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RESEARCH ARTICLE

Elucidating the Identity of *Rasbora notura-paviana-vulgaris* Species-Complex in Peninsular Malaysia Through Geometric Morphometric

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Abstract The *sumatrana-elegans* species-group in Peninsular Malaysia is a subject of interest due to their history of intricating and interchanging taxonomy. In Peninsular Malaysia, three species and two body forms within the *sumatrana-elegans* species-group was identified to form a unique species-complex collectively referred to as '*Rasbora notura-paviana-vulgaris'*. Geometric morphometric was applied to elucidate the identity of the species-complex, and indicated that the species-complex is statistically similar. Presence of one species with geographical polymorphisms may exist within the species-complex but the actual identity of some species cannot be fully determined. Hence, this study suggested that geometric morphometric need to correlates with other biological fields to obtain a more conclusive outcome. This could provide researchers with more reliable evidence on elucidating identity of cryptic species-complexes for future studies.

Keywords: Cryptic species, landmark-based, interspecific group, *Rasbora*, Sundaland.

Introduction

The term 'species-complex' is used for members of species that are morphologically closely related and thus, are indistinguishable from one another [52]. Studies have anticipated that species-complex can be the result of homologous morphologies, presence of cryptic species, species variations, wide distributional range [30], taxonomic inflation [28], and species hybridisation [8]. Therefore, the species-complex serves as useful classification rank in understanding the relationships among the species within the group, and their distribution. The rank of classification has also applied across kingdoms of Fungi (e.g., mold *Aspergillus niger* [36]), Plantae (*Pagamea guianensis* [52]), and as well some taxa of fish (e.e., damselfish, *Dascyllus aruanus-abudafur* [51], barb, *Barbodes binotatus-banksi* [21]).

The species-complex of *Rasbora notura-paviana-vulgaris*, is a complex of rasboras or '*seluang*' from Peninsular Malaysia. This species-complex comprises of three species and two body forms; the *Rasbora notura*, *R.* cf. *notura*, *R. paviana*, *R.* cf. *paviana* and *R. vulgaris* from the *sumatrana-elegans* species group. *Rasbora notura* and *R.* cf. *notura* [42] formed a smaller complex; *Rasbora notura*-complex and classified into the *hosii* subgroup [46]. The *Rasbora paviana* and *R.* cf. *paviana* [74] formed a smaller complex namely the *Rasbora paviana*-complex. The *Rasbora paviana*-complex were further classified into the *lateristriata* subgroup [46], alongside *R. vulgaris* [19]. Taxonomic confusion within this species-complex has been ongoing for decades since this species-complex exhibits homologous morphologies. Respective species within the species-complex exhibits typical *sumatrana-elegans* traits; distinct caudal fin blotch, presence of supra-anal blotch and typical black midlateral stripe [46]. Preliminary surveys across Peninsular Malaysia suggests that distinction in

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morphologies of the caudal fin blotch, width, and extension of the midlateral stripe are the only possible way to practically distinguish members of this species-complex. For instance, *Rasbora paviana* and *R. vulgaris* midlateral stripe extends anteriorly from the caudal fin blotch and reach the posterior portion of the operculum [46]. However, the only way to morphologically distinguish the two species is based on the conspicuity and width of the midlateral stripe, such that the stripe for *Rasbora paviana* is broader compared to *R. vulgaris* [46]. Consistencies in morphologies between the three species and two body forms have led to their referral as the '*Rasbora notura*-*paviana*-*vulgaris* species-complex' in this study. Furthermore, the extensive use of the temporary species name '*Rasbora sumatrana*' to identify members of this species-complex has led to more taxonomic confusion [2, 41]. This extensive use of temporary species name persisted until the description of *Rasbora notura* by Kottelat [42].

Geometric morphometric is a landmark-based morphometric approach that characterised a statistical structure of variation and covariation [57]. This statistical structure is important in biological terms, and has been used extensively to elucidate taxonomic issues. In this approach, geometric shapes were recorded in two and three dimensions by morphological landmarks or simply 'landmarks' [55]. These landmarks were recorded in *x* and *y* coordinates that corresponds to vectors, areas, and degrees of freedom (d.f.) to form a set of spatial distributional data; the partial warp scores. Partial warp scores acted as a variable that visualise changes in shapes as non-linear [55, 56]. Due to its capability to visualise spatial distribution data in two and three dimensions, this method is able to distinguish small-scale variation. This makes the geometric morphometric approach more efficient to elucidate taxonomic problem compared to traditional morphometric approach [40, 56, 67]. Various ichthyofaunal studies have applied geometric morphometric to elucidate taxonomic issues, from distinguishing fishes' population [38], body sizes [18], morphological structures [21], external meristic structures [53], skeletal structures [17, 32, 73], to identification of fishes' ecology and habitats [13].

Cryptic morphologies exhibit by members of the *Rasbora notura*-*paviana*-*vulgaris* species-complex has led to numerous taxonomic perplexities, i.e., misidentification of *Rasbora paviana* as '*Rasbora* sp.' From Tasik Kenyir [16], and *R.* cf. *paviana* as '*R. sumatrana*' from Tembat Forest Reserve [25]. Therefore, we applied landmark-based geometric morphometric to elucidate the species-complex by visualising their body shapes in two dimensions. By visualising their body shapes, we can see if the species-complex is statistically the same or different. Additionally, this study also aimed to determine the identity of two unconfirmed species; *Rasbora* cf. *notura* and *R.* cf. *paviana* reported within the region. In doing so, we hope to elucidate, determine and acknowledge the identity of the unconfirmed species statistically, whether the unconfirmed species are a form of unique geographical variation, or an entirely different species. We examined specimens collected from primary and secondary sources that was collected along the Peninsular Malaysia prior to and during this study.

Materials and Methods

Sample and Data Collection

This study examined specimens obtained from primary and secondary sources. Primary sources were obtained through sample collections from 46 localities across Peninsular Malaysia (Figure 1). Secondary data were obtained from preserved specimens examined from the Universiti Malaysia Terengganu Zoological Collection (UMTZC) and samples loaned from Universiti Malaya (UM), Kuala Lumpur. Samples examined were identified by referring to Rainboth [54] and Zakaria-Ismail *et al.* [75].

