

## Research Article

# Morphometric Analysis of Sumatran, Kalimantan, and Javan *Cyrtodactylus*, which were Labelled as *Cyrtodactylus marmoratus*, Revealed Undescribed Species

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### ABSTRACT

*Cyrtodactylus marmoratus* is originally described based on the specimen from Java. Due to the marbled body colour pattern and the similarity in morphology, many specimens from outside of Java have been identified as *C. marmoratus*. The ongoing research, both molecular and morphological studies, showed that *C. marmoratus* is restricted to Java. The taxonomic status of specimens labelled as *C. marmoratus* from outside Java remains unresolved. Here, we study the morphometric and meristic of Javan, Sumatran, and Kalimantan *Cyrtodactylus* which were labelled as *C. marmoratus* to reveal their taxonomic status. We examined 11 morphometric and 19 meristic characters in 51 specimens at Museum Zoologicum Bogoriense (MZB) originally from, Java, Sumatra, and Kalimantan labelled as *C. marmoratus* as well as other recognized species. Principal Component Analysis (PCA) results show that *C. marmoratus* from Java differs from previous specimens which labelled as *C. marmoratus* from Sumatra and Kalimantan. The PCA results also show that *C. marmoratus* from Martabe differs from *C. marmoratus* Java which is supported by statistical analysis on interorbital, HeadW, HeadD, tubercle on the ventrolateral fold, dorsal tubercle and ventral scales. We hypothesized that *Cyrtodactylus* from Martabe is a suspected undescribed species-await formal description, and overall molecular analyses are needed for future study.

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### INTRODUCTION

The genus *Cyrtodactylus* (Gray 1827) is the most diverse genera among gekkonids with 305 validated species (Uetz et al. 2021), and it is widely distributed in India, Indochina, Sundaland, Wallacea and Papua (Wood et al. 2012; Grismer et al. 2020). Despite the diversity of *Cyrtodactylus* is relatively high, several species are difficult to recognize because of their morphological similarity to other known species (Davis et al. 2021). The diversity of *Cyrtodactylus* in Sumatra, Java and Borneo islands is still underestimated and much remains undescribed species (O'Connell et al. 2019; Davis et al. 2021). Currently, Sumatra consists of seven recognized species (*C. agamensis*, *C. lateralis*,

*C. quadrivirgatus*, *C. semicinctus*, *C. psarops*, *C. consobrinus* and *C. marmoratus* (Harvey et al. 2015), whereas Borneo consists of 14 species (*C. consobrinus*, *C. malayanus*, *C. baluensis*, *C. pubisulcus*, *C. cavernicolus*, *C. ingeri*, *C. matsuii*, *C. hantu*, *C. limajalur*, *C. miriensis*, *C. muluensis*, *C. quadrivirgatus*, *C. philippinicus* and *C. yoshii*) (Hikida 1990; Davis et al. 2019; Uetz et al. 2021) and Java consists of three species (*C. marmoratus*, *C. semiadii*, *C. petani*) (Uetz et al. 2021; Riyanto et al. 2020).

The Java island has a diversity of *Cyrtodactylus* that need further research to reveal hidden species. O'Connel et al (2019) provide the phylogenetics tree of *Cyrtodactylus* on Sumatra and West Java, which West Java has one putative new species in *C. marmoratus* group. However, the dispersal pattern of *C. marmoratus* group in West Java remained unresolved. In this case, *C. marmoratus* is a widely distributed species that can be found in Sumatra, Java, Borneo, Malay Peninsula, and West Papua. Meanwhile, Dring (1979) transferred all specimens of *C. marmoratus* from the Malay Peninsula and Singapore to *C. quadrivirgatus*. The type locality of *C. marmoratus* was mentioned from Java. Mecke et al. (2016b) were done redescription the type series of *C. marmoratus*, which is then based on the compatibilities of morphological characters. Subsequently, Riyanto et al. (2020) determined the specimens from Cibodas as the “true *marmoratus*. Both of Mecke et al (2016b) and Riyanto et al (2022) agree that *C. marmoratus* is restricted to Java.

The taxonomic status of *C. marmoratus* outside Java is remain unresolved. Mecke et al. (2016a) redescription of *C. marmoratus* from Sulawesi resulted that the Sulawesi population belong to *C. fumosus*. These results indicated that the specimens were identified as *C. marmoratus* from Sumatra and Borneo suspected to be different species. In this paper, we examined museum specimens which were labelled as *C. marmoratus* to the revealed taxonomic status of *C. marmoratus* in Sumatra and Kalimantan.

## MATERIALS AND METHODS

### Materials

We follow Riyanto et al. (2020) to identify specimens from Cibodas (West Java) as the true *C. marmoratus* due to the similarity in its morphology to the recent type series description by Mecke et al. (2016b). A total of 51 specimens collected from Kalimantan and Sumatra which have labelled and have similar pattern to *C. marmoratus* were examined. We included *C. consobrinus*, *C. malayanus*, and *C. lateralis* as the comparisons. All specimens examined here are stored in Museum Zoologicum Bogoriense (MZB) (Table 1), localities information presented in Figure 1. We applied a methylene blue in 70% ethanol to stain the skin of specimens to get clear visualization of some minute structures, such as sub-digital scales and pores following Harvey et al. (2015).

