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Morphological analysis of the endemic freshwater halfbeak *Dermogenys orientalis* (Weber, 1894) in Maros-Pangkep Karst Area, South Sulawesi, Indonesia

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Abstract. *Umar MT, Omar SBA, Hidayani AA, Ashad ANA, Gazali M, Umar W, Andriyono S, Tenriulo A, Moore AM. 2024. Morphological analysis of the endemic freshwater halfbeak* Dermogenys orientalis *(Weber, 1894) in Maros-Pangkep Karst Area, South Sulawesi, Indonesia. Biodiversitas 25: 3056-3066.* The viviparous halfbeak *Dermogenys orientalis* (Weber, 1894) is a freshwater fish endemic to the Maros-Pangkep Karst Area in South Sulawesi, Indonesia. Halfbeaks have a unique shape with a beak-like upper jaw considerably longer than the lower jaw. To date, research on the biology of this fish has been limited, in particular with respect to morphology. This study aims to analyze morphological (morphometric, and meristic) characteristics of *D. orientalis* populations in the Pattunuang, Bantimurung, and Leang-Leang rivers by sex. Morphological identification was carried out by comparing the morphology of fish originating from the Maros-Pangkep Karst Area based on the characteristics of the fish obtained and carried out in-situ. Morphometric analysis was performed using Stepwise Discriminant Analysis. Phenotypic distance between populations was inferred using Predicted Group Membership and Pairwise Group Comparison. Equality of Group Means Test was applied to discriminant morphometric traits and the t-test (α=0.05) to meristic traits. All statistical tests were performed using SPSS software version 22.0. The results showed that *D. orientalis* was sexually dimorphic and viviparous. In addition to the male andropodium, *D. orientalis* exhibited sexual dimorphism in body shape, and females were significantly longer (standard length) than males. The species characters identification found in this study were 13 and 19 characters for males and females respectively. The results of the t-test on the meristic character data that have been obtained, the mean values of three meristic traits (pectoral, anal and caudal fin ray counts) differed significantly between groups.

Keywords: *Dermogenys orientalis,* endemic halfbeak, karst area, morphology, morpho-meristic

INTRODUCTION

The Indonesian island of Sulawesi, situated in the heart of Wallacea between Asia and Australia, hosts many extant native species, many of which are restricted range endemic taxa, despite significant habitat degradation and the introduction of many alien species (Tweedley et al. 2013; Miesen et al. 2016; Hasan et al. 2021; Ndobe et al. 2023). At least 120 endemic aquatic species (fish and invertebrates) have been identified in Sulawesi's ancient lakes alone (Struebig et al. 2022). Additional species still being discovered in other Sulawesi lakes and rivers, including Sulawesi endemic freshwater taxa and diadromous taxa such as amphidromous gobies that are now considered native to Sulawesi (Huylebrouck et al. 2014; Kobayashi et al. 2020; Hasan et al. 2021; Gani et al. 2021, 2022; Ndobe et al. 2022, 2023; Nurjirana et al. 2022, 2023; Utama et al. 2024). Sulawesi endemic fishes mostly belong to three families: Tematherinidae (sailfin silversides), Adrianichthyidae (ricefishes), and Zenarchopteridae (halfbeaks) (Miesen et al. 2016). Halfbeaks of the genus *Dermogenys* (family Zenarchopteridae, order Beloniformes) are viviparous fish with a characteristic elongated lower jaw (Kobayashi et al. 2020). The mandibular elongation process occurs at the developmental stage and in adult fish. The tip of the lower jaw is bright red or orange in many species due to carotenoid pigments, particularly zeaxanthin, astaxanthin, and beta-doradexanthin (Kusumah et al. 2016). First described as *Hemiramphus orientalis* Weber, 1984, *Dermogenys orientalis* is one of the halfbeaks endemic to the freshwaters of Sulawesi Island (Omar et al. 2020). The known *D. orientalis* is distribution includes several regions in the southwestern part of Sulawesi, including the Maros-Pangkep Karst Area (Weber 1984; Meisner 2001; Samsudin 2017; Omar et al. 2020, 2021).

The Maros-Pangkep karst in the Bantimurung Bulusaraung National Park is the second largest and most beautiful in the world after the karst area in China (Rahman 2022; Hakim et al. 2023). The Maros-Pangkep Karst Area has unique geomorphology with some of the best cone karst formations in the world (Putri et al. 2020). In general, freshwater ecosystems in karst areas are subject to change and can become degraded or lost due to the poor performance of karst rock in filtering contaminants from human, livestock, and industrial sewage and wastewater (Kolda et al. 2020). The biodiversity of karst areas is special and unique because they contain endemic, rare, and protected species that have adapted to the karst environment and are typically found in isolated populations that are extremely limited in terms of geographic extent and found at low densities and/or low abundance (Putri et al. 2020; Yang et al. 2021).

The halfbeak *D. orientalis* is one of several fish endemic to the Maros-Pangkep Karst Area (Omar et al. 2021). Due to its attractive shape, color, and behavior, *D. orientalis* is traded as an ornamental fish (Kusumah et al. 2016; Samsudin et al. 2018). Exploitation for the aquarium trade is thought to be a major driver of the observed decrease in abundance and diversity of native fish species in the region, while capture for research may also represent a threat to the declining populations (Nur et al. 2019). In addition to the direct threat from capture fisheries, *D. orientalis* populations are also at risk from indirect anthropogenic threats such as habitat degradation (e.g. siltation) and the introduction of alien species (Kusumah et al. 2016). To date, captive breeding of *D. orientalis* for conservation purposes (e.g. re-stocking) has not yet been undertaken. There is a need to conserve the endemic fish populations, including *D. orientalis*, and their habitat in the unique Maros-Pankep Karst Area (Kudsiah et al. 2022).