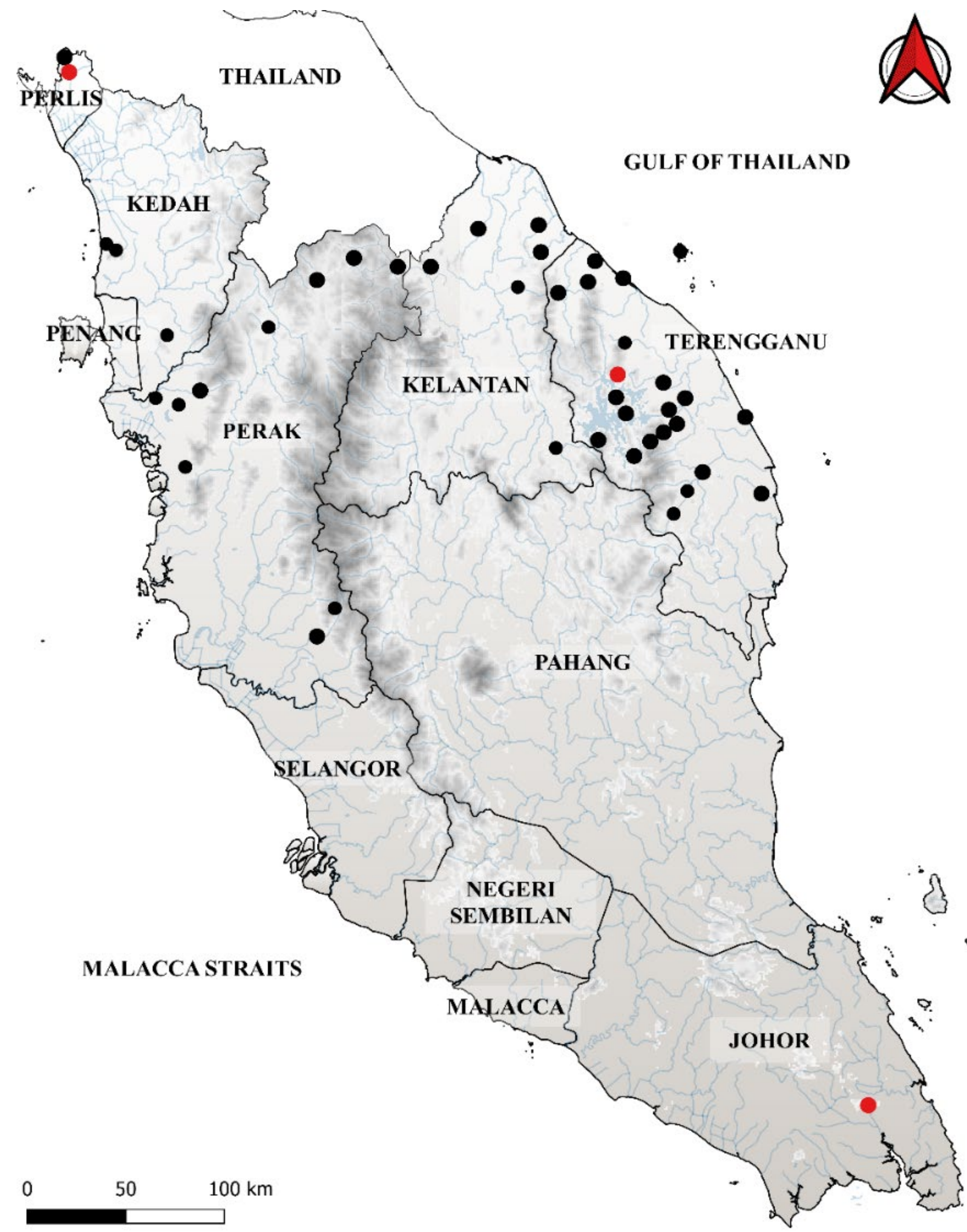

Figure 1. Map showing the sources for primary and secondary data examined in Peninsular Malaysia. Red circle indicated primary study sites surveyed during this study. Black circle indicated secondary study sites surveyed prior to and during this study

Geometric Morphometric

For this study, we utilised the landmark-based geometric morphometric which utilised a set of landmarks plotted in *x* and *y* coordinates [57]. Eighteen landmarks were predetermined before images preparation (Figure 2). Images for each specimen were taken and uploaded into the tpsUtil ver. 1.81 software [58] for compilation and transformation. Predetermined landmarks were manually plotted in a clockwise direction using tpsDig2 ver. 2.32 software [59]. The plotting direction was predetermined and plotted in a systematic manner (clockwise direction) to avoid technical error. This procedure is crucial, as inconsistencies in number, position of landmarks and irregular direction of landmarks plotting will produce an abnormal spatial distribution data.

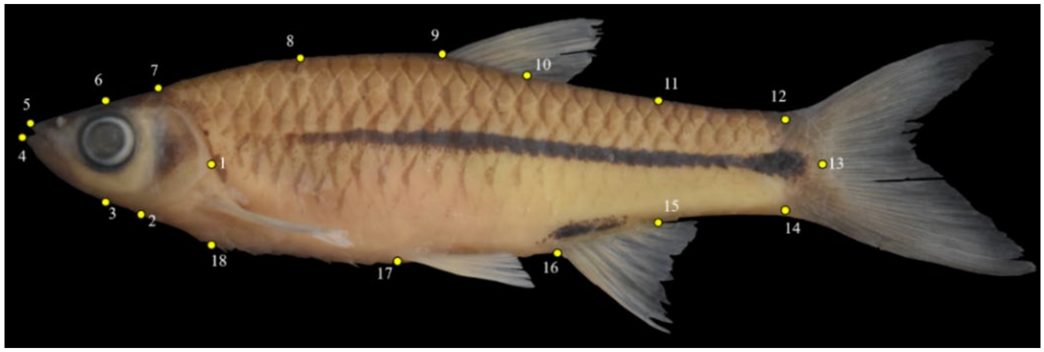

Figure 2. Landmark-based for geometric morphometric. Yellow dots represent the landmarks plotted for this study. The numbering of the landmarks represents the sequence of landmarks plotted

Images plotted were appended into a single tps file using tpsUtil ver. 1.81 software, and uploaded into the tpsRelw ver. 1.74 software [60] to generate the Generalised Procrustes Analysis (GPA) landmark superimposition method. This method removed non-shape variables (partial warp scores) and generated a general consensus [1]. The general consensus is the 'average body shape' produced based on coordinates obtained through landmarks plotted of each individual of each species. Partial warp scores removed by GPA landmark superimposition method were used to generated the relative warp scores. Relative warp scores (principal component data, PC) are the spatial distribution data produced by each landmark (*x* and *y* coordinates) in corresponds to vectors, areas, angles, general consensus and degrees of freedom (d.f.) [11]. GPA landmark superimposition method will produce twice PC values than original number of landmarks [50]. Hence, a total of 36 PC values is generated (18 landmarks) in this study. However, PCA disregards four PC values due to four degrees of freedom and only generates 32 PC values. The four degrees of freedom are the rotations (1 d.f.), scales (1 d.f.), and translations (2 d.f.) [50].