### Methods

#### Morphological data

Measurements were taken with Mitutoyo® dial callipers to the nearest 0.1

Table 1. Locations, sample-sizes and grouping into primary Operational Taxonomic Units (OTUs).

Localities	Sample size	Species ID	Primary OTU
Bukit Lawang, Sumatra	2	<i>C. consobrinus</i>	<i>C. consobrinus</i>
Mt. Bondang Murung, Central Kalimantan	1	<i>C. consobrinus</i>	<i>C. consobrinus</i>
Mt. Meratus, East Kalimantan	2	<i>C. consobrinus</i>	<i>C. consobrinus</i>
Seulawah Agam, Aceh	6	<i>C. lateralis</i>	<i>C. lateralis</i>
Ketambe, Aceh, Sumatra	1	<i>C. lateralis</i>	<i>C. lateralis</i>
Bukit Lawang, Sumatra	1	<i>C. lateralis</i>	<i>C. lateralis</i>
Bentung Kerihun, West Kalimantan	1	<i>C. malayanus</i>	<i>C. malayanus</i>
Maruwai, Central Kalimantan	3	<i>C. malayanus</i>	<i>C. malayanus</i>
Meratus, Central Kalimantan	2	<i>C. malayanus</i>	<i>C. malayanus</i>
Kutai, East Kalimantan	2	<i>C. malayanus</i>	<i>C. malayanus</i>
Kerinci National Park, Jambi, Sumatra	3	<i>C. marmoratus</i>	<i>C. marmoratus</i> (Kerinci)
Cibodas, Bogor, West Java	11	<i>C. marmoratus</i>	<i>C. marmoratus</i> (Java)
Nunukan, East Kalimantan	3	<i>C. marmoratus</i>	<i>C. marmoratus</i> (Nunukan)
Martabe, Sumatra	8	<i>C. marmoratus</i>	<i>C. marmoratus</i> (Martabe)
Kubu Perahu, Lampung, Sumatra	2	<i>C. marmoratus</i>	<i>C. marmoratus</i> (Lampung)
Mandau, Siak, Riau, Sumatra	3	<i>C. marmoratus</i>	<i>C. marmoratus</i> (Riau)
Kutai Kartanegara, East Kalimantan	1	<i>C. marmoratus</i>	<i>C. marmoratus</i> (Kutai)
Sebangau, Palangkaraya, Central Kalimantan	1	<i>C. marmoratus</i>	<i>C. marmoratus</i> (Kutai)

mm, we followed Grismer et al. (2012) by measuring 11 external body characters: snout-vent length (SVL), measured from the tip of snout to the cloaca opening; tail length (TailL), measured from the cloaca opening to the tip of the original tail; axilla to groin length (AGL), measured from the arm to groin, specimen in supine position; head length (HeadL), measured from the posterior margin of the retroarticular process of the lower jaw to the snout; head width (HeadW), maximum wide measured the angle of the jaws; head