Comprehensive study and assessment of the morphological characteristics of a species can support the development of a conservation strategy at relevant local levels (Zaccara et al. 2019; Hasan et al. 2022). Fishes in the genus *Dermogenys* are typically limited to specific freshwater and estuarine habitats, including major rivers such as the Mekong and the waterways of the Indonesian and Philippine Islands (Samsudin et al. 2018). While some halfbeak species have quite extensive natural geographic distribution, others have restricted geographical distributions (Samsudin et al. 2018). Furthermore, morphological identification of *Dermogenys* can be quite challenging due to the small size of the individuals and overlapping morphological characteristics within this genus (Samsudin et al. 2018).

The halfbeak *D. orientalis* has a restricted distribution in the Maros-Pangkep Karst Area, South Sulawesi, Indonesia. Nonetheless, populations are found in several river systems or watersheds (Nur et al. 2019), and sexual dimorphism (modified anal fin forming an andropodium) is a diagnostic trait of the viviparous genus *Dermogenys* (Meisner 2001). Sexual dimorphism or morphological variations between the sexes can arise through evolutionary and ecological processes, for example when each sex has developed different habits and related functional adaptations (Acar and Kaymak 2023). Diversification selection may facilitate morphological differences between the sexes, while the different reproductive life histories of males and females can both limit and drive dimorphism in terms of form and the degree of between-population divergence (Dorado et al. 2012). However, the morpho-meristic characteristics of *D. orientalis* have not been characterized in detail at population level, including differences between males and females. Therefore, the purpose of this study was to describe and compare the morphology and morpho-meristic of male and female *D. orientalis* halfbeaks in three rivers within the Maros-Pangkep Karst Area.

MATERIALS AND METHODS

Study area

Specimens of the halfbeak *D. orientalis* were obtained from collectors in three rivers in the Maros and Pangkajene dan Kepulauan (Pangkep) karst area, South Sulawesi, Indonesia, namely the Bantimurung River, Pattunuang River and Leang-Leang River (Table 1, Figures 1 and 2). The samples comprised 30 males and 30 females from each sampling site. Morphological identification was conducted according to the guidelines in Huylebrouck et al. (2012).

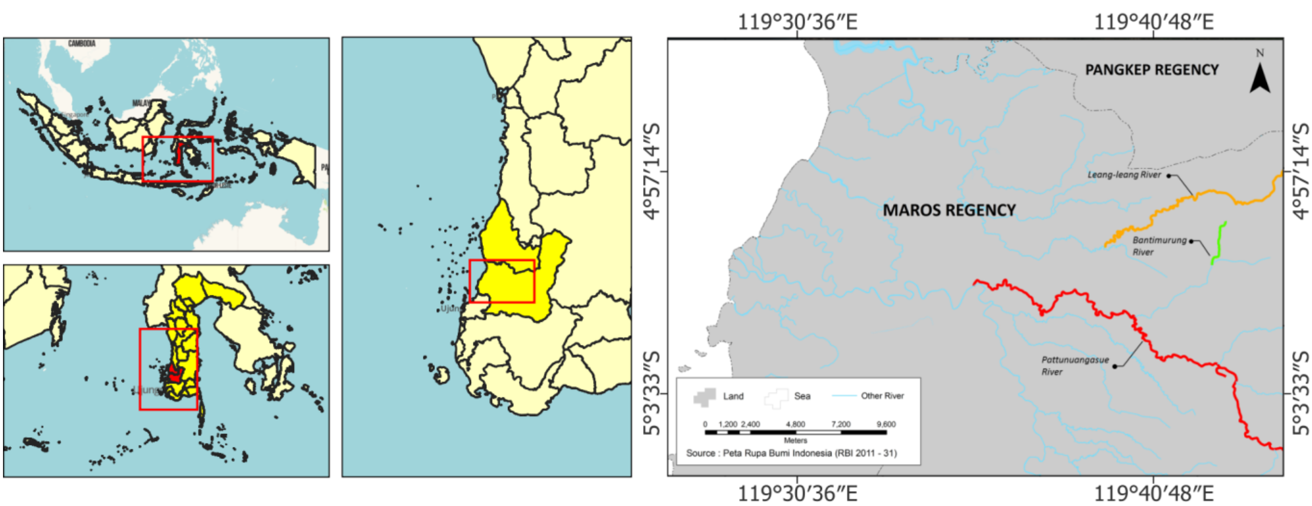

Figure 1. Location of Maros-Pangkep Karst Area of Maros and Pangkajene dan Kepulauan (Pangkep) districts, South Sulawesi, Indonesia

Procedures

Morphological identification

Morphological identification at the species level was carried out in situ at each site in the Maros-Pangkep Karst Area based on external characteristics. Specimens identified as *D. orientalis* and collected for this study were photographed using a digital camera.

Morpho-meristic analysis

The morphometric traits and meristic counts in this study were determined following the method of Huylebrouck et al. (2012), as shown in Tables 2 and 3. These parameters were coded to facilitate data collection and analysis (Figure 3).