After generation of the principal component (PC) values, the values were uploaded into the Paleontological Statistics (PAST) ver. 4.0 software [33] for multivariate normality test. Multivariate normality test determined that the distribution data is not normal (p-value less than 0.05). The data is transformed using Box-Cox transformation. The new PC values generated by Box-Cox transformation is analysed the second time through multivariate normality test to check for normal distribution. Multivariate normality test on the new PC values was indicated as not normal and ignored. Abnormality in normality test is due to the inconsistencies in sample size [64]. Further data transformation is not advisable as to avoid the data from becoming more complicated to comprehend. After multivariate normality test, PC1 and PC2 values were then utilised to plot the PCA scatterplot graphs. The scatterplot graphs were visualised into two graphs (95% ellipses and convex hulls) by manual plotting through Microsoft Excel. 95% ellipses derived from the much larger 95% confidence ellipses. But unlike 95% confidence ellipses, 95% ellipses are the smallest ellipses which could cover its much larger derivatives [12]. Convex hulls are the smallest 'envelopes' on a geometrical plane that enclosed specific sets of data in a ubiquitous structure [7]. After PCA scatterplot graphs visualisation, PC1 and PC2 values were uploaded into the PAST software for permutational analysis of covariance (PERMANOVA). PERMANOVA were conducted with permutational N 9999. For permutational N 9999, species are considered geometrically consistent if p-value obtained is more than 0.0001. The landmark-based geometric morphometric analysis followed protocol provided by [50].

Results

Principal Component Analysis (PCA) Scatterplot Graphs

A total of 392 individuals were examined in this study, which comprised of 74 individuals of *Rasbora* cf. *notura*, 18 individuals of *R.* cf. *paviana*, 100 individuals of *R. notura*, *R. paviana* and *R. vulgaris* respectively. PCA scatterplots shows high consistency in body shapes between the species-complex (Figure 3). *Rasbora notura* share the most consistencies, mostly overlapping with all four species as depicted by the overlapping in 95% ellipses and convex hulls. PCA scatterplots also shows that *Rasbora notura* and *R.* cf. *notura* share the same body shapes, depicted by the large overlap in 95% ellipses and convex hulls (Figure 3). Similarly, *Rasbora vulgaris* and *R.* cf. *paviana* also share the same body shapes, largely overlapping as depicted by the 95% ellipses and convex hulls. *Rasbora paviana* shows the least consistencies in body shapes with *R.* cf. *notura* and *R.* cf. *paviana*, depicted by the partial overlapping in 95% ellipses and convex hulls (Figure 3).

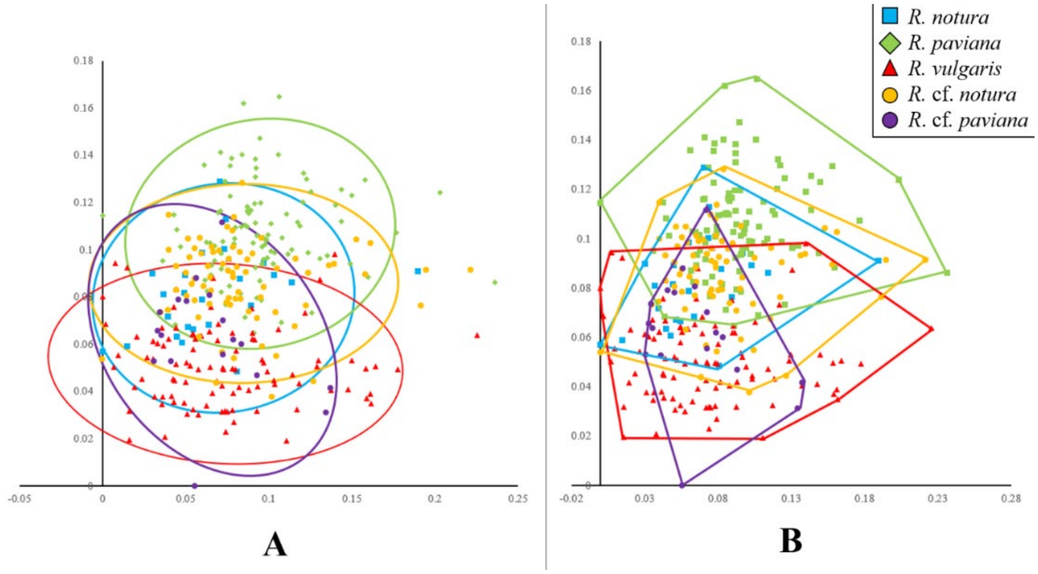

Figure 3. Scatterplot of principal component analysis (PCA) for *Rasbora notura*-*paviana*-*vulgaris* species-complex. (A) 95% ellipses scatterplot. (B) Scatterplot with convex hulls. Coloured shapes within the PCA scatterplots represents the individuals of respective species examined in this study

Permutational Analysis of Covariance (PERMANOVA)

PERMANOVA showed no difference in spatial distribution data (p-value > 0.0001) between the species-complex. Table 1 shows that PERMANOVA for the species-complex are consistent. *Rasbora notura*, *R. paviana* and *R. vulgaris* share the same spatial distribution data (p-value 0.0001). Spatial distribution data provided by PERMANOVA (Table 1) is barely enough to depict that the three species are statistically similar, and still distinguishable from one another. *Rasbora* cf. *notura* shared the most consistencies (p-value 0.0163) with *R. notura*, depicting the similarities in spatial distribution data between the two species (Table 1). *Rasbora* cf. *paviana* shared a high consistency (p-value 0.2822) with *R. vulgaris*, depicting that the two species are similar in terms of spatial distribution data. PERMANOVA also shows that *Rasbora* cf. *paviana* shared the least consistency (p-value 0.0001) with *R. paviana*, depicting that the species is most distinct with *R. paviana* than *R. vulgaris* in terms of spatial distribution data (Table 1).

Table 1. Permutational Multivariate Analysis of Variance (PERMANOVA) N is 9999 for *Rasbora notura*-*paviana*-*vulgaris* species-complex, where; significant difference = p-value less than 0.0001

	R. notura	*R. paviana*	*R. vulgaris*	*R.* cf. *notura*	*R.* cf. *paviana*
R. notura		0.0001	0.0001	0.0163	0.0284
R. paviana	0.0001		0.0001	0.0001	0.0001
R. vulgaris	0.0001	0.0001		0.0001	0.2822
R. cf. *notura*	0.0163	0.0001	0.0001		0.0028
R. cf. *paviana*	0.0284	0.0001	0.2822	0.0028	

Discussion

Morphological similarities within closely related species have been a persisting issue in the studies of *Rasbora* spp. Hence, numerous approaches have been applied to solve these issues such as conventional [24, 46], genetics [45], and geometric morphometric [29]. Reports of occurrences of this species-complex which was not from their known distributional range has led to further misidentification issues in Peninsular Malaysia [2, 41]. Hence, geometric morphometric was utilised to visualise if the species-complex's body shapes and spatial distribution data can be distinguished statistically.

Identity of *Rasbora notura, R. paviana*, and *R. vulgaris*

The overlapping of PCA scatterplots and p-values by PERMANOVA presumptively indicated that the species-complex is similar in terms of body shapes and spatial distribution data. The consistencies also indicated a possibility that the species-complex is a form of geographical variations. From the PCA scatterplots, there is a consistent in trend (Figure 3) between the overlapping of scatterplots between *Rasbora notura-paviana* and *R. notura-vulgaris*. This confirmed that the species-complex is statistically similar to one another with a slight deviation. *Rasbora paviana-vulgaris* has a slightly overlapping in body shapes but the spatial distribution data provided by PERMANOVA (p-value 0.0001) indicated that the pair is similar.

Based on the species-complex's distinction in morphologies, there is also a possibility of geographical variation. The geographical distribution and distinct isolation between the three species congruent with Olvido and Mousseau [49]. Geographically, the species-complex is known to occupied range with distinct biogeographical significance [70, 75]. *Rasbora paviana* occupied most of the northern region; from Perlis to northern Pahang [5, 24, 75]. *Rasbora notura* occupied most of the eastern coast region from Kelantan and reach as far as Johor [46, 75]. *Rasbora vulgaris* occupied most of the western coast region and were known to reach as far as Negeri Sembilan. Biogeographically, this distribution pattern congruent with the paleo-drainage of Siam River which extends from Vietnam into Peninsular Malaysia, Singapore and empties into the Gulf of Thailand through the Singapore Straits [65, 70]. The species-complex possibly occupied Peninsular Malaysia region through the extension of this paleo-drainage. Formation of unique morphological variation by geographically isolated population is probably due to the rise of sea level during the Last Glacial Maximum between 11 500 to 11 000 years ago [70]. This also explains why species within this species-complex exhibits cryptic morphologies despite being traditionally restricted within their distributional range.

However, consistencies in spatial distribution data are particularly common among closely related species [31, 61, 63]. The high consistencies (Figure 3) may not be a proper indication that the species-complex is indeed one species with three geographical variations. Theoretically, the species-complex may also share similar body shapes with other species within its clades such as the *argyrotaenia* and *semilineata* species groups [31, 61, 69]. Geometric morphometric analyses conducted may be very informative in providing us with information on the species-complex that we cannot obtain through conventional procedures. This method preserves information in terms of two and three-dimensional which is normally lost or ignored when conventional procedures are utilised [21, 55].

However, the geometric morphometric approach has its own limitation. This is because geometric morphometric circled around the concept that species from the same clade can exhibit similar body shape [26, 31, 61]. Furthermore, this method lacks the means to properly distinguish interspecific relationship without more convincing evidence such as genetics [26, 31, 61]. Numerous fish species were also known to exhibit similar morphologies but were proven to be genetically distinct. Such case was proven by phylogenetic studies conducted on *Rasbora caudimaculata* with *R. trilineata* by Liao *et al*. [45], and *Channa limbata* and *C. gachua* by Conte-Grand *et al*. [14]. Additionally, studies conducted by Guill *et al*. [31] on relationship between phylogeny and geometric morphometric in darters (family Percidae) shows that ecologically distinct fish species within the same clade can still exhibit similar spatial distribution data.

Hence, in order to properly distinguish the *Rasbora notura-paviana-vulgaris* species-complex, geometric morphometric studies need to be correlates with phylogenetics [35]. In doing so, we are able to properly determine if the species-complex are actually three distinct species, or one species with three unique geographical variation. Additionally, if the species-complex were proven to be similar phylogenetically, it is suggested that the members of the species-complex is renamed and referred to as '*Rasbora paviana*'. Taxonomically, *Rasbora paviana* [74] was named and described earlier than *R. vulgaris* [19] and *R. notura* [42]. This makes '*Rasbora vulgaris*' and '*R. notura*' junior synonym to '*R. paviana*' if the case for geographical variation is true. Hence, this study has decided to retained the species name for respective species until it can be proven through molecular studies.

Additionally, this study shows that taxonomic studies for *Rasbora* spp. is still far from settle despite being a major focus for decades where it was considered to be relatively advance through the works of Howes [37], Fang *et al*. [22], Liao *et al*. [45], Lumbantobing [46], and Sholihah *et al*. [69]. This also gave us the perspective that a group of similar looking species may or may not be the same species. Hence, various field of studies such as ecology, molecular, morphology and morphometric need to be correlates with one another in order to properly elucidate taxonomic problem within a group of similar looking species.

Identity of *Rasbora* cf. *notura*

High consistency in PCA scatterplots and PERMANOVA presumptively indicated that the *Rasbora notura* and *R.* cf. *notura* are similar species. The overlapping in body shapes visualised by PCA scatterplots and significantly similar in spatial distribution data (p-value 0.0163) between *Rasbora* notura and *R.* cf. *notura* shows that the two species are undoubtedly similar statistically. This presumptively indicated that the *Rasbora* cf. *notura* is a form of variation of the *R. notura.* This finding is important because morphologically, the two species are slightly different from one another (Figure 4). *Rasbora notura* exhibits a distinct diamond-shaped (four-sides polygon) caudal fin blotch, whereas *R.* cf. *notura* exhibits a distinct triangular-shaped (three-sides polygon) caudal fin blotch (Figure 5).

This finding shows that the application of geometric morphometric is reliable in determining the presence of geographical variation from two morphologically distinct fish species. The statistical consistencies obtained through the application of geometric morphometric congruent to studies conducted by Joseph and Jayasangkar [39] and Binashikhbubkr *et al*. [10]. Joseph and Jayasangkar [39] utilised a twelve landmark points for landmark-based geometric morphometric to determine the identity of two geographically distinct populations of threadfin breams (*Nemipterus mesoprion*) from India. The study determined that the two populations are statistically similar despite being geographically distant. Binashikhbubkr *et al*. [10] also utilises landmark-based geometric morphometric to study seven morphologically distinct population of mackerel tuna (*Euthynnus affinis*) from Peninsular Malaysia. The study determined that four morphologically distinct population of *E. affinis* collected along the eastern coast shoreline is similar statistically

Figure 4. Live specimens of *Rasbora notura* species-complex collected from Sekayu, Hulu Terengganu district, Terengganu, Peninsular Malaysia prior to this study. Differences in colouration shown in this figure is due to lighting during fish photography. The colouration of the two species appeared similar in the wild. (A) Photo of *Rasbora notura* (typical *R. notura*). (B) Photo of *Rasbora* cf. *notura*. Photos by Mohamad Aqmal-Naser

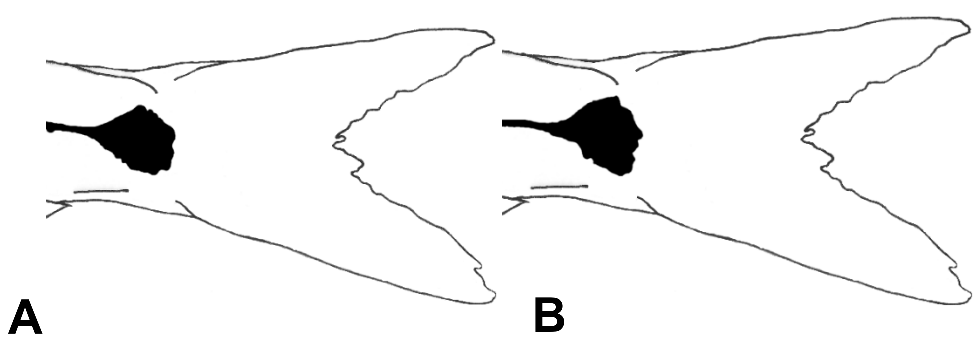

Figure 5. Illustration of caudal fin blotch of the *Rasbora notura*-complex reported from Peninsular Malaysia. (A) Caudal fin blotch of the *Rasbora notura.* (B) Caudal fin blotch of the unconfirmed species of *Rasbora notura* (*R.* cf. *notura*)

The indication of *Rasbora* cf. *notura* as a form of variation to the *R. notura* is highly anticipated due to their homologous morphologies and geographical range. In terms of distributional range, *Rasbora* cf. *notura* was only collected alongside *R. notura* in the eastern coast region of Peninsular Malaysia. The species' distributional range however, cannot be fully determined as the species is yet to be acknowledge to the public. There is a possibility that the species was recorded and referred to as '*Rasbora notura*', but no explicit description regarding its collection was mention. This case is surprisingly common among genus *Rasbora*, where unconfirmed species was left unacknowledged due to imminent taxonomic perplexities [43]. Hence, the extension of the *Rasbora* cf. *notura* distributional range is only limited to the individuals collected and stored in UMTZC. Additionally, individuals identified as *Rasbora* cf. *notura* is also relatively rare, even within its known distributional localities. Only 74 individuals were identified and examined through primary and secondary sources from UMTZC.

The indication of *Rasbora* cf. *notura* as a variation to the *R. notura* is critical. This is because *Rasbora notura* is infamous for its diamond-shaped caudal fin blotch, where it subsequently became a unique trait for the *sumatrana-elegans* species group in Peninsular Malaysia [42]. Introduction of *Rasbora* cf. *notura* as a form of variation for the *R. notura* will definitely change the species' description in the literature sense. Hence, this study suggested that the description of *Rasbora notura* as "exhibiting a diamond-shaped caudal fin blotch" were revised to as "polygonal-shaped caudal fin blotch". This is more coherent as *Rasbora* cf. *notura* exhibits a three-sides polygonal (triangular) shaped caudal fin blotch in contrast to the typical four-sides polygonal (diamond or rhombus) caudal fin blotch exhibits by *R. notura.*

Although geometric morphometric suggested that *Rasbora* cf. *notura* is possibly a form of variation to the typical *R. notura*, the disproportion of sample size may affect the discriminating analysis [48]. Harris [34] stated that the total individuals minus total variables must be more than 30 in order to secure an adequate sample size. Referring to suggestion by Harris [34], the sample size of *Rasbora* cf. *notura* is effectively adequate (sample size 56). However, the findings may not be 100 percent accurate as the number of individuals examined for *Rasbora notura* is disproportionally large (100 individuals) compared to *R.* cf. *notura* (74 individuals). Additionally, the inconsistencies in sample size were indicated during multivariate normality test [64]. Both original distribution data and transformed data shows an abnormal distribution (p-value<0.05). Hence, it is suggested that the total number of individuals must be consistent and adequate in order to improve and obtain solid results for geometric morphometrics. It is undoubtedly that a large number of individuals is better, but it is more presentable to have the same sample size for each species of interest. Additionally, it also presentable to correlates geometric morphometric with other fields, especially genetics and ecology. This is although geometric morphometric is very informative, we need to take note that physiological and environmental factors also plays an important impact on determining fishes' morphologies [9, 23, 66, 72]. With this finding, we identified the elusive *Rasbora* cf. *notura* as a form of variation for the *R. notura*. These variations were also distinguishable by their caudal fin blotches; where *Rasbora notura* exhibits a diamond-shaped (or rhombus-shaped) caudal fin blotch, and the *R.* cf. *notura* exhibits a triangular-shaped caudal fin blotch. The identities of these variations were also retained until it is proven otherwise through a more reliable approach.

Identity of *Rasbora* cf. *paviana*

Based on the PCA scatterplots and PERMANOVA, this study has presumptively distinguished *Rasbora* cf. *paviana* from *R. paviana* and *R. vulgaris*. The PCA scatterplots and PERMANOVA conducted indicated that *Rasbora* cf. *paviana* is statistically similar to *R. vulgaris*. This presumptively indicated that the unconfirmed species is possibly a form of variation of *Rasbora vulgaris*. The overlapping and consistencies in p-value between *Rasbora* cf. *paviana* and *R. vulgaris* is very significant (p-value 0.2822) in contrast to *R. paviana* (p-value 0.0001). The PERMANOVA for *Rasbora* cf. *paviana* and *R. paviana* is too inconsistent, and just barely enough to indicate that their spatial distribution data is similar. This finding congruent to the study on eight species of electric fishes from two clades; Mormyridae and Apterontidae [27]. The study utilised landmark-based geometric morphometric and indicated that the eight species are statistically similar although they were morphologically classified into two distinct clades [27]. Ford *et al*. [27] also remarked that the morphological convergence between the clades is possibly superficial. Although this study indicated that *Rasbora* cf. *paviana* is statistically consistent with *R. vulgaris*, morphological and geographical factors contradicted the claim. In terms of morphologies, *Rasbora* cf. *paviana* is very distinct from *R. vulgaris*, where the unconfirmed species exhibits a wide black midlateral stripe that reaches the middle portion of the midhumeral region (Figure 6). In contrast, *Rasbora vulgaris* exhibits a narrow black midlateral stripe, that reaches the posterior portion of the operculum opening. Morphologically, the stripe exhibit by *Rasbora* cf. *paviana* is more consistent with *R. paviana* than *R. vulgaris* (Figure 6).

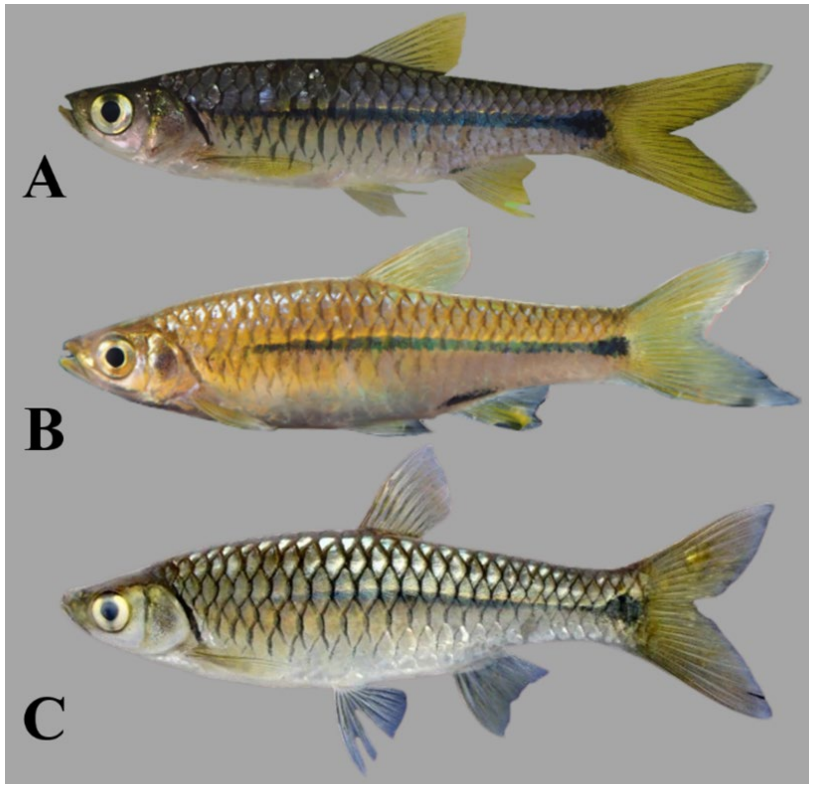

Figure 6. Photos of *Rasbora paviana*, *R. vulgaris* and *R.* cf. *paviana* obtained from secondary sources prior to this study. (A) Live specimen of *Rasbora paviana*, collected from Perlis State Park, Perlis. (B) Live specimen of *Rasbora* cf. *paviana* collected from Tasik Kenyir, Hulu Terengganu district, Terengganu, Peninsular Malaysia. Photos by Mohamad Aqmal-Naser. (C) Photo of *Rasbora vulgaris* collected from vicinity of Kampung Pengkalan Batu, Kedah. Photo obtained from Fishes of Mainland Southeast Asia (FiMSeA)

Geographically, *Rasbora* cf. *paviana* is relatively rare even within its known localities of occurrences in Kelantan dan Terengganu. Similar to *Rasbora* cf. *notura*, individuals of *R.* cf. *paviana* examined for this study was only collected and stored in UMTZC. No known literature has reported the occurrence of this species. Hence, the presence of this species was not publicly acknowledged and the full extension its distributional range is not known. In contrast to *Rasbora* cf. *paviana*, *R. vulgaris* distributional range is well known throughout the western coast region but relatively underestimated [75]. This species is widely distributed from Perak to Penang and possibly reaches as far as Negeri Sembilan [3, 6, 42, 44, 46, 62, 68, 75]. Despite its wide distributional range, *Rasbora vulgaris* is absent from the eastern coast region. The most eastern locality that ever recorded the species' occurrences is in Royal Belum State Park, Perak [4, 20, 47]. This further contradicted the claim that *Rasbora* cf. *paviana* is a form of variation of *R. vulgaris*. However, there is a possibility that *Rasbora* cf. *paviana* do occurred in Perak, given its undetermined distribution and *R. vulgaris* underestimated distributional range. But that remained a mere speculation.

On the other hand, this study also presumptively indicated that *Rasbora* cf. *paviana* is not a variation of *R. paviana*. PCA scatterplots and PERMANOVA indicated that the two species are the least consistent compared to *Rasbora vulgaris* (Figure 3). Aside from elucidating distinct population, geometric morphometric is also proven to be reliable in distinguishing cryptic species that superficially resembles other species. Steffan *et al*. [71] has utilised the landmark-based geometric morphometric to properly distinguish the steambed salamander (*Eurycea subfluvicola*), a species that superficially resembles *E. multiplicata.* The two salamander species were proven to be statistically and genetically distinct although they exhibit similar morphologies on different stages of their life [71]. On the other hand, *Rasbora paviana* morphology is fundamental for the identity of *R.* cf. *paviana*. *Rasbora* cf. *paviana* superficially resembles *R. paviana* with one slight deviation; morphology of black midlateral stripe (Figure 6). *Rasbora paviana* exhibits a linear black midlateral stripe which extends anteriorly from the caudal fin blotch and reaches just behind the posterior end of the operculum opening. In contrast, *Rasbora* cf. *paviana* exhibits a much 'shorter' stripe, extending anteriorly and reaches just at the middle portion of the midhumeral region.

Hence, this study has decided to retained and referred to the unconfirmed species as '*R*asbora cf. *paviana*', and not as a variation of either *R. vulgaris* or *R. paviana*. Although geometric morphometric gave us an insight into the potential identity of *Rasbora* cf. *paviana*, this study was restricted by the limited sample size. This is due to the extremely rare occurrences of *Rasbora* cf. *paviana*, even within region normally associated with the species. Additionally, sample of *Rasbora vulgaris* examined does not represent the whole Peninsular Malaysia due to the lack of samples from southern Selangor and Negeri Sembilan. This study also lacks a more reliable method, particularly genetic also led to difficulties to properly determine the identity of *Rasbora* cf. *paviana*. It is advisable for future studies to make sure the sample size is adequate for species comparison. Unexplored localities also need to be studied so researchers may collect a full representative of the species within a small region. Additionally, utilisation of more advance approaches such as genetics and geometric morphometric analyses on skeletal structures is advisable to thoroughly elucidate and determine the identity of unconfirmed species that superficially resembles other species. Despite the definite results indicated by geometric morphometric, this study is unable to properly determine the true identity of *Rasbora* cf. *paviana* and the species name is retained.

Conclusions

Application of landmark-based geometric morphometric has proven to be reliable in elucidating the identity of the *Rasbora notura-paviana-vulgaris* species-complex. Definite statistical values provided by the approach also prove to be informative in determining which species is most and least consistent with one another. Despite the definite findings provided by the landmark-based geometric morphometric, the species-complex's cryptic morphologies and wide distributional range prevented this study from fully determining the identity of the species-complex. Hence, it is crucial to correlates the geometric morphometric with conventional and genetic approaches to obtain a more reliable result.

Conflicts of Interest

Authors verified and declared that there is no conflict of interest regarding the submission and publication of this paper.

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Materials Examined

Rasbora notura

JOHOR • 1; Kota Tinggi district, Gunung Panti; 2022; Aqmal-Naser *et al*. leg.; JSL 03 • 1; same collection data as for preceding; JSL 11. KELANTAN • 5; Gua Musang district; Kuala Koh, Kelantan National Park; 15 Sept. 2003; Yati and Amirrudin leg.; UMTZC 5817. TERENGGANU • 6; Dungun district, Chemerong Felda Semaring; 7 Oct. 2003; Yati and Amirrudin leg.; UMTZC 6477 • 17; Dungun district, Kampung Pasir Raja; 22 May 2006; Amirrudin *et al*. leg.; UMTZC 6531 • 2; same collection data as for preceding; 7 June 2004; Amirrudin *et al*. leg.; UMTZC 6535 • 4; same collection data as for preceding; 8 June 2004; Amirrudin *et al*. leg.; UMTZC 8592 • 1; Kuala Paka; 2 Mar. 2007; Amirrudin leg.; UMTZC 6703 • 1; Sungai Panchur Pinang; 23 May 2006; Amirrudin *et al*. leg.; UMTZC 6666 • 1; Hulu Terengganu district, Sungai Embong; 8 Feb. 2013; UMTZC 7342 • 2; Kuala Berang; UMTZC 3776 • 6; same collection data as preceding; 24 Aug. 2005; El and Mullen leg.; UMTZC 6755 • 3; same collection data as preceding; 27 July 2005; Elmi *et al*. leg; UMTZC 6812 • 5; Tasik Kenyir, Sungai Ikan; 7 Sept. 2018; Fahmi-Ahmad *et al*. leg.; UMTZC 7687 • 8; Sekayu, Sekayu Recreational Forest, Sungai Peres; 12 Nov. 2012; Syed and Amirrudin leg.; UMTZC 7187 • 9; Sungai Por; 19 Jan.

2008; Annie leg.; UMTZC 6140-43 • 3; same collection data as preceding; 21 Nov. 2007; Annie leg.; UMTZC 6217 • 1; same collection data as preceding; 9 June 2007; Lara leg.; UMTZC 6300 • 3; same collection data as preceding; 1 May 2017; Aqmal-Naser leg.; UMTZC 7353 • 1; same collection data as preceding; Hajar and Nabilah leg.; UMTZC 7619 • 14; same collection data as preceding; Uncatalogued • 1; swamp near Sekayu; 13 Dec. 2005; UMTZC 6195 • 2; Marang district, Merchang, swamp near Merchang; UMTZC 8492-94 • 1; Setiu district, Lata Payong; UMTZC 6358 • 1; same collection data as preceding; 18 May 2009; Amirrudin leg.; UMTZC 7890 • 1; same collection data as preceding; Uncatalogued.