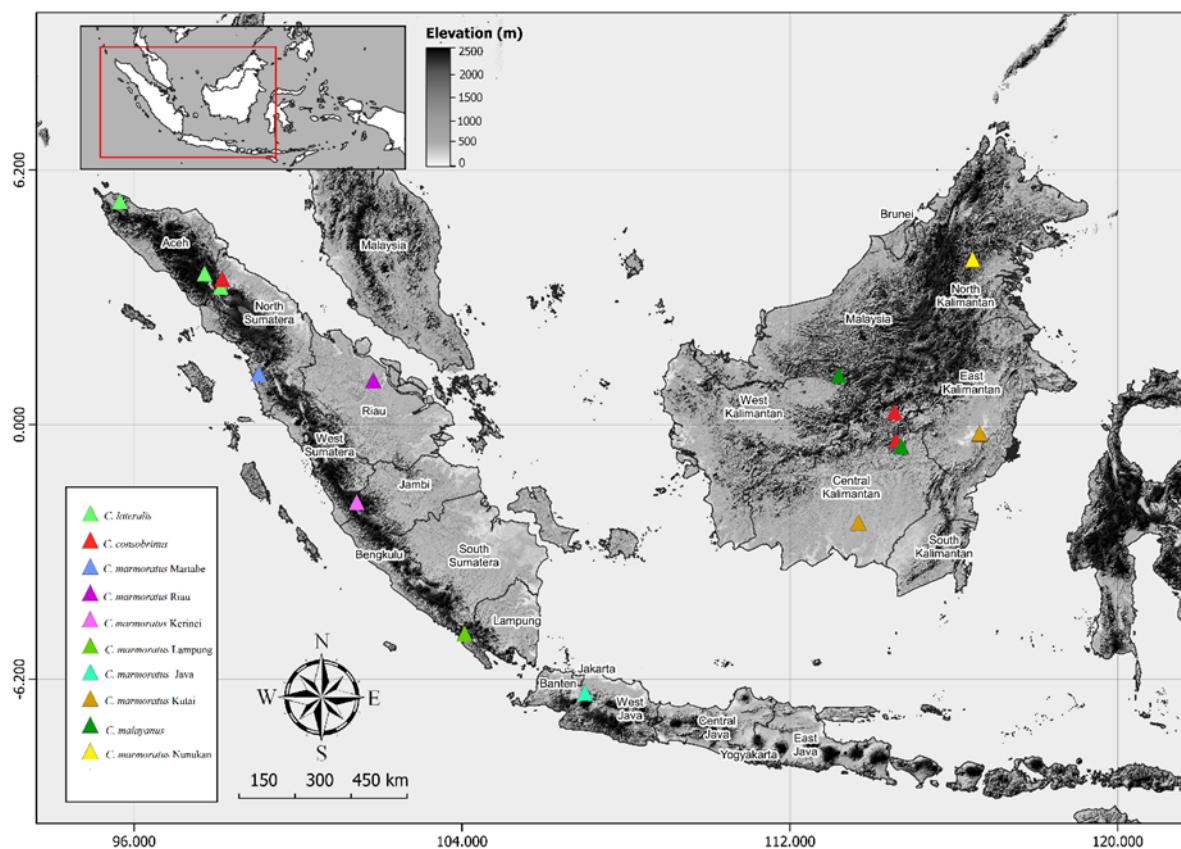


Figure 1. Distribution on the Sunda land (Sumatra, Java, and Kalimantan) of the 10 OTUs specimens used in this study. Map modified by QGIS 3.16 Hannover following this website: <https://www.qgis.org/en/site/forusers/download.html>.

depth (HeadD), the maximum height of head measured from the top-to-bottom side; eye diameter (EyeD), the greatest horizontal diameter of the eyeball; eye to ear distance (EyeEar), measured from the anterior edge of the ear opening to the posterior edge of the eyeball; eye to snout distance (EyeS), measured from anterior margin of the eye ball to the snout; eye to nostril distance (SnEye), measured between the anterior margin of the eyeball to the posterior margin of the nares; interorbital distance (InteroD), measured between the anterior edges of the orbit; ear length (EarL), the greatest length of the ear opening; and internarial distance (IN), measured between the nares.

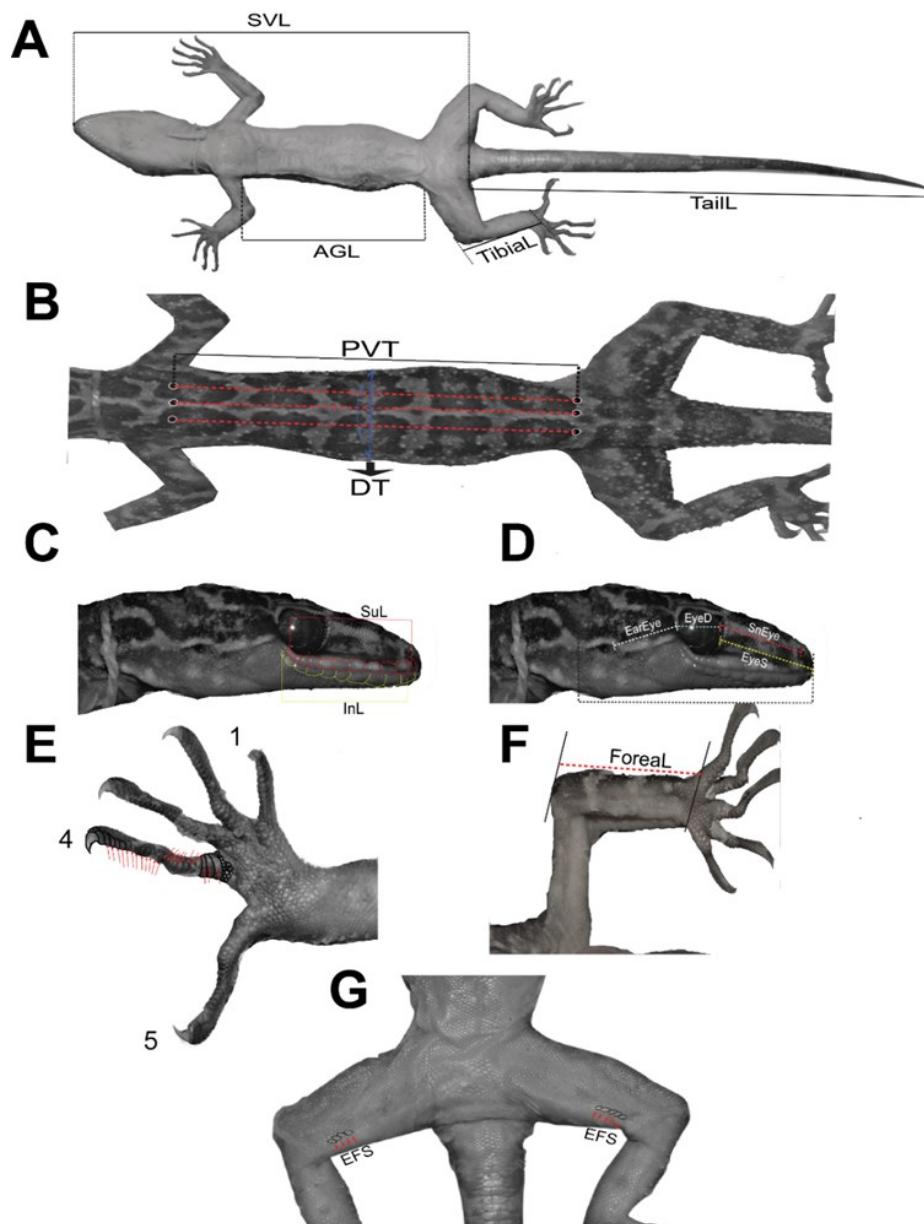
We counted the number of supralabials (SuL), number of infralabials (InL), number of dorsal tubercles (DT), number of paravertebral tubercles (PVT), number of ventral scales between lateral body folds at midbody (VS), number of pores at femoral (FP), number of pores at precloacal (PP), number of precloacal and femoral pores which continuous arranged (PFP), and number of subdigital lamellae under 4<sup>th</sup> toe were counted following [Bauer et al. \(2010\)](#) under a stereoscope (AmScope, magnification 10x to 60x). All measurements and counts were taken on the right side. The illustration for measurement and counted meristic characters is presented in Figure 2. We followed [Riyanto et al. \(2020\)](#) for checked the presence of tubercle on upper (TubBrachium) and lower arms (TubAntebrachium), presence of tubercle on ventrolateral fold, presence of enlarged post cloacal scales and number of tubercle post cloaca. We followed [Mecke et al. \(2016b\)](#) and checked the presence of enlarged femoral scales (EFS), enlarged precloacal scales (EPS), enlarged median subcaudal (SubC) and the condition of precloacal depressions. A groove is always longitudinal and relatively narrow, with some or all of the precloacal scales (usually pore-bearing) on the left and right sides in contact with each other or narrowly separated. The groove may have an entire length slit shape, or a “Λ” shape with the depression broadening posteriorly. Meanwhile, pit is a triangular depression, with most or all the posterior enlarged precloacal scale series widely separated from each other.