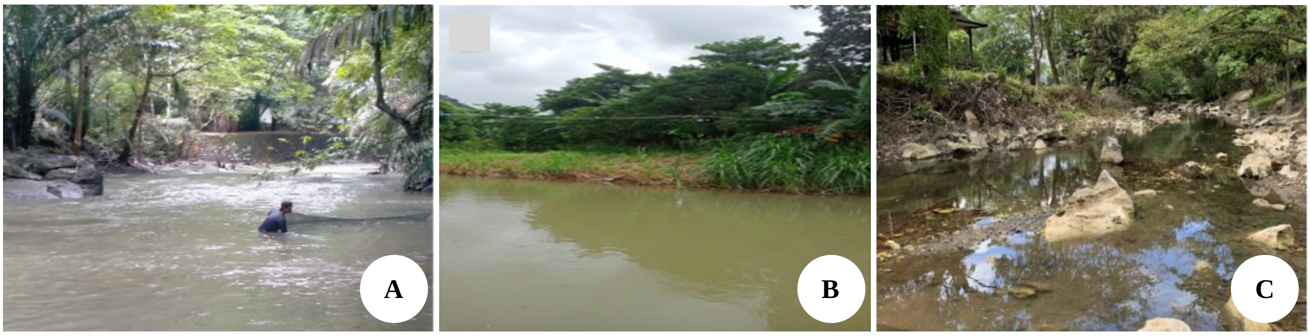

Figure 2. Halfbeak habitat at sampling sites in the Maros-Pangkep Karst Area of South Sulawesi, Indonesia: A. Bantimurung River; B. Pattunuang River; C. Leang-Leang River

Table 1. Coordinates and description of sampling locations

River	Coordinates	Site description
Bantimurung	5°01’10.575” S, 119°40’06.069” E	Fast water flow, with rocky, sandy and muddy substrates
Pattunuang	5°03’08.615’ S, 119°43’04.112” E	Stagnant water flow, with rocky, sandy and muddy substrates
Leang-Leang	4°58’43.035’ S, 119°40’27.132” E	Stagnant water flow, with rocky, sandy and muddy substrates

Table 2. Morphometric characteristics measured for the halfbeak *D. orientalis*

Morphometric trait	
Trait (abbreviation)	**Description**
Standard Length (SL)	The distance between the leading edge of the mouth and the base of the caudal fin
Total Length Including Beak (TL)	The distance between the leading edge of the mouth and the rear end of the caudal fin
Lower Jaw Length Brembach (LJLB)	The distance between the leading edge of the mouth and the leading edge of the maxilla
Lower Jaw Length (LJL)	The distance from the leading edge of the lower jaw to the base of the lower jaw
Upper Jaw Length (UJW)	The distance from the leading edge of the maxilla to the base of the maxilla
Bony Orbital Diameter (ORBL)	The distance to the center line of the eye sockets
Head Length (HDL)	The distance between the leading edge of the maxilla and the rear end of the operculum
Snout To Pectoral-Fin Distance (SN-P)	The distance between the leading edge of the maxilla and the base of the pectoral fins
Snout To Ventral-Fin Distance (SN-V)	The distance between the leading edge of the maxilla and the base of the ventral fins
Body Depth at Pectoral-Fin Base (BDP)	The distance between the upper body surface and the lower body surface past the base of the pectoral fins
Body Depth at Ventral-Fin Base (BDV)	The distance between the upper body surface and the lower body surface that passes through the base of the ventral fins
Depth of Caudal Peduncle (P_1-C)	The distance measured between the two bases of the caudal fin
Ventral-Fin to Caudal-Fin Distance (V-C)	The distance between the base of the ventral fins and the base of the caudal fin
Length of Pectoral Fin (LPF)	The distance between the base of the pectoral fins and the tip of the pectoral fins
Length of Pectoral-Fin Base (LPFB)	The distance between the bases of the pectoral fins
Length of Dorsal Fin (LDF)	The distance between the base of the dorsal fin and the tip of the dorsal fin
Length of Dorsal-Fin Base (LDFB)	The distance from the base of the dorsal fin
Length of Ventral Fin (LVF)	The distance between the base of the ventral fins and the tip of the ventral fins
Length of Ventral-Fin Base (LVFB)	The distance between the bases of the ventral fins
Length of Anal fin (LAF)	The distance between the base of the anal fin and the tip of the anal fin
Length of Anal-Fin Base (LAFB)	The distance from the base of the anal fin
Length of Caudal fin (LCF)	The distance between the base of the caudal fin and the tip of the rear caudal fin