Rasbora paviana

KEDAH • 1; Kuala Muda and Yan district, Gunung Jerai; 6 Apr. 2006; Amirrudin *et al*. leg.; UMTZC 5216 • 2; Yan district, Sungai Perigi; 6 June 2005; Amirrudin *et al*. leg.; UMTZC 5028. KELANTAN • 6; Jeli district; Sungai Buloh; 7 Feb. 2008; Amzar leg.; UMTZC 5807 • 3; same collection data as preceding; 18 Nov. 2007; Amzar leg.; UMTZC 5863 • 1; MARA Junior Science College (MRSM) Jeli; 13 Sept. 2007; Amzar leg.; UMTZC 5870 • 10; Tanah Merah district, Sungai Jedok; 20 Sept. 2007; Amzar leg.; UMTZC 5821 • 5; Sungai Jegor; 23 March 2019; Aqmal-Naser *et al*. leg.; UMTZC 7520 • 3; Pasir Puteh district, Jeram Linang; 13 Aug. 2018; Fahmi-Ahmad *et al*. leg.; UMTZC 7559-60 • 4; Jeram Pasu; March 2018; Amirrudin *et al*. leg.; UMTZC 8390-91. PERAK • 6; Larut, Matang and Selama district, Sungai Beriah Kiri; 1 Aug. 2005; Amirrudin leg.; UMTZC 8515 • 1; Taiping district, Sungai Jelutong; 12 March 2000; UMTZC 5295. PERLIS • 10; Kaki Bukit district, Perlis State Park; 2022; Aqmal-Naser *et al*. leg; Uncatalogued • 2; Teluk Meranti; 28 Sept. 1999; Amirrudin leg.; UMTZC 5018 • 6; Sungai Wang Burma; 31 Jan. 2008; Amirrudin *et al*. leg.; UMTZC 8287-88 • 4; same collection data as preceding; 4 Aug. 2008; Amirrudin *et al*. leg.; UMTZC 8408-10. TERENGGANU • 2; Hulu Terengganu district, Sungai Ular; 15 Jan. 2016; Syed *et al*. leg.; UMTZC 7801-4 • 3; Tasik Kenyir, Sungai Cacing; 1 July 2017; Syed *et al*. leg.; UMTZC 7783 • 5; Sungai Lawit; 8 Aug. 2017; Syed *et al*. leg.; UMTZC 7665 • 2; Sungai Saok; 7 Sept. 2017; Syed *et al*. leg.; UMTZC 7720 • 1; Sungai Siput; 5 Sept. 2017; Syed *et al*. leg.; UMTZC 7648 • 5; Sungai Ikan; 7 Sept. 2018; Fahmi-Ahmad *et al*. leg.; UMTZC 7687 • 2; Kampung Tembila; 23 Sept. 2017; Fahmi-Ahmad *et al*. leg.; UMTZC 7198 • 2; Besut district, Lata Belatan Recreational Forest; 18 Feb. 2005; UMTZC 6310 • 7; same collection data as preceding; 18 Feb. 2005; UMTZC 6332 • 1; Lata Tembakah; Uncatalogued • 6; Kuala Nerus district, Pulau Redang; 2022; Rasul leg.; UMKL 12860.

Rasbora vulgaris

PERAK • 7; Gunung Bongkok; 7 Aug. 2008; Amirrudin *et al*. leg.; UMTZC 8376 • 4; same collection data as preceding; 7 Aug. 2008; Amirrudin *et al*. leg.; UMTZC 8378 • 1; Hulu Perak district, Gerik; 3 Aug. 2005; Amirrudin *et al*. leg.; 31 July 2005; UMTZC 5262 • 17; Taiping district, Pondok Tanjung, Sungai Jelutong; 31 July 2005; UMTZC 5275 • 1; Redang Panjang; 13 Dec. 2000; UMTZC 5199 • 30; Royal Belum State Park, Sungai Purun; 20 June 2007; Amirrudin leg.; UMTZC 5359 • 30; Sungai Royal Belum; 20 June 2007; Amirrudin leg.; UMTZC 5373 • 8; Batang Padang district, Sungkai, Sungai Suar; 17 July 2014; Amirrudin *et al*. leg.; UMTZC 5241 • 3; Pahau Recreational Forest; 6 Aug. 2012; Aqmal-Naser and Amirrudin leg.; UMTZC 7381.

Rasbora cf. *notura*

TERENGGANU • 1; Hulu Terengganu district, Sungai Embong; 8 Feb. 2013; UMTZC 7342 • 1; Kuala Berang; UMTZC 3776 • 1; same collection data as preceding; 24 Aug. 2005; El and Mullen leg.; UMTZC 6755 • 1; Tasik Kenyir, Sungai Ikan; 7 Sept. 2018; Fahmi-Ahmad *et al*. leg.; UMTZC 7687 • 1; Sekayu; 8 Sept. 2006; UMTZC 6130 • 2; Sekayu Recreational Forest, Sungai Peres; 5 July 2017; UMTZC 7961 • 4; Sungai Por; 19 Jan. 2008; Annie and Fahmi-Ahmad leg.; UMTZC 6140-42 • 3; same collection data as preceding; 21 Nov. 2007; Annie and Joe leg.; UMTZC 6217 • 11; same collection data as preceding; 6 Sept. 2007; Lara and Amirrudin leg.; UMTZC 6300 • 5; same collection data as preceding; Hajar and Nabilah leg.; UMTZC 7619 • 7; same collection data as preceding; Uncatalogued • 1; swamp near Sekayu; 13 Dec. 2005; UMTZC 6195 • 8; Dungun district, Felda Semaring Chemerong; 7 Oct. 2003; Yati and Amirrudin leg.; UMTZC 6477 • 3; Kampung Pasir Raja; 25 May 2006; Amirrudin *et al*. leg.; UMTZC 6531 • 5; same collection data as preceding; 7 June 2004; Amirrudin *et al*. leg.; UMTZC 6535 • 2; same collection data as preceding; 6 June 2004; Amirrudin *et al*. leg.; UMTZC 6617 • 1; same collection data as preceding; 8 June 2004; Amirrudin *et al*. leg.; UMTZC 8541 • 10; same collection data as preceding; 8 June 2004; Amirrudin *et al*. leg.; UMTZC 8592 • 2; Sungai Panchur Pinang; 23 May 2006; Amirrudin *et al*. leg.; UMTZC 6666 • 1; Setiu district, Lata Payong; 12 Oct. 2003; Yati and Amirrudin leg.; UMTZC 6353 • 1; same collection data as preceding; 21 Jan. 2006; Amirrudin leg.; UMTZC 6386 • 2; same collection data as preceding; 18 May 2009; Amirrudin leg.; UMTZC 7890 • 1; same collection data as preceding; Uncatalogued.

Rasbora cf. *paviana*

KELANTAN • 1; Tanah Merah district, Sungai Jegor; 23 March 2019; Aqmal-Naser ***et al***. leg.; UMTZC 7520. TERENGGANU • 1; Besut district, Lata Belatan Recreational Forest; 18 Feb 2005; UMTZC 6310 • 1; same collection data as preceding; 18 Feb. 2005; UMTZC 6332 • 4; same collection data as preceding; Amirrudin ***et al***. leg.; UMTZC 7077 • 1; Hulu Terengganu district, Sungai Cacing; 1 July 2017; Syed ***et al***. leg.; UMTZC 7783 • 5; Sungai Ikan; 7 Sept. 2018; Fahmi-Ahmad ***et al***. leg.; UMTZC 7687 • 2; Sungai Lawit; 8 Aug. 2017; Syed ***et al***. leg.; UMTZC 7665 • 1; Sungai Papan; 9 Sept. 2020; Syed ***et al***. leg.; UMTZC 8689.

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