### Data analysis

Specimens were divided into a priori Operational Taxonomic Units (OTUs) as a representing putative species due to the upon locations and obvious differences in morphology, and localities. As the consequence, all specimens labelled as *C. marmoratus* both from Kalimantan and Sumatra were relabelled to primary OTUs with added to their respective localities (Table 1).

All morphometric characters before their inclusion in the statistical analyses were adjusted by divided to SVL. We follow [Zar \(2010\)](#) for the small sample size, in performing separate Kruskal-Wallis one-way analysis of variance tests for each of nine morphometric ratios and 15 meristic characters to detect statistical differences between OTUs. The characters which have significant statistical differences will be performed to Dunn test. We performed statistical analysis only specimens which were labelled as *C. marmoratus*. Homogeneity of the priori-OTUs examined by Principal Com-

ponent Analysis (PCA) followed by ordination of specimens along their first two Principal Components (PCs) and the resulting pattern was inspected visually. A biplot of the principal component scores were used to examine the morphometric differentiation between OTU. All statistical analyses were performed in R. (version 4.1.2) (R Core Team 2021).



**Figure 2.** Illustration of measured characters in *Cyrtodactylus*. **A.** Ventral view of the body, **B.** Dorsal view of the body, **C & D.** Lateral view of the head, **E.** View of the subdigital lamellae under 4<sup>th</sup> toe, **F.** Ventral view of the forelimb, **G.** View of enlarged femoral scales.