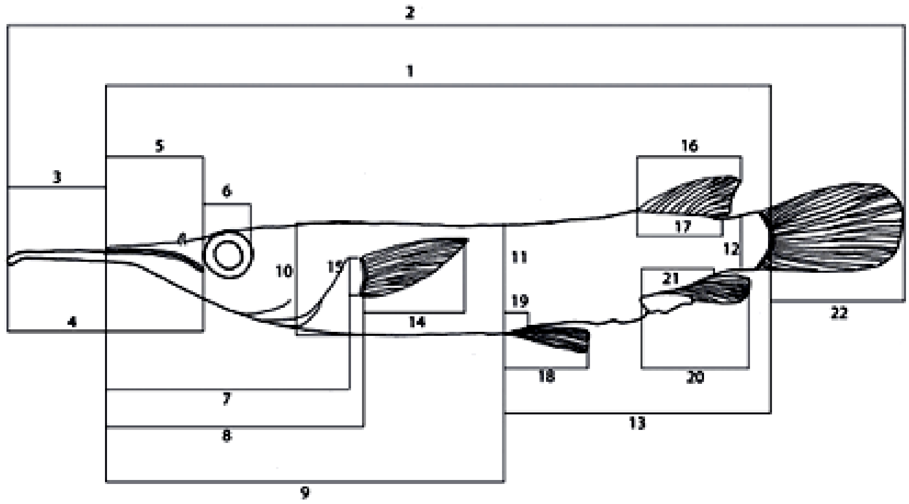

Figure 3. Schematic diagram showing morphometric characteristics used in halfbeak identification (Dorado et al. 2012)

Table 3. Meristic counts recorded for the halfbeak *D. orientalis*

Meristic count	
Code	**Description**
A	Number of anal fin rays
C	Number of caudal fin rays
D	Number of dorsal fin rays
P	Number of pectoral fin rays
V	Number of ventral fin rays

The specimens collected were divided into 10 classes based on standard length (SL, in mm) following Omar (2013). Morphometric character data were standardized to reduce bias using the following equation (Elliott et al. 1995):

$$Ms = Mo\ (Ls/Lo)b$$

Where: Ms=standardized measurement, Mo=measured character length, Ls=mean standard length of all fish in each group (6 groups, by sex and river), Lo=measured standard length of the specimen, b=exponent calculated from the logarithmic linear regression of the equation M=aLb for the sex/river group in question, where M is the length of the character and L is the Standard Length (SL), with all measurements in mm.

Data analysis

The morphometric and meristic data were tabulated and presented as mean ± Standard Deviation (SD). Differences between populations and sex were tested using Predicted Group Membership (PGM) analysis, and a discriminant test was used to evaluate the significance of the differences between the morphometric characteristics of the sampled halfbeak *D. orientalis* populations in the Bantimurung River, Pattunuang River, and Leang-Leang River at a confidence level of 95% (α=0.05) (Elliott et al. 1995). The meristic characters (counts) were compared using the Student's t-test (α=0.05) (Omar 2013). Data analyses were conducted in SPSS version 22.0

RESULTS AND DISCUSSION

Morphological identification

The typical morphology of *D. orientalis* can be seen in Figure 4 and sexual dimorphism in anal fin structure in Figure 5. The modified anal fin forming an andropodium (Figure 5.A) is typical of males in the genus *Dermogenys*. The fin ray counts for male and female *D. orientalis* from the Bantimurung, Pattunuang, and Leang-Leang rivers are shown in Table 4 together with ranges reported in the scientific literature.

Figure 4. The halfbeak *D. orientalis* Weber, 1894 (Figure adapted from Omar et al. 2021)

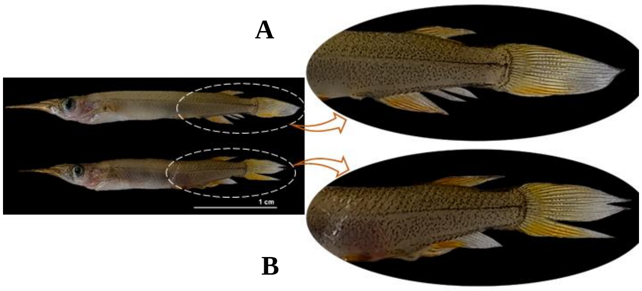

Figure 5. Morphological differences (sexual dimorphism) between (A) male and (B) female *Dermogenys orientalis*

The body form of the specimens collected were consonant with the original description (Weber 1894) and re-description by Meisner (2001); in particular, the slender body form, elongated lower jaw, and modified anal fin (andropodium) of male specimens. Live specimens conformed to the limited color description in Weber (1894), having a brownish body color and a darker stripe from the operculum to the base of the caudal fin. Preserved specimens from this study were white to (pale) tan in color, with a thin stripe following the lateral line, and scattered melanophores on the body and fins, as described by Meisner (2001); they also resemble the plate in Kottelat et al. (1993) showing preserved *D. orientalis* specimens.

Morphometric and meristic (morpho-meristic) analysis

The Canonical Discriminant Function (CDF) plot shows a clear grouping by sex and river (Figure 6). The centroid groupings for males and females were most distinct in fish from the Leang-Leang River. The pattern was similar for males and females from the Bantimurung and Pattunuang Rivers, although a few males from the Bantimurung River had similar centroid characteristics to males from the Pattunuang River. The CDF plot also indicates that the population from each river has distinctive centroid characteristics.

The Predicted Group Membership (PGM) analysis (Table 5) shows that the discriminant function mostly assigned both female and male *D. orientalis* collected from each of the three rivers to the correct location/sex group. All Leang-Leang River specimens were correctly assigned. The specimens from the other two rivers were less well differentiated, with 6.7% of male fish from the Bantimurung River population assigned to the Pattunuang River male population, and 3.3% of female fish from the Pattunuang River population assigned to the Leang-Leang River female population.

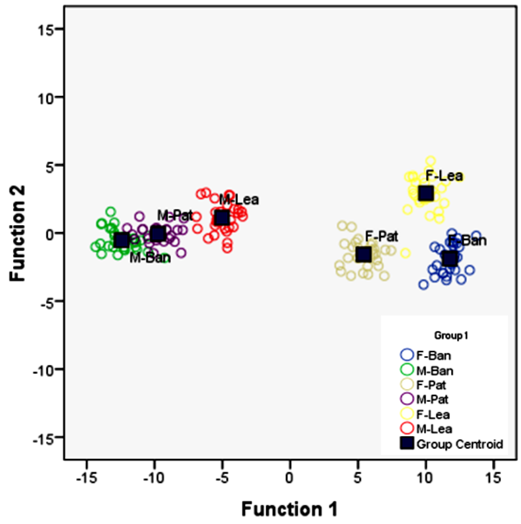

Figure 6. Canonical Discriminant Function Scatter plot for male and female *Dermogenys orientalis* from the Bantimurung River, Leang-Leang River, and Pattunuang River populations. Note: M: Male; F: Female; Ban: Bantimurung River; Leah: Leang-Leang River; Pat: Pattunuang River

Table 4. Meristic characters of male and female *Dermogenys orientalis* from three rivers in the Maros-Pangkep Karst Area and ranges reported by other studies

Sex (n=30)		Number of fin rays				
		Pectoral (P)	**Ventral (V)**	**Anal (A)**	**Caudal (C)**	**Dorsal (D)**
Bantimurung River						
Male	Minimum	9	5	14	19	10
	Maximum	12	6	17	21	12
	Mode	11	6	15	21	10
Female	Minimum	10	5	14	18	9
	Maximum	12	6	17	22	12
	Mode	11	6	16	21	10
Pattunuang River						
Male	Minimum	9	5	14	18	9
	Maximum	11	6	16	21	11
	Mode	10	6	15	20	11
Female	Minimum	9	5	14	18	10
	Maximum	11	6	17	21	11
	Mode	10	6	15	21	11
Leang-Leang River						
Male	Minimum	10	5	12	18	8
	Maximum	12	6	16	21	12
	Mode	11	6	13	21	11
Female	Minimum	10	5	12	18	9
	Maximum	12	6	16	21	12
	Mode	10	6	14	18	11
Published count ranges						
Weber (1984)[a]		no data		15-16	no data	9-10
Meisner (2001)[b]		10-12	no data	15-17	no data	10-11
Kottelat et al. (1993)[c]		no data	no data	15-16	no data	9-12
Hidayani et al. (2024)[d]		9-12	5-6	15-17	17-20	10-11

Note: [a] original description based on 32 specimens from 3 locations in southwestern Sulawesi, presumably the type specimen and paratypes; [b] Lectotype, 30 paralectotypes and 653 non-type specimens; [c] Based on literature review, including documents not available during this study; [d] Three DNA barcoding voucher specimens

Table 5. Predicted Group Membership (PGM) analysis of *Dermogenys orientalis* by site (river) and sex

Classification		Code	Predicted group membership						Total
			F_Ban	M_Ban	F_Pat	M_Pat	F_Lea	M_Lea	
Cross-validated	Count	F-Ban	30	0	0	0	0	0	30
		M-Ban	0	27	0	3	0	0	30
		F-Pat	0	0	30	0	0	0	30
		M-Pat	0	2	0	28	0	0	30
		F-Lea	0	0	1	0	29	0	30
		M-Lea	0	0	0	0	0	30	30
	%	F-Ban	100	0	0	0	0	0	100
		M-Ban	0	90	0	10	0	0	100
		F-Pat	0	0	100	0	0	0	100
		M-Pat	0	6.7	0	93.3	0	0	100
		F-Lea	0	0	3.3	0	96.7	0	100
		M-Lea	0	0	0	0	0	100	100

Note: 96.7% of specimens sampled were correctly assigned to their group of origin and 96.7% of cross-validated grouped cases were correctly assigned. M: Male; F: Female; Ban: Bantimurung River; Pat: Pattunuang River; Lea: Leang-Leang River

Table 6. PGC analysis of phenotypic distance between *Dermogenys orientalis* populations based on morphometric traits

Code		F_Ban	M_Ban	F_Pat	M_Pat	F_Lea	M_Lea
F_Ban	F		688.699	48.724	546.236	31.884	345.517
	Sig.			<0.0001	<0.0001	<0.0001	<0.0001
M_Ban	F			377.046	11.534	603.538	79.393
	Sig.	<0.0001		<0.0001	<0.0001	<0.0001	<0.0001
F_Pat	F	48.724	377.046		272.528	50.336	140.246
	Sig.	<0.0001	<0.0001		<0.0001	<0.0001	<0.0001
M_Pat	F	546.236	11.534	272.528		468.275	34.443
	Sig.	<0.0001	<0.0001	<0.0001		<0.0001	<0.0001
F_Lea	F	31.884	603.538	50.336	468.275		278.240
	Sig.	<0.0001	<0.0001	<0.0001	<0.0001		<0.0001
M_Lea	F	345.517	79.393	140.246	34.443	278.240	
	Sig.	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	

Note: F : Female; M : Male; Tires: Bantimurung River; Pat: Pattunuang River; Lea : Leang-Leang River

The Pairwise Group Comparison (PGC) analysis by site and sex revealed significant between-group differences, in particular between the sexes. The degree of difference between male and female fish was highest in the Bantimurung River population followed by the Leang-Leang River population (Table 6).

Morphological characters that differed between groups and could be used as identifiers (potential discriminant traits) were analyzed using Equality of Group Means (EGM) analysis (Table 7). All 22 traits measured differed significantly (P<0.05), between the populations in three rivers in the Maros-Pangkep Karst Area.

Most traits measured differed significantly between male and female *D. orientalis* (Table 8). The Bantimurung River female group had the highest values for 13 characters, while the lowest values for 19 characters were from the Bantimurung River male group. Furthermore, the mean length of females was longer than that of male fish overall and for each river.

The meristic count ranges and mean values were mostly similar for all six site/sex groups in this study (Table 4). However, some counts differed significantly between site and/or sex groups (Table 9).

Table 7. Equality of group mean test results for 22 morphometric traits of 3 *Dermogenys orientalis* populations

Trait	Wilks' Lambda	F	df1	Sig
N1	.316	75.372	5	<0.0001
N2	.029	1.182E3	5	<0.0001
N3	.504	34.205	5	<0.0001
N4	.368	59.873	5	<0.0001
N5	.531	30.732	5	<0.0001
N6	.573	25.889	5	<0.0001
N7	.373	58.509	5	<0.0001
N8	.248	105.617	5	<0.0001
N9	.076	420.933	5	<0.0001
N10	.284	87.674	5	<0.0001
N11	.313	76.362	5	<0.0001
N12	.558	27.555	5	<0.0001
N13	.180	158.119	5	<0.0001
N14	.393	53.755	5	<0.0001
N15	.869	5.268	5	<0.0001
N16	.458	41.128	5	<0.0001
N17	.588	24.349	5	<0.0001
N18	.647	18.967	5	<0.0001
N19	.773	10.213	5	<0.0001
N20	.296	82.866	5	<0.0001
N21	.443	43.762	5	<0.0001
N22	.372	58.803	5	<0.0001

Table 8. Mean values of discriminant morphometric traits that could be used for distinguishing between *Dermogenys orientalis* populations by sex

Distinguishing characters	Description	Mean standardized value					
		F_Ban	M_Ban	F_Pat	M_Pat	F_Lea	M_Lea
N1	Standard Length (SL)	53.979	33.961	48.663	36.122	52.290	40.703
N2	Total Length Including Beak (TL)	71.976	46.620	65.688	49.174	71.068	55.776
N3	Lower Jaw Length Brembach (LJLB)	8.300	6.438	7.878	6.373	9.241	7.514
N4	Lower Jaw Length (LJL)	13.403	9.401	12.360	10.034	14.925	13.141
N5	Upper Jaw Length (UJW)	6.273	4.147	5.581	4.570	7.156	6.083
N6	Bony Orbital Diameter (ORBL)	3.217	2.258	3.104	2.532	3.232	3.036
N7	Head Length (HDL)	13.144	7.763	11.861	9.298	13.830	12.362
N8	Snout to Pectoral-Fin Distance (SN-P)	17.625	11.439	16.487	13.173	17.607	16.409
N9	Snout to Ventral-Fin Distance (SN-V)	33.307	20.592	30.249	22.708	32.620	24.955
N10	Body Depth at Pectoral-Fin Base (BDP)	7.818	4.982	7.633	5.910	7.458	6.664
N11	Body Depth at Ventral-Fin Base (BDV)	7.979	4.980	7.361	5.660	7.644	6.700
N12	Depth of Caudal Peduncle	3.844	2.687	3.755	2.966	3.512	3.307
N13	Ventral-Fin to Caudal-Fin Distance (V-C)	20.455	12.518	17.770	12.565	19.710	14.251
N14	Length of Pectoral Fin	8.967	5.740	8.295	6.356	8.856	8.471
N15	Length of Pectoral-Fin Base	3.126	2.652	3.130	2.579	2.544	2.555
N16	Length of Dorsal Fin	7.955	5.215	7.490	5.618	7.990	7.197
N17	Length of Dorsal-Fin Base	6.122	3.849	5.376	3.942	5.537	5.225
N18	Length of Ventral Fin	4.186	2.816	3.473	2.728	3.921	3.610
N19	Length of Ventral-Fin Base	1.303	0.877	1.210	0.724	0.862	0.905
N20	Length of Anal Fin	6.028	3.460	5.159	4.501	8.423	5.089
N21	Length of Anal-Fin Base	8.168	4.730	6.972	5.670	6.524	5.880
N22	Length of Caudal fin	10.026	6.420	9.286	7.271	10.169	9.118

Note: for each trait, yellow highlight: highest value and magenta highlight: lowest value

Table 9. Independent pairwise t-tests of *Dermogenys orientalis* meristic counts in the Pattunuang, Bantimurung, and Leang-Leang Rivers

Comparison test	P	V	A	D	C
	Sig. (p)	Sig. (p)	Sig. (p)	Sig. (p)	Sig.(p)
F-Ban vs M-Ban	0.62	1.00	0.49	0.94	0.37
F-Ban vs F-Pat	0.00*	1.00	0.04*	0.23	0.98
F-Ban vs M-Pat	0.00*	1.00	0.02*	0.58	0.99
F-Ban vs F-Lea	0.08	1.00	0.00*	0.94	0.04*
F-Ban vs M-Lea	1.00	0.59	0.00*	0.94	0.37
M-Ban vs F-Pat	0.04*	1.00	0.83	0.76	0.78
M-Ban vs M-Pat	0.00*	1.00	0.75	0.97	0.13
M-Ban vs F-Lea	0.87	1.00	0.00*	1.00	0.00*
M-Ban vs M-Lea	0.62	0.55	0.00*	1.00	0.00*
F-Pat vs M-Pat	0.87	1.00	1.00	0.99	0.84
F-Pat vs F-Lea	0.47	1.00	0.00*	0.76	0.00*
F-Pat vs M-Lea	0.00*	0.59	0.00*	0.76	0.10
M-Pat vs F-Lea	0.45	1.00	0.00*	0.97	0.16
M-Pat vs M-Lea	0.00*	0.54	0.00*	0.97	0.72
F-Lea vs M-Lea	0.08	0.42	1.00	1.00	0.92

Note: *: significant difference (P<0.05), F-Ban: Female from Bantimurung River, M-Ban: Male from Bantimurung River, F-Pat: Female from Pattunuang River, M-Pat: Male from Pattunuang River, F-Lea: Female from Leang-Leang River, M-Lea: Male from Leang-Leang River

The traits with significant differences were the pectoral fin ray count (P), the anal fin ray count (A) and the caudal fin ray count (C). Ventral and dorsal fin ray counts did not differ significantly between any of the sex/site groups. Some traits differed between male and female *D. orientalis* in each of the three rivers as well as between rivers. Meristic count traits of the Bantimurung River population differed more from those in the other two rivers than the Pattunuang River and Leang-Leang River populations did from each other.

Discussion

Morphological identification

The genus *Dermogenys* is distinguished from other genera in the Hemiramphidae by several diagnostic characters, including morphometric, meristic and reproductive traits, in particular the modified anal fin (andropodium) in males (Meisner 2001). Initially, *Dermogenys* was included in the family Hemiramphidae, but due to its viviparous reproduction mode, is now included in the family Zenarchopteridae (Senarat et al. 2019). In adult males, anal fin rays one through seven are modified into andropodium to orient the male genital papillae which extend towards the female gonopore during internal fertilization; the second anal fin is most visibly modified, with a terminal segment called a spicule (Huylebrouck et al. 2014). Details of the andropodium structure vary between species, however all maintain the role of the andropodium in facilitating the transfer of spermatozeugmata during copulation (Kraemer et al. 2019).

General traits of the genus *Dermogenys* include a slender body, a mandibular elongation process during the juvenile phase that can continue in adult fish, a uni-serial conical maxillary row of teeth extending medially in a concave row from the outermost row of teeth to a point about halfway along the premaxilla and a distinct geniculus on the second anal fin in males starting at segment three or four (Meisner 2001). A bright red or orange coloration at the tip of the lower jaw comes from carotenoid pigments such as zeaxanthin, astaxanthin, and beta-doradexanthin (Collette and Bemis 2018). *Dermogenys* halfbeak males tend to be brightly colored and aggressive, while females are generally less colorful (Samsudin 2017).

Male *Dermogenys* also generally have black pigment at the distal end of the dorsal fin, at the base of the pectoral fins, and at the base and distal tip of the ventral fins in males (Samsudin 2017). *Dermogenys* halfbeaks are active swimmers and very sensitive to environmental cues, with a unique olfactory organ enabling them to detect any chemical changes in their environment, and mechanoreceptive neuromasts in the mandible for detecting movement; these traits probably help, inter alia, in avoiding predators (Samsudin 2017). However, identification keys remain complex and challenging due to the small size and similar appearance of *Dermogenys* species, while identification based on the andropodium in males requires radiographic methods and appropriate staining techniques (Samsudin et al. 2018).

The specimens collected in this study displayed traits consonant with the original description by Weber (1894), which was translated into English and expanded with additional details by Meisner (2001). These include body shape with a slender body, an oval caudal fin, an elongated lower jaw with a rostrum and shorter but wider upper jaw which is longer than it is wide. They also displayed diagnostic characters including dorsal-fin origin above anal-fin rays 6 or 7; males had a short, ventrally curved spiculus segmented to the distal tip and lacked a bony cap on the spines of the second anal-fin, while in females melanophores anterior to the anal fins formed a narrow, diffuse U-shape extending anteriorly to the anus.

Of the five types of viviparity (I-V), species in the genus *Dermogenys* generally exhibit types I or type II, distinguished by the way embryos are stored in the female reproductive tract and how they obtain nutrition from the female parent's endogenous egg yolk (Meisner 2001). *D. orientalis* exhibits type II half-beak viviparity, and thread-like sperm is a diagnostic trait (Meisner 2001). The reproductive mode of *D. orientalis* and *D. bispina* is similar (Reznick et al. 2007). They each carry two or three developing young, with sperm bundle morphology observed in *D. orientalis* from southwest Sulawesi similar to that described for *D. bispina* (some identified as *D. pusilla*) from East Kalimantan, Java, Vietnam, Thailand, Myanmar, and Bangladesh. Studies of ovarian structure have found that embryonic development in this species is completely intrafollicular, indicating likely close kinship between *D. bispina* and *D. orientalis* (Meisner and Collette 1998), with intrafollicular gestation, up to 36 embryos in each ovary, and an oocyte diameter of 0.7 mm (Kusumah et al. 2016). Although reproductive aspects were not observed in detail during this study, the morpho-meristic differences between the sexes could be related to the viviparous reproductive mode.

Morphometric and meristic (morpho-meristic) analysis

Morphometric characteristics and meristic counts are helpful in the identification, classification, and genetic studies of fish species (Hossain et al. 2022). In contrast to morphometrics which emphasizes the measurement of fish body parts, meristics involves calculating the number of fish body parts (Oetama et al. 2020). Morphometric and meristic characters can also be used to compare life histories, morphological trends of fish populations, and evaluate individual welfare (Azad et al. 2018; Rahman et al. 2019).

The reported meristic count ranges from other studies (Table 3) are incomplete and differ slightly between studies (Kottelat et al. 1993; Meisner 2001; Hidayani et al. 2024), but are similar to those found in this study. The between-site and sex differences in this study indicate that it is possible that differences between previous studies could be related to the origin and sex of the specimens sampled.

The CDF scatter plot and PGM analysis indicate that each of the six *D. orientalis* site/sex groups has unique characteristics. However, some male fish from the Bantimurung River population had similar characteristics to males from the Pattunuang River population, and a few female fish from the Pattunuang River resembled females from the Leang-Leang River population. One likely reason for these similarities is that these three rivers are part of the same watershed, within the Pattunuang Asue natural tourist area. The main rivers flowing through this area are the Maros River and Pangkep River (with an upstream area in the east of Barru District), both of which flow from east to west and empty into the Makassar Strait (Permana et al. 2018). The source of the Leang-Leang River is on a limestone hill to the east of the Leang-Leang Prehistoric Archaeological Park, and also flows east to west. Before reaching Lambatorang Hill, this river forks in two; the southerly branch crosses the Lambatorang Hill through Ponore and Voclus, becoming the Deppa River, while the northern branch of the Deppa River flows through Appajeng Village. The Leang-Leang River flows north of karst features including the Jin Cave, Barugaya 1 Cave, and Barugaya 2 Cave. In Bontolebang Village, the Leang-Leang River merges with the Cabalak River to become the Galaggara River which flows into the Makassar Strait. The Bantimurung River and Pattunuang River both flow through Samangki Village in Simbang District (Wardhani et al. 2022). The Pattunuang River is seasonal, with a small debit during the dry season while during the rainy season the flow can be quite strong. The Bantimurung River is used for paddy field irrigation and to supply Maros capital district with potable water (Dassir et al. 2021). Migration between rivers is probably rare but is most likely to occur during the rainy season. Albeit limited, the similarity in characters between specimens from the Bantimurung and Pattunuang rivers (around 10%) and the Pattunuang and Leang-Leang rivers (around 3.3%) could be related to such migrations. Habitat could also play a role. *D. orientalis* prefer calm waters with a varied vegetation (Kusumah et al. 2016). A study in the Leang-Leang River found that the habitat of these halfbeaks typically has silt, sand, and rocky substrate, with depths ranging from 5 cm to 1 m, calm water flow, and river banks surrounded by trees (Kusumah et al. 2016). The characteristics of *D. orientalis* habitat in the Pattunuang River and Bantimurung River are generally similar.

The PGC analysis also indicates that although there are similarities in the characteristics of *D. orientalis* populations in the Bantimurung River and Pattunuang River, and between these two and the Leang-Leang River population, these fish populations each have their own unique characteristics. This is based on the high value of the degree of difference for both male and female fish (≥50). Intra-species variations in fish morphology, including sexual dimorphism, can be caused by genetic and other factors that affect phenotype, and such differences often correspond to differences in habits and/or habitat which can influence fish body shape (Acar and Kaymak. 2023). In particular, morphological characters can show high plasticity in response to environmental conditions, such as food abundance, temperature, turbidity, depth, and water flow, as well as differences in feeding behavior (Campang and Ocampo 2015). Differences in morphological characters leading to sexual dimorphism can be caused by evolutionary forces because the two sexes may have different habits and/or habitat according to their functional adaptations.

This study confirms that *D. orientalis* displays sexual dimorphism in both size, as is typical of the genus *Dermogenys* (Meisner 2001), and in body (centroid) shape. In this study, standard lengths ranged from 17.3-66.0 mm SL for females compared to 15.0- 36.7 cm for male fish. A similar disparity in size, with females tending to be larger than males, has been reported in other halfbeaks (Meisner 2001), including the genus *Dermogenys* (Samsudin 2017) and the closely-related genus *Angkahamphus* (Huylebrouck et al. 2012).

The meristic characteristics of fish species tend to remain constant throughout their lifecycle, which shows that meristic character does not depend on body size (Zubia et al. 2015; Kamboj and Kamboj 2019). However, environmental factors can influence and cause between-population differences in meristic counts (Kottelat et al. 1993), while genetic factors can also affect fish morphology (Matthews 1998). The differences in meristic counts between *D. orientalis* populations in the three rivers sampled could be due to differences in habitat characteristics and their effects on phenotype (e.g. on physiology or gene expression), or from genetic differences (e.g. from stochastic processes or differential selection pressures).

In conclusion, there were significant differences in morphometric characters between male and female *Dermogenys orientalis* halfbeaks sampled from three rivers in the Maros-Pangkep Karst Area, and between rivers for each sex. Male halfbeaks were generally smaller than females in all three rivers. There were significant differences between site/sex groups in the mean values of three meristic counts (pectoral, anal and caudal fin rays). These results indicate that the populations in the three rivers are likely separate stocks, and that *D. orientalis* exhibits sexual dimorphism in body shape in addition to the modified anal fin (andropodium) of male halfbeaks.

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