | 1.9 |
| Body width | 30 | 12.9 | 18.6 | 14.9 | 1.7 | 14 | 11.7 | 14.2 | 12.7 | 0.7 | 13 | 13.6 | 16.0 | 14.6 | 0.7 | 10 | 13.0 | 14.6 | 13.7 | 0.5 |
| Caudal peduncle depth | 30 | 9.7 | 11.5 | 10.6 | 0.5 | 14 | 11.6 | 13.8 | 12.3 | 0.7 | 13 | 10.2 | 11.4 | 10.8 | 0.4 | 10 | 12.0 | 13.2 | 12.7 | 0.4 |
| Caudal peduncle length | 30 | 14.6 | 16.3 | 15.6 | 0.5 | 13 | 13.9 | 16.1 | 15.0 | 0.8 | 13 | 14.6 | 16.4 | 15.6 | 0.7 | 10 | 16.5 | 18.3 | 17.4 | 0.6 |
| Predorsal length | 30 | 45.3 | 50.0 | 47.9 | 1.1 | 14 | 49.8 | 52.5 | 50.9 | 0.7 | 13 | 45.9 | 49.5 | 48.1 | 1.1 | 10 | 47.1 | 49.6 | 48.3 | 0.8 |
| Prepelvic length | 30 | 36.3 | 39.5 | 38.1 | 0.9 | 13 | 38.5 | 40.5 | 39.3 | 0.6 | 13 | 36.8 | 40.0 | 38.7 | 1.0 | 10 | 36.4 | 39.1 | 37.9 | 0.9 |
| Preanal length | 30 | 49.4 | 53.9 | 51.9 | 1.4 | 14 | 49.7 | 53.3 | 51.0 | 0.9 | 13 | 49.4 | 52.1 | 50.6 | 1.0 | 10 | 47.7 | 50.1 | 48.7 | 0.8 |
| Pectoral fin length | 17 | 17.1 | 19.9 | 18.4 | 0.8 | 14 | 18.9 | 21.1 | 19.9 | 0.7 | 13 | 16.2 | 18.5 | 17.7 | 0.7 | 0 |  |  |  |  |
| Pelvic fin length | 23 | 14.6 | 18.2 | 16.1 | 1.0 | 14 | 17.8 | 23.4 | 21.0 | 1.6 | 13 | 16.9 | 19.9 | 18.1 | 0.9 | 10 | 15.0 | 17.5 | 15.9 | 0.8 |
| Spine length of first dorsal fin | 24 | 8.6 | 11.6 | 10.3 | 0.9 | 14 | 8.7 | 12.0 | 10.3 | 0.9 | 13 | 10.3 | 11.7 | 10.9 | 0.4 | 8 | 9.4 | 12.1 | 10.9 | 1.0 |
| Spine length of second dorsal fin | 23 | 7.0 | 11.4 | 8.9 | 1.0 | 14 | 7.8 | 13.0 | 9.9 | 1.4 | 13 | 8.4 | 11.2 | 9.6 | 0.9 | 10 | 8.3 | 12.4 | 9.9 | 1.3 |
| Spine length of anal fin | 24 | 6.6 | 9.6 | 7.9 | 0.8 | 11 | 8.6 | 10.2 | 9.3 | 0.5 | 12 | 6.5 | 8.4 | 7.7 | 0.6 | 9 | 7.1 | 8.8 | 7.8 | 0.6 |
| Dorsal fin base length | 30 | 38.6 | 43.5 | 40.7 | 1.5 | 14 | 34.7 | 42.2 | 39.1 | 2.0 | 13 | 38.5 | 41.0 | 40.0 | 0.8 | 10 | 37.0 | 39.9 | 38.3 | 1.0 |
| Second dorsal fin base length | 30 | 24.1 | 29.3 | 26.4 | 1.2 | 14 | 22.1 | 28.6 | 25.2 | 1.9 | 13 | 24.1 | 28.6 | 26.2 | 1.1 | 10 | 24.2 | 27.0 | 25.5 | 0.9 |
| Anal fin base length | 30 | 33.9 | 40.4 | 37.7 | 2.0 | 14 | 37.4 | 44.1 | 40.4 | 2.0 | 13 | 35.4 | 40.0 | 38.2 | 1.3 | 10 | 39.7 | 43.6 | 41.3 | 1.3 |
| Anal fin height |  |  |  |  |  | 4 | 19.7 | 22.2 | 20.6 | 1.1 |  |  |  |  |  |  |  |  |  |  |


| Lateral scales | 35-37 | 34-37 | 35-36 | 34-36 |
| :---: | :---: | :---: | :---: | :---: |
| Transverse scales | 7-8 | 9-10 | 10 | 10 |
| Predorsal scales | 15-16 | 14-19 | 16-18 | 14-18 |
| Cheek scales | 11-18 | 12-16 | 14-19 | 13-15 |
| Dorsal rays | IV-VI + I, 12-19 | IV-VI + I, 12-15 | $\mathrm{IV}-\mathrm{V}+\mathrm{I}, 14-16$ | IV-V + I, 13-16 |
| Anal rays | I,21-24 | I,20-24 | I,22-24 | I,21-25 |
| Pectoral rays | 13-15 | 12-14 | 13-15 | 14-15 |
| Pelvic rays | I,5 | I,5 | I,5 | I,5 |
| Total gillrakers on first arch | 16-19 | 16-17 | 16-20 | 15-16 |


|  | Melanotaenia arguni |  |  |  |  | Melanotaenia batanta |  |  |  |  | Melanotaenia boesemani |  |  |  |  | Melanotaenia catherinae |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Material examined |  |  |  |  | Material examined |  |  |  |  | Material examined |  |  |  |  | Material examined |  |  |  |  |
| SL (mm) | 54.8-72.6 |  |  |  |  | 73.9-110.0 |  |  |  |  | 54.7-86.9 |  |  |  |  | 58.1-79.8 |  |  |  |  |
| in \% standard length | n | min | max | mean | SD | n | min | max | mean | SD | n | min | max | mean | SD | n | min | max | mean | SD |
| Head length | 15 | 24.2 | 26.9 | 25.2 | 0.7 | 15 | 23.6 | 25.3 | 24.7 | 0.5 | 13 | 25.5 | 28.5 | 27.1 | 0.9 | 8 | 25.6 | 26.7 | 26.0 | 0.4 |
| Snout length | 15 | 8.3 | 9.1 | 8.7 | 0.3 | 15 | 9.2 | 9.5 | 9.4 | 0.1 | 13 | 7.8 | 8.7 | 8.4 | 0.3 | 8 | 8.5 | 9.1 | 8.8 | 0.2 |
| Interorbital width | 15 | 8.3 | 9.0 | 8.7 | 0.2 | 15 | 8.8 | 9.6 | 9.2 | 0.2 | 13 | 8.3 | 9.5 | 8.8 | 0.3 | 8 | 9.7 | 10.4 | 10.0 | 0.3 |
| Eye diameter | 15 | 6.6 | 7.2 | 7.0 | 0.2 | 15 | 7.0 | 7.8 | 7.5 | 0.2 | 13 | 8.6 | 10.7 | 9.5 | 0.5 | 8 | 8.5 | 9.1 | 8.9 | 0.2 |
| Body depth | 15 | 30.7 | 33.8 | 32.2 | 1.0 | 15 | 31.3 | 36.7 | 33.9 | 1.7 | 13 | 34.0 | 44.7 | 37.5 | 3.5 | 8 | 29.0 | 36.0 | 32.7 | 2.3 |
| Body width | 15 | 11.0 | 13.0 | 11.9 | 0.6 | 15 | 12.7 | 14.0 | 13.2 | 0.4 | 13 | 11.4 | 15.5 | 14.0 | 1.1 | 8 | 13.7 | 15.2 | 14.5 | 0.6 |
| Caudal peduncle depth | 15 | 10.0 | 10.8 | 10.4 | 0.3 | 15 | 11.6 | 12.9 | 12.2 | 0.4 | 13 | 9.8 | 12.4 | 10.9 | 0.9 | 7 | 13.5 | 14.9 | 13.9 | 0.5 |
| Caudal peduncle length | 15 | 14.1 | 16.1 | 15.4 | 0.6 | 14 | 14.1 | 15.5 | 14.9 | 0.4 | 13 | 15.4 | 18.7 | 17.1 | 1.0 | 8 | 14.3 | 15.5 | 15.0 | 0.4 |
| Predorsal length | 15 | 49.8 | 52.1 | 50.7 | 0.9 | 15 | 50.8 | 52.9 | 51.7 | 0.7 | 13 | 49.1 | 54.4 | 51.8 | 1.4 | 8 | 49.6 | 51.0 | 50.2 | 0.5 |
| Prepelvic length | 15 | 36.8 | 39.7 | 38.3 | 0.9 | 15 | 34.8 | 37.2 | 36.3 | 0.6 | 13 | 40.0 | 42.0 | 40.9 | 0.7 | 8 | 38.6 | 40.0 | 39.2 | 0.6 |
| Preanal length | 14 | 49.7 | 52.9 | 51.3 | 1.0 | 15 | 44.6 | 48.0 | 46.5 | 1.1 | 13 | 51.3 | 57.6 | 53.4 | 1.6 | 8 | 49.2 | 50.0 | 49.5 | 0.3 |
| Pectoral fin length | 15 | 18.1 | 20.9 | 19.5 | 0.7 | 14 | 19.1 | 21.1 | 20.3 | 0.7 | 3 | 16.9 | 18.8 | 17.7 | 1.0 | 0 |  |  |  |  |
| Pelvic fin length | 15 | 16.2 | 20.2 | 17.7 | 1.2 | 15 | 21.1 | 25.2 | 22.5 | 1.2 | 13 | 13.8 | 16.7 | 14.8 | 1.0 | 2 | 17.6 | 17.9 | 17.8 | 0.2 |
| Spine length of first dorsal fin | 15 | 9.4 | 11.8 | 10.7 | 0.7 | 13 | 9.9 | 11.8 | 11.0 | 0.7 | 10 | 9.8 | 12.2 | 11.0 | 0.9 | 7 | 9.2 | 10.5 | 9.7 | 0.4 |
| Spine length of second dorsal fin | 15 | 8.6 | 12.1 | 10.4 | 1.2 | 14 | 8.1 | 11.3 | 9.6 | 0.9 | 10 | 7.5 | 11.0 | 8.7 | 1.0 | 7 | 8.7 | 9.4 | 9.1 | 0.3 |
| Spine length of anal fin | 15 | 7.2 | 9.5 | 8.5 | 0.6 | 12 | 7.1 | 9.9 | 8.8 | 0.9 | 9 | 7.4 | 9.7 | 8.4 | 0.9 | 3 | 7.5 | 8.6 | 8.1 | 0.5 |
| Dorsal fin base length | 14 | 34.7 | 41.4 | 38.0 | 2.1 | 15 | 36.3 | 39.2 | 37.1 | 0.9 | 12 | 33.5 | 37.4 | 36.1 | 1.1 | 8 | 38.0 | 39.7 | 38.7 | 0.6 |
| Second dorsal fin base length | 14 | 22.0 | 26.8 | 24.2 | 1.7 | 15 | 22.6 | 26.3 | 23.9 | 1.0 | 12 | 22.1 | 24.7 | 23.3 | 0.7 | 8 | 25.2 | 27.8 | 26.5 | 0.9 |
| Anal fin base length | 14 | 37.0 | 42.3 | 39.7 | 1.6 | 15 | 44.0 | 50.5 | 46.7 | 2.0 | 12 | 32.2 | 37.3 | 35.6 | 1.6 | 8 | 41.0 | 45.1 | 42.8 | 1.6 |
| Anal fin height | 15 | 11.3 | 16.3 | 13.5 | 1.3 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |


| Lateral scales | $34-37$ | $34-35$ | $33-36$ | $7-8$ |
| :--- | :---: | :---: | :---: | :---: |
| Transverse scales | $10-11$ | 10 | $15-16$ | $10-12$ |
| Predorsal scales | $16-18$ | $16-18$ | IV-V $+\mathrm{I}, 11-14$ | 10 |
| Cheek scales | $14-20$ | $11-15$ | $\mathrm{I}, 18-22$ | $13-17$ |
| Dorsal rays | $\mathrm{IV}-\mathrm{V}+\mathrm{I}, 12-16$ | $\mathrm{IV}-\mathrm{VI}+\mathrm{I}, 12-15$ | $\mathrm{IV}-\mathrm{V}+\mathrm{I}, 12-15$ |  |
| Anal rays | $\mathrm{I}, 20-24$ | $\mathrm{I}, 26-29$ | $\mathrm{I}, 21-23$ |  |
| Pectoral rays | $12-15$ | $13-15$ | $13-14$ |  |
| Pelvic rays | $\mathrm{I}, 5$ | $\mathrm{I}, 5$ |  |  |
| Total gillrakers on first arch | $17-18$ | $17-18$ | $16-17$ | $14-18$ |


|  | Melanotaenia fasinensis |  |  |  |  | Melanotaenia fredericki |  |  |  |  | Melanotaenia irianjaya |  |  |  |  | Melanotaenia kokasensis |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Material examined |  |  |  |  | Material examined |  |  |  |  | Material examined |  |  |  |  | Material examined |  |  |  |  |
| SL (mm) | .9-120.2 |  |  |  |  | 55. |  |  |  |  | 39.6-102. |  |  |  |  | 49.1-57.2 |  |  |  |  |
| in \% standard length | n | min | max | mean | SD | n | min | ma | mean | SD | $n$ | min | max | mean | SD | $n$ | min | max | mean | SD |
| Head length | 13 | 23.1 | 25.0 | 24.5 | 0.5 | 11 | 23.7 | 25.4 | 24.5 | 0.5 | 14 | 25.3 | 27.0 | 25.9 | 0.5 | 3 | 25.9 | 26.7 | 26.2 | 0.4 |
| Snout length | 13 | 9.2 | 9.5 | 9.3 | 0.1 | 11 | 7.7 | 8.4 | 8.2 | 0.2 | 14 | 9.2 | 10.3 | 9.6 | 0.4 | 3 | 8.3 | 8.6 | 8.5 | 0.2 |
| Interorbital width | 13 | 7.6 | 8.2 | 7.9 | 0.2 | 12 | 8.0 | 8.4 | 8.2 | 0.1 | 14 | 8.3 | 9.4 | 8.9 | 0.3 | 3 | 9.0 | 9.2 | 9.1 | 0.1 |
| Eye diameter | 13 | 6.4 | 8.1 | 7.4 | 0.5 | 12 | 7.4 | 8.5 | 7.8 | 0.3 | 14 | 7.4 | 8.4 | 7.9 | 0.3 | 3 | 8.2 | 8.7 | 8.5 | 0.3 |
| Body depth | 13 | 27.8 | 37.9 | 33.0 | 2.5 | 11 | 26.3 | 33.0 | 29.8 | 2.2 | 13 | 28.6 | 38.1 | 33.6 | 2.7 | 3 | 30.1 | 31.4 | 30.8 | 0.6 |
| Body width | 13 | 12.1 | 14.2 | 12.8 | 0.5 | 11 | 11.5 | 12.9 | 12.4 | 0.4 | 12 | 12.5 | 15.3 | 13.5 | 0.9 | 3 | 11.3 | 11.8 | 11.6 | 0.3 |
| Caudal peduncle depth | 13 | 10.1 | 10.8 | 10.4 | 0.2 | 12 | 9.3 | 11.0 | 10.2 | 0.6 | 14 | 9.7 | 11.1 | 10.5 | 0.4 | 3 | 11.2 | 11.5 | 11.4 | 0.1 |
| Caudal peduncle length | 13 | 13.3 | 15.6 | 14.6 | 0.8 | 11 | 13.0 | 17.7 | 15.5 | 1.3 | 14 | 14.4 | 17.6 | 15.9 | 1.0 | 3 | 17.5 | 18.9 | 18.0 | 0.8 |
| Predorsal length | 13 | 48.1 | 49.8 | 48.8 | 0.6 | 12 | 47.7 | 51.9 | 50.1 | 1.3 | 13 | 50.0 | 52.5 | 51.2 | 0.7 | 3 | 49.6 | 49.7 | 49.7 | 0.1 |
| Prepelvic length | 13 | 34.5 | 38.8 | 36.2 | 1.1 | 12 | 33.9 | 39.5 | 36.5 | 1.9 | 11 | 36.8 | 38.7 | 37.6 | 0.6 | 3 | 37.8 | 38.5 | 38. | 0.4 |
| Preanal length | 13 | 45.6 | 48.4 | 46.8 | 0.9 | 12 | 45.4 | 53.0 | 48.1 | 2.5 | 13 | 48.5 | 52.5 | 50.1 | 1.2 | 3 | 50.2 | 50.6 | 50.4 | 0.2 |
| Pectoral fin length | 11 | 17.4 | 19.9 | 18.6 | 0.8 | 10 | 17.6 | 21.2 | 19.2 | 1.0 | 13 | 18.6 | 20.9 | 19.9 | 0.7 | 3 | 18.2 | 20.0 | 19.3 | 0.9 |
| Pelvic fin length | 11 | 17.0 | 19.5 | 18.5 | 0.8 | 11 | 16.1 | 19.3 | 17.1 | 0.9 | 9 | 20.6 | 24.9 | 22.4 | 1.5 | 3 | 16.3 | 17.9 | 17.0 | 0.8 |
| Spine length of first dorsal fin | 13 | 10.0 | 12.7 | 11.1 | 0.9 | 10 | 12.0 | 13.9 | 12.8 | 0.6 | 6 | 12.3 | 13.6 | 13.0 | 0.5 | 3 | 12.3 | 12.9 | 12.6 | 0.3 |
| Spine length of second dorsal fin | 13 | 7.3 | 11.6 | 9.3 | 1.2 | 9 | 11.7 | 13.7 | 12.6 | 0.7 | 6 | 12.3 | 14.1 | 13.2 | 0.7 | 3 | 10.8 | 13.1 | 11.9 | 1.2 |
| Spine length of anal fin | 12 | 7.0 | 8.8 | 8.1 | 0.7 | 9 | 8.9 | 9.6 | 9.2 | 0.2 | 6 | 9.8 | 11.6 | 10.5 | 0.6 | 3 | 8.7 | 9.8 | 9.1 | 0.6 |
| Dorsal fin base length | 13 | 39.0 | 42.2 | 40.4 | 1.1 | 11 | 34.7 | 38.8 | 36.8 | 1.4 | 12 | 35.0 | 37.7 | 36.5 | 1.0 | 3 | 33.6 | 37.1 | 35.5 | 1.8 |
| Second dorsal fin base length | 13 | 25.9 | 29.5 | 27.2 | 1.0 | 11 | 21.0 | 24.6 | 23.0 | 1.1 | 9 | 21.1 | 23.7 | 22.8 | 0.9 | 3 | 21.0 | 23.1 | 22.2 | 1.1 |
| Anal fin base length | 13 | 40.6 | 48.4 | 42.9 | 2.3 | 11 | 36.1 | 43.0 | 39.9 | 2.2 | 14 | 36.4 | 43.5 | 39.5 | 2.4 | 3 | 37.4 | 37.9 | 37.6 | 0.3 |
| Anal fin height |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

Anal fin height

| Lateral scales | 37-39 | 36-39 | 35-39 | 36-38 |
| :---: | :---: | :---: | :---: | :---: |
| Transverse scales | 9 | 7-8 | 10 | 10 |
| Predorsal scales | 17-19 | 16-19 | 17-19 | 16-17 |
| Cheek scales | 14-18 | 13-16 | 13-16 | 14 |
| Dorsal rays | IV-VI + I, 14-17 | V-VI + I, 12-16 | IV-VI + I, 12-16 | $\mathrm{IV}-\mathrm{V}+\mathrm{I}, 12-14$ |
| Anal rays | I,24-27 | I,24-25 | I,22-26 | I,23 |
| Pectoral rays | 13-15 | 13-15 | 13-15 | 13-14 |
| Pelvic rays | I,5 | I,5 | I,5 | I,5 |
| Total gillrakers on first arch | 17-19 | 13-16 | 19-21 | 16-19 |


|  | Melanotaenia misoolensis |  |  |  |  | Melanotaenia multiradiata |  |  |  |  | Melanotaenia parva |  |  |  |  | Melanotaenia salawati |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Material examined |  |  |  |  | Material examined |  |  |  |  | Material examined |  |  |  |  | Material examined |  |  |  |  |
| SL (mm) | 46.1-77.4 |  |  |  |  | 64.1-89.9 |  |  |  |  | 50.7-67.0 |  |  |  |  | 68.0-91.6 |  |  |  |  |
| in \% standard length | n | min | max | mean | SD | n | min | max | mean | SD | n | min | max | mean | SD | n | min | max | mean | SD |
| Head length | 8 | 25.4 | 26.6 | 26.1 | 0.5 | 14 | 24.5 | 26.3 | 25.5 | 0.5 | 8 | 25.3 | 27.6 | 26.3 | 0.8 | 16 | 23.9 | 25.1 | 24.7 | 0.4 |
| Snout length | 8 | 8.6 | 9.0 | 8.8 | 0.1 | 14 | 8.9 | 9.7 | 9.3 | 0.2 | 8 | 8.2 | 9.1 | 8.7 | 0.3 | 16 | 8.5 | 9.1 | 8.8 | 0.2 |
| Interorbital width | 8 | 9.0 | 9.5 | 9.3 | 0.2 | 14 | 7.7 | 8.3 | 8.0 | 0.2 | 8 | 8.7 | 9.5 | 9.1 | 0.2 | 16 | 8.6 | 9.2 | 8.9 | 0.2 |
| Eye diameter | 8 | 8.4 | 9.9 | 9.1 | 0.5 | 14 | 6.7 | 7.4 | 7.1 | 0.2 | 8 | 7.9 | 8.4 | 8.2 | 0.2 | 16 | 6.9 | 7.9 | 7.5 | 0.3 |
| Body depth | 8 | 29.1 | 34.1 | 31.7 | 1.7 | 14 | 27.1 | 30.5 | 28.7 | 1.0 | 7 | 32.7 | 37.5 | 35.0 | 1.8 | 16 | 32.1 | 37.9 | 34.4 | 1.6 |
| Body width | 8 | 12.5 | 14.1 | 13.1 | 0.5 | 14 | 11.2 | 12.6 | 12.0 | 0.4 | 8 | 13.8 | 15.9 | 15.1 | 0.7 | 16 | 12.5 | 13.7 | 13.3 | 0.3 |
| Caudal peduncle depth | 7 | 10.7 | 11.3 | 10.9 | 0.2 | 14 | 9.3 | 10.0 | 9.7 | 0.2 | 8 | 11.6 | 12.5 | 12.1 | 0.4 | 16 | 11.0 | 12.6 | 11.9 | 0.5 |
| Caudal peduncle length | 7 | 15.6 | 16.5 | 16.1 | 0.4 | 14 | 14.1 | 15.9 | 15.0 | 0.5 | 8 | 16.8 | 19.4 | 17.8 | 0.9 | 16 | 15.7 | 16.7 | 16.2 | 0.3 |
| Predorsal length | 8 | 48.1 | 51.2 | 49.5 | 0.9 | 13 | 49.5 | 50.9 | 50.3 | 0.4 | 7 | 50.8 | 52.8 | 51.3 | 0.7 | 16 | 51.4 | 54.8 | 52.2 | 0.9 |
| Prepelvic length | 7 | 37.9 | 39.1 | 38.5 | 0.4 | 14 | 36.3 | 38.6 | 37.5 | 0.7 | 8 | 38.3 | 41.0 | 39.8 | 1.1 | 16 | 34.5 | 37.2 | 35.9 | 0.6 |
| Preanal length | 8 | 48.5 | 51.4 | 49.4 | 0.9 | 14 | 48.6 | 50.8 | 49.8 | 0.7 | 8 | 50.6 | 53.3 | 52.1 | 0.9 | 16 | 44.2 | 48.1 | 46.3 | 1.1 |
| Pectoral fin length | 8 | 18.4 | 20.4 | 19.5 | 0.8 | 14 | 16.9 | 19.2 | 18.5 | 0.6 | 8 | 18.1 | 19.3 | 18.8 | 0.5 | 13 | 20.2 | 22.5 | 21.4 | 0.7 |
| Pelvic fin length | 8 | 16.9 | 19.7 | 18.0 | 1.1 | 14 | 16.4 | 21.8 | 17.9 | 1.5 | 8 | 15.1 | 17.3 | 16.1 | 0.8 | 15 | 18.5 | 22.0 | 20.4 | 1.1 |
| Spine length of first dorsal fin | 8 | 10.2 | 12.2 | 11.2 | 0.7 | 14 | 10.5 | 12.4 | 11.5 | 0.6 | 8 | 9.4 | 11.4 | 10.1 | 0.6 | 14 | 9.5 | 12.2 | 10.7 | 0.7 |
| Spine length of second dorsal fin | 8 | 9.4 | 13.3 | 10.5 | 1.2 | 14 | 10.0 | 13.6 | 11.4 | 1.0 | 8 | 8.1 | 10.7 | 8.9 | 0.9 | 15 | 8.6 | 11.7 | 10.2 | 1.0 |
| Spine length of anal fin | 8 | 9.0 | 11.1 | 9.7 | 0.7 | 13 | 7.9 | 10.0 | 8.9 | 0.6 | 7 | 7.1 | 8.9 | 7.7 | 0.7 | 15 | 7.4 | 9.7 | 8.7 | 0.7 |
| Dorsal fin base length | 8 | 37.3 | 40.5 | 38.5 | 1.1 | 14 | 34.7 | 38.7 | 36.4 | 1.0 | 8 | 33.8 | 37.4 | 36.1 | 1.2 | 16 | 33.7 | 36.1 | 35.1 | 0.7 |
| Second dorsal fin base length | 8 | 22.7 | 24.3 | 23.5 | 0.6 | 14 | 21.7 | 24.9 | 23.5 | 0.9 | 8 | 20.7 | 24.7 | 22.8 | 1.5 | 16 | 19.7 | 22.3 | 21.0 | 0.9 |
| Anal fin base length | 8 | 38.4 | 42.1 | 39.9 | 1.3 | 14 | 37.6 | 41.1 | 39.0 | 1.1 | 8 | 33.1 | 38.2 | 35.9 | 1.7 | 16 | 43.9 | 48.3 | 45.6 | 1.3 |
| Anal fin height | 4 | 13.7 | 15.5 | 14.6 | 0.7 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |


| Lateral scales | $34-36$ | $36-39$ | $34-36$ |
| :--- | :---: | :---: | :---: |
| Transverse scales | 10 | $10-11$ | 10 |
| Predorsal scales | $14-18$ | $16-19$ | $14-18$ |
| Cheek scales | $13-16$ | $13-17$ | $10-13$ |
| Dorsal rays | $\mathrm{IV}-\mathrm{VI}+\mathrm{I}, 13-14$ | $\mathrm{IV}-\mathrm{VI}+\mathrm{I}, 13-16$ | $\mathrm{~V}-\mathrm{VI}+\mathrm{I}, 11-13$ |
| Anal rays | $\mathrm{I}, 23-26$ | $\mathrm{I}, 24-27$ | $\mathrm{I}, 19-23$ |
| Pectoral rays | $13-14$ | $15-16$ | $12-14$ |
| Pelvic rays | $\mathrm{I}, 5$ | $\mathrm{I}, 5$ | I |
| Total gillrakers on first arch | $16-19$ | $18-19$ | 10 |


|  | Melanotaenia synergos |  |  |  |  | Melanotaenia urisa |  |  |  |  | Melanotaenia veoliae |  |  |  |  | Melanotaenia wanoma |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Material examined |  |  |  |  | Material examined |  |  |  |  | Material examined |  |  |  |  | Material examined |  |  |  |  |
| SL (mm) | 57.7-67.1 |  |  |  |  | 57.4-87.8 |  |  |  |  | 53.9-92.3 |  |  |  |  | 59.6-72.8 |  |  |  |  |
| in \% standard length | n | min | max | mean | SD | n | min | max | mean | SD | n | min | max | mean | SD | n | min | max | mean | SD |
| Head length | 5 | 25.4 | 26.3 | 25.8 | 0.4 | 17 | 23.7 | 25.2 | 24.5 | 0.4 | 16 | 25.3 | 27.0 | 25.9 | 0.5 | 18 | 24.7 | 26.4 | 25.6 | 0.6 |
| Snout length | 5 | 9.2 | 9.6 | 9.3 | 0.2 | 17 | 7.6 | 8.7 | 8.4 | 0.3 | 16 | 8.0 | 9.1 | 8.7 | 0.3 | 18 | 8.0 | 9.1 | 8.6 | 0.3 |
| Interorbital width | 5 | 9.8 | 10.3 | 10.0 | 0.2 | 17 | 7.9 | 8.8 | 8.5 | 0.2 | 16 | 9.0 | 9.5 | 9.2 | 0.1 | 18 | 8.4 | 9.0 | 8.7 | 0.2 |
| Eye diameter | 5 | 7.9 | 8.3 | 8.1 | 0.1 | 17 | 8.0 | 9.0 | 8.4 | 0.3 | 16 | 6.3 | 7.9 | 7.4 | 0.4 | 18 | 7.3 | 7.8 | 7.6 | 0.1 |
| Body depth | 5 | 33.2 | 34.6 | 33.9 | 0.5 | 17 | 27.0 | 34.2 | 30.6 | 2.1 | 16 | 30.8 | 37.5 | 33.8 | 1.8 | 18 | 28.7 | 32.8 | 30.7 | 1.1 |
| Body width | 5 | 13.2 | 13.8 | 13.5 | 0.2 | 17 | 10.0 | 11.2 | 10.6 | 0.4 | 16 | 11.3 | 12.6 | 11.9 | 0.4 | 18 | 11.4 | 13.5 | 12.4 | 0.7 |
| Caudal peduncle depth | 5 | 13.5 | 14.1 | 13.8 | 0.2 | 17 | 8.6 | 10.0 | 9.6 | 0.4 | 16 | 10.3 | 11.7 | 11.0 | 0.5 | 18 | 10.0 | 11.1 | 10.6 | 0.3 |
| Caudal peduncle length | 5 | 15.8 | 18.2 | 17.2 | 1.0 | 17 | 16.3 | 19.0 | 17.4 | 1.0 | 16 | 16.5 | 17.7 | 16.9 | 0.4 | 18 | 14.0 | 16.1 | 15.4 | 0.6 |
| Predorsal length | 5 | 47.5 | 49.5 | 48.7 | 0.8 | 17 | 50.6 | 54.5 | 52.3 | 0.9 | 16 | 49.5 | 52.1 | 50.6 | 0.9 | 16 | 47.3 | 49.5 | 48.4 | 0.8 |
| Prepelvic length | 5 | 38.7 | 40.4 | 39.5 | 0.7 | 16 | 36.3 | 39.2 | 37.3 | 0.7 | 16 | 36.9 | 38.0 | 37.5 | 0.4 | 17 | 38.3 | 40.4 | 39.2 | 0.7 |
| Preanal length | 5 | 48.5 | 49.8 | 49.1 | 0.5 | 17 | 47.0 | 49.1 | 48.3 | 0.7 | 16 | 47.4 | 49.3 | 48.3 | 0.6 | 17 | 49.6 | 52.8 | 50.9 | 1.1 |
| Pectoral fin length | 0 |  |  |  |  | 15 | 15.2 | 17.4 | 16.2 | 0.6 | 13 | 18.1 | 20.7 | 19.5 | 0.7 | 18 | 18.7 | 20.7 | 19.6 | 0.6 |
| Pelvic fin length | 4 | 17.1 | 18.5 | 17.8 | 0.6 | 17 | 11.0 | 13.7 | 12.5 | 0.6 | 15 | 16.4 | 20.1 | 19.0 | 1.0 | 18 | 16.3 | 19.5 | 17.6 | 0.9 |
| Spine length of first dorsal fin | 4 | 8.3 | 8.9 | 8.7 | 0.3 | 17 | 9.0 | 12.8 | 10.7 | 1.2 | 15 | 10.2 | 12.8 | 11.7 | 0.7 | 17 | 10.2 | 12.1 | 11.3 | 0.5 |
| Spine length of second dorsal fin | 4 | 7.0 | 8.9 | 7.8 | 0.9 | 17 | 8.3 | 14.3 | 10.7 | 1.8 | 16 | 7.9 | 11.2 | 9.7 | 0.9 | 18 | 9.2 | 12.9 | 10.6 | 1.1 |
| Spine length of anal fin | 2 | 5.9 | 7.9 | 6.9 | 1.4 | 16 | 7.1 | 8.5 | 7.8 | 0.3 | 15 | 9.1 | 11.3 | 10.0 | 0.6 | 17 | 9.1 | 10.4 | 9.6 | 0.3 |
| Dorsal fin base length | 5 | 38.6 | 41.1 | 39.4 | 1.0 | 16 | 30.8 | 35.7 | 33.7 | 1.6 | 15 | 36.7 | 39.9 | 38.0 | 1.1 | 18 | 36.8 | 40.5 | 38.7 | 1.0 |
| Second dorsal fin base length | 5 | 25.2 | 27.3 | 26.1 | 0.8 | 16 | 20.4 | 23.5 | 22.0 | 1.0 | 15 | 23.2 | 25.8 | 24.3 | 0.9 | 18 | 24.3 | 27.5 | 25.6 | 1.1 |
| Anal fin base length | 5 | 41.6 | 43.3 | 42.3 | 0.7 | 16 | 35.4 | 41.3 | 38.1 | 1.6 | 15 | 37.9 | 45.1 | 41.3 | 1.8 | 18 | 36.0 | 41.4 | 39.3 | 1.3 |
| Anal fin height |  |  |  |  |  | 17 | 6.8 | 9.9 | 8.5 | 0.9 | 11 | 12.7 | 16.6 | 14.3 | 1.3 | 18 | 11.9 | 17.4 | 13.2 | 1.2 |


| Lateral scales | 32-33 | 36-39 | 34-37 | 34-36 |
| :---: | :---: | :---: | :---: | :---: |
| Transverse scales | 10 | 10-11 | 10-11 | 10-11 |
| Predorsal scales | 15-17 | 18-20 | 17-18 | 15-17 |
| Cheek scales | 13-18 | 13-16 | 12-14 | 14-18 |
| Dorsal rays | IV-VI + I, 11-12 | $\mathrm{IV}-\mathrm{V}+\mathrm{I}, 12-15$ | IV-V + I, 12-13 | IV-VI + I, 14-15 |
| Anal rays | I,18-21 | I,21-23 | I,22-27 | I,22-25 |
| Pectoral rays | 13-14 | 13-14 | 12-13 | 13-14 |
| Pelvic rays | I,5 | I,5 | I,5 | I,5 |
| Total gillrakers on first arch | 14-18 | 17-18 | 18-20 | 15-16 |


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