## RESULTS AND DISCUSSION

### Results

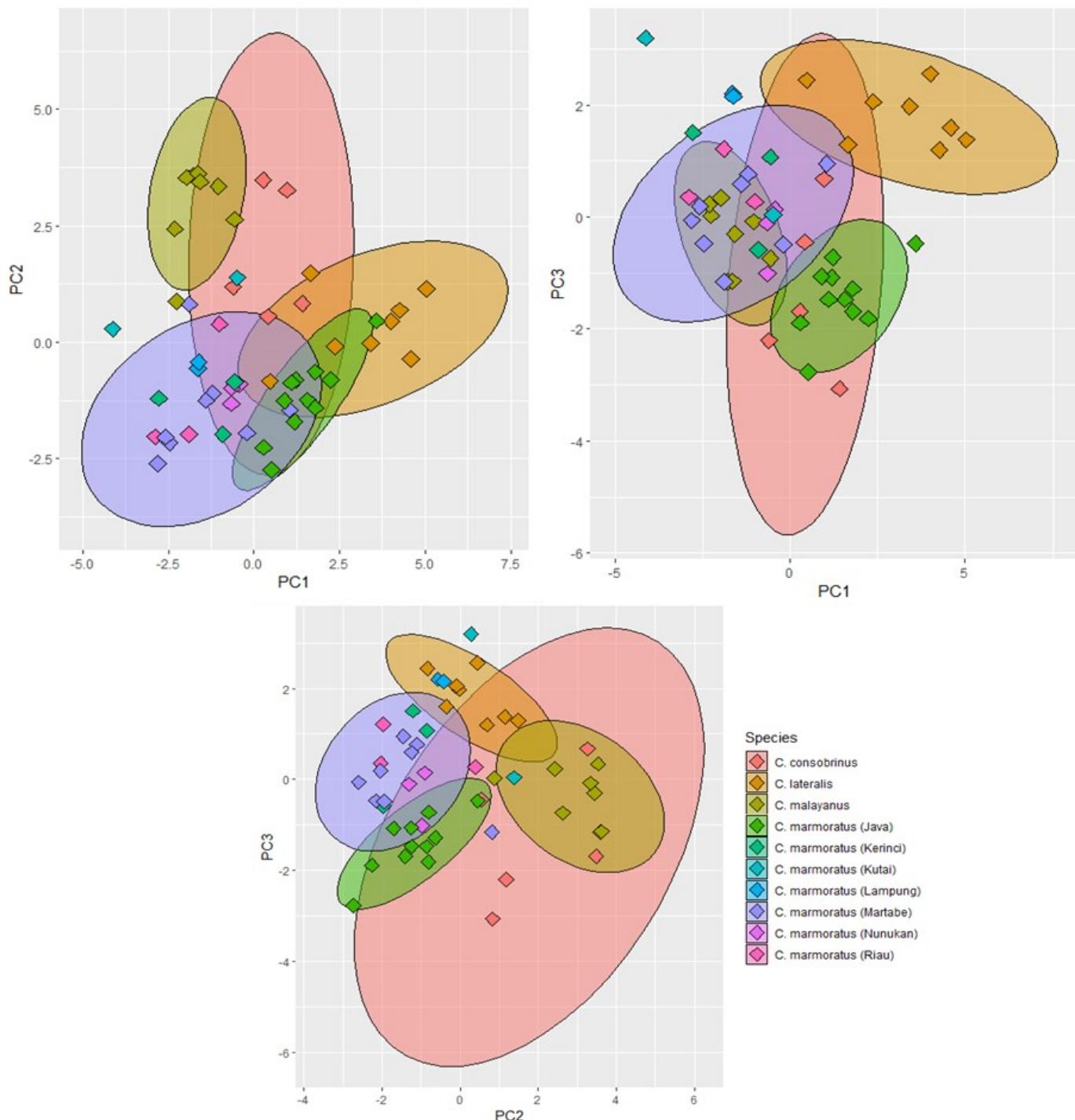
Principal component analysis showed that five components reach 58,5 % for explaining the variation and the total eigenvalue reach 14.0438 (Table 2). In the first PC, morphometric characters have the highest positive correlation including HeadW, HeadD, SnEye, EyeS, and IO, meanwhile, in meristic characters only VS has the highest positive correlation. In contrast, spines

Table 2. Summary analysis of principal component analysis score of Sumatran, Kalimantan and Javan *Cyrtodactylus*

Character	PC1	PC2	PC3	PC4	PC5
AGL/SVL	0.156979329	-0.1047731520	-0.017577464	0.161303205	-0.07102509
HeadL/SVL	0.247976590	0.1548045588	0.152607599	0.154439302	-0.12785407
HeadW/SVL	0.387401006	-0.0007062378	-0.152955681	-0.093274456	0.01332827
HeadD/SVL	0.321194914	-0.1247859036	-0.146126871	0.042263714	-0.03890982
EyeS/SVL	0.339506083	0.0374904712	0.113425315	0.013576318	-0.11152219
EyeD/SVL	-0.048223921	0.2631359450	0.039981276	0.325266169	0.24191758
SnEye/SVL	0.328166997	0.1025988828	0.117406218	-0.006155799	0.10230859
EarEye/SVL	0.159169926	0.1081510718	0.047441474	0.020439091	-0.08187862
IO/SVL	0.257882384	-0.0991033079	-0.401818209	0.153104059	0.19897514
TubLA	-0.005029344	-0.1951094491	0.386515065	-0.119819618	0.38423815
SubCa	0.105099365	-0.4090890411	0.211396239	-0.131384872	-0.15510277
Spines	-0.304670099	-0.0819113423	-0.299208775	0.255526172	0.05072730
SuL	-0.124357557	0.3223170942	0.163640764	-0.241888743	0.13300855
InL	0.075308957	0.0722428672	-0.037937543	-0.293111049	0.33601431
TubBrachium	-0.138683850	0.2024149568	-0.143979780	0.049260554	-0.23023212
TubAntebrachium	0.040920158	0.2024149568	-0.134921092	-0.232552812	-0.03316241
PVT	-0.184273135	-0.1186416582	0.091083435	0.359726487	-0.30461448
DT	-0.251274883	-0.0516968099	0.120578545	-0.289238110	-0.05011188
VS	0.281242210	0.1980686805	0.006832648	-0.194381401	-0.22696191
Toe4 <sup>th</sup>	-0.030271656	0.2419296242	-0.278781743	-0.155091016	-0.05536596
EFS	0.014774424	-0.3248167963	0.039410353	-0.195999762	-0.32730647
EPS	0.130307246	0.0208115941	0.127516061	0.370515709	0.31658363
Enlarge Post Cloaca Scale	0.002137374	0.2472410278	0.501559727	0.094961333	-0.03050341
Tubercle Post Cloaca	0.056978099	0.1950744514	0.137696274	0.228704799	-0.36339726
Standard deviation	2.1260	1.8790	1.5649	1.41876	1.23757
Proportion of variance	0.1883	0.1471	0.1020	0.08387	0.06382
Cumulative proportion	0.1883	0.3354	0.4375	0.52134	0.58516
Eigenvalue	4.51973073	3.53071478	2.44891599	2.01287319	1.53156920

and DT have the highest negative correlation. In the second PC, EyeD, SuL, and Toe4<sup>th</sup> showed the highest positive correlation on the morphometric and meristic characters whereas SubCa and EFS showed the highest negative correlation. The highest positive correlation on the third PC are enlarged post cloaca scales and TubLa while IO and spines showed the highest negative correlation. In the fourth and fifth PC, EyeD and EPS showed similar value of positive correlation, while EPS character has the highest positive correlation in the fourth PC and TubLa in the fifth PC, respectively.

Principal component analysis based on the nine morphometric characters and 15 meristic characters (PC1–PC2, PC1–PC3, and PC2–PC3 (Figure 3) showed that there are five distinct OTUs, i.e. *C. malayanus*, *C. consobrinus*, *C. lateralis*, *C. marmoratus* from Martabe and *C. marmoratus* from Java. It clear that *C. marmoratus* (specimens originally from Cibodas, West Java) is differs from specimens previously labelled as “marmoratus” that originally from Martabe. We hypothesized that *C. marmoratus* frrom Martabe is suspected undescribed species. It is considered by statistical difference on interorbital, HeadW, HeadD, tubercle on ventrolateral fold, dorsal tubercle and ventral scales. The comparison of morphometric and meristic among *C. marmoratus* group are presented in table 3 and 4.



**Figure 3.** Principal component analysis biplot of morphometric variation in primary OTUs, each point represents an individual specimen.

Referring to the biplots on three PC (Figure 3), show that the *C. marmoratus* from Java is clearly different from other specimens which labelled as *C. marmoratus* as well as other recognized species. It means similarity on dorsal color pattern is not supported as a diagnostic character to distinguish *C. marmoratus*. *Cyrtodactylus marmoratus* is easily distinguished from the other OTUs in this study by the following combination of characters such as the absence of tubercles on the upper arms, subcaudal not enlarged, presence of enlarged precloacofemoral, vary in arrangement of precloacal and femoral pores vary continuous and not, and presence of groove precloacal depression in male (Table 5).

**Table 3.** Summary statistics of Kruskal-Wallis and Dunn test of the morphometric characters on the specimens which were labelled as *C. marmoratus*.

<b>Head Length</b>	<b>Z</b>	<b>P.adj</b>	<b>Head Depth</b>	<b>Z</b>	<b>P.adj</b>
Java – Kerinci	2.01355599	0.2312949	Java – Kerinci	2.35080182	0.098348294
Java - Kutai	0.85096053	0.7536924	Java - Kutai	2.61591570	0.093437952
Java – Lampung	1.68301082	0.2771190	Java – Lampung	1.99187798	0.162345567
Java – Martabe	-0.34151660	0.9051182	Java – Martabe	3.49598294	0.009918697
Java – Riau	2.24023648	0.2020011	Java – Riau	2.35080182	0.131131058
Java – Nunukan	1.52256573	0.3356519	Java – Nunukan	2.24169287	0.104921161
Kerinci – Kutai	-0.72011152	0.8250486	Kerinci – Kutai	0.52548679	1.000000000
Kerinci – Lampung	-0.01946247	0.9844722	Kerinci – Lampung	0.000000000	1.000000000
Kerinci – Martabe	-2.17162431	0.2091881	Kerinci – Martabe	0.13777677	1.000000000
Kerinci – Riau	0.26111648	0.8775819	Kerinci – Riau	0.000000000	1.000000000
Kerinci – Nunukan	-0.39167473	0.9734180	Kerinci – Nunukan	-0.08703883	1.000000000
Kutai – Lampung	0.63960215	0.7836469	Kutai – Lampung	-0.47970161	1.000000000
Kutai – Martabe	-1.02815479	0.7090464	Kutai – Martabe	-0.48879490	1.000000000
Kutai – Riau	0.95366121	0.7145358	Kutai – Riau	-0.52548679	1.000000000
Kutai – Nunukan	0.36978700	0.9338978	Kutai – Nunukan	-0.60333668	1.000000000
Lampung – Martabe	-1.83719463	0.2779609	Lampung – Martabe	0.11798498	1.000000000
Lampung – Riau	0.25301216	0.8716474	Lampung – Riau	0.000000000	1.000000000
Lampung - Nunukan	-0.33086205	0.8642068	Lampung - Nunukan	-0.07784989	1.000000000
Martabe - Riau	2.39975617	0.2460899	Martabe - Riau	-0.13777677	1.000000000
Martabe – Nunukan	1.69924682	0.3124544	Martabe – Nunukan	-0.24274955	1.000000000
Nunukan – Riau	0.65279121	0.8301314	Nunukan – Riau	0.08703883	1.000000000
<b>Head Width</b>	<b>Z</b>	<b>P.adj</b>	<b>Eye Diameter</b>	<b>Z</b>	<b>P.adj</b>
Java – Kerinci	1.7955026	0.254007779	Java – Kerinci	1.4481733	0.23838004
Java - Kutai	2.1685722	0.210806224	Java - Kutai	1.8973268	0.13483124
Java – Lampung	1.8218528	0.287604735	Java – Lampung	-1.9162370	0.14525419
Java – Martabe	4.0894495	0.000908036	Java – Martabe	-1.4208134	0.23305654
Java – Riau	3.0503705	0.023998717	Java – Riau	0.6298562	0.61692013
Java – Nunukan	1.9319013	0.280201349	Java – Nunukan	-1.6614317	0.18446931
Kerinci – Kutai	0.5449992	0.946218101	Kerinci – Kutai	0.5644117	0.60109765
Kerinci – Lampung	0.2530353	0.933614382	Kerinci – Lampung	-2.6468964	0.04264797
Kerinci – Martabe	1.0793503	0.841294828	Kerinci – Martabe	-2.3684483	0.06252007
Kerinci – Riau	1.0010383	0.831621814	Kerinci – Riau	-0.6527912	0.63480640
Kerinci – Nunukan	0.1088085	0.913354376	Kerinci – Nunukan	-2.4806066	0.05508680
Kutai – Lampung	-0.2665253	0.975678110	Kutai – Lampung	-2.9315098	0.07083692
Kutai – Martabe	0.2949895	1.000000000	Kutai – Martabe	-2.6799445	0.05154406
Kutai – Riau	0.3503566	1.000000000	Kutai – Riau	-1.1482859	0.35119076
Kutai – Nunukan	-0.4476779	0.981578488	Kutai – Nunukan	-2.7831337	0.05652844
Lampung – Martabe	0.6321203	0.922789472	Lampung – Martabe	1.0281548	0.39883859
Lampung – Riau	0.6423205	0.993997027	Lampung – Riau	2.0630222	0.11733156
Lampung - Nunukan	-0.1557141	0.968496142	Lampung - Nunukan	0.4281744	0.66852414
Martabe - Riau	0.1279473	0.943100215	Martabe - Riau	1.5811524	0.19922558
Martabe – Nunukan	-0.9481223	0.800490153	Martabe – Nunukan	-0.6232759	0.58921939
Nunukan – Riau	0.8922298	0.781766571	Nunukan – Riau	1.8278154	0.14191225

**Table 3.** Contd.

<b>Interorbital</b>	<b>Z</b>	<b>P.adj</b>
Java – Kerinci	1.66143166	0.4058324877
Java - Kutai	2.40159971	0.0856986879
Java – Lampung	1.22286180	0.5811274881
Java – Martabe	4.17380216	0.0006290716
Java – Riau	2.75252112	0.0413968328
Java – Nunukan	2.80707559	0.0524931847
Kerinci – Kutai	0.83688636	0.6039846680
Kerinci – Lampung	-0.15569979	1.0000000000
Kerinci – Martabe	1.26623411	0.7190024721
Kerinci – Riau	0.87038828	0.6204502492
Kerinci – Nunukan	0.91390769	0.6887338511
Kutai – Lampung	-0.90610304	0.6385422996
Kutai – Martabe	0.11798498	1.0000000000
Kutai – Riau	-0.05838742	1.0000000000
Kutai – Nunukan	-0.01946247	0.9844721731
Lampung – Martabe	1.26412474	0.6185557719
Lampung – Riau	0.93419873	0.7354229173
Lampung - Nunukan	0.97312368	0.7711476177
Martabe - Riau	-0.21650635	1.0000000000
Martabe – Nunukan	-0.16401996	1.0000000000
Nunukan – Riau	-0.04351941	1.0000000000

**Table 4.** Summary statistics of Kruskal-Wallis and Dunn test of the meristic characters of specimens which were labelled as *C. marmoratus*.

<b>Tubercle on Ventrolateral Fold</b>	<b>Z</b>	<b>P.adj</b>	<b>Dorsal Tubercle</b>	<b>Z</b>	<b>P.adj</b>
Java – Kerinci	-2.7692096	0.03933473	Java – Kerinci	-1.2612422	0.36263779
Java - Kutai	0.2346403	0.95023595	Java - Kutai	-1.8120993	0.18367351
Java – Lampung	-2.3464027	0.09951698	Java – Lampung	-3.0666295	0.04546227
Java – Martabe	-3.3480083	0.01709286	Java – Martabe	-2.6231004	0.04574514
Java – Riau	-1.7538328	0.18540472	Java – Riau	-2.6321577	0.05939114
Java – Nunukan	-2.7692096	0.05900209	Java – Nunukan	0.4386929	0.73045078
Kerinci – Kutai	2.1734327	0.08924331	Kerinci – Kutai	-0.6260202	0.65631389
Kerinci – Lampung	0.0000000	1.00000000	Kerinci – Lampung	-1.6824292	0.21579985
Kerinci – Martabe	-3.3480083	0.93727903	Kerinci – Martabe	-0.5869309	0.65012510
Kerinci – Riau	0.8099905	0.73140483	Kerinci – Riau	-1.0936122	0.44281746
Kerinci – Nunukan	0.0000000	1.00000000	Kerinci – Nunukan	1.3560791	0.33423216
Kutai – Lampung	-1.9840635	0.12402800	Kutai – Lampung	-0.9643651	0.50229439
Kutai – Martabe	-2.1959559	0.11799943	Kutai – Martabe	0.2202482	0.82567788
Kutai – Riau	-1.4489551	0.30943525	Kutai – Riau	-0.3521363	0.76097282
Kutai – Nunukan	-2.1734327	0.10411719	Kutai – Nunukan	1.8389342	0.19777459
Lampung – Martabe	0.3137080	0.93109409	Lampung – Martabe	1.4400842	0.31467150
Lampung – Riau	0.7244776	0.75724805	Lampung – Riau	0.7042727	0.63165766
Lampung - Nunukan	0.0000000	1.00000000	Lampung - Nunukan	2.8953432	0.03976814
Martabe – Riau	0.6105533	0.81224299	Martabe - Riau	-0.7320150	0.64982318
Martabe – Nunukan	-0.3663320	0.99976430	Martabe – Nunukan	2.2224239	0.09189135
Nunukan – Riau	0.8099905	0.79789618	Nunukan – Riau	-2.4496913	0.06005106

**Table 4.** Contd.

<b>Paravertebral</b>	<b>Z</b>	<b>P.adj</b>	<b>Ventral Scales</b>	<b>Z</b>	<b>P.adj</b>
<b>Tubercles</b>					
Java – Kerinci	-0.1546255	0.87711658	Java – Kerinci	1.7871873	0.17245017
Java – Kutai	1.1474557	0.43958832	Java - Kutai	-1.3160638	0.35920050
Java – Lampung	1.8448045	0.22773095	Java – Lampung	2.6511092	0.04211964
Java – Martabe	-2.7163266	0.04620753	Java – Martabe	2.9177854	0.02467688
Java – Riau	-1.1971005	0.44151043	Java – Riau	0.1991295	0.84216144
Java – Nunukan	1.0524509	0.43888909	Java – Nunukan	1.1300600	0.38767645
Kerinci – Kutai	1.0765704	0.45500899	Kerinci – Kutai	-2.3833939	0.07204609
Kerinci – Lampung	1.6637906	0.20192399	Kerinci – Lampung	0.9572648	0.47380710
Kerinci – Martabe	-1.7155831	0.20122287	Kerinci – Martabe	0.2831803	0.81589052
Kerinci – Riau	-0.8316074	0.53239014	Kerinci – Riau	-1.2668319	0.35912696
Kerinci – Nunukan	0.9629138	0.46982707	Kerinci – Nunukan	-0.5242063	0.66330717
Kutai – Lampung	0.5360563	0.65422700	Kutai – Lampung	3.0495901	0.04812231
Kutai – Martabe	-2.7122540	0.03508436	Kutai – Martabe	2.9946073	0.02885383
Kutai – Riau	-1.8203827	0.20610224	Kutai – Riau	1.2503050	0.34115010
Kutai – Nunukan	-0.2153141	0.87099858	Kutai – Nunukan	1.9145295	0.16665760
Lampung – Martabe	-3.3903175	0.01466046	Lampung – Martabe	-0.8628530	0.47956380
Lampung – Riau	-2.4076029	0.06744207	Lampung – Riau	-2.0903536	0.12805116
Lampung - Nunukan	-0.8025343	0.52159547	Lampung - Nunukan	-1.4261291	0.32304526
Martabe - Riau	0.7126268	0.55542283	Martabe - Riau	-1.8110371	0.18410467
Martabe – Nunukan	2.8769009	0.04216818	Martabe – Nunukan	-0.9153969	0.47247807
Nunukan – Riau	-1.7945212	0.19091628	Nunukan – Riau	-0.7426256	0.53399312
<b>Supralabial</b>	<b>Z</b>	<b>P.adj</b>	<b>Enlarged Femoral Scales</b>	<b>Z</b>	<b>P.adj</b>
Java – Kerinci	-1.83487298	0.23283579	Java – Kerinci	0.000000	1.00000000000
Java - Kutai	-2.29250012	0.15313761	Java - Kutai	1.935782	0.1851303342
Java – Lampung	-3.12703613	0.03708143	Java – Lampung	0.000000	1.00000000000
Java – Martabe	-2.03680405	0.21876583	Java – Martabe	0.000000	1.00000000000
Java – Riau	-2.46293416	0.14469548	Java – Riau	0.000000	1.00000000000
Java – Nunukan	-1.34955297	0.46504348	Java – Nunukan	4.569196	0.0001028158
Kerinci – Kutai	-0.62126485	0.70143330	Kerinci – Kutai	1.630074	0.2164800825
Kerinci – Lampung	-1.32400707	0.43283496	Kerinci – Lampung	0.000000	1.00000000000
Kerinci – Martabe	0.36735791	0.78844176	Kerinci – Martabe	0.000000	1.00000000000
Kerinci – Riau	0.50101951	0.76138267	Kerinci – Riau	0.000000	1.00000000000
Kerinci – Nunukan	0.38715144	0.81508478	Kerinci – Nunukan	3.644957	0.0014040396
Kutai – Lampung	-0.64151294	0.72966527	Kutai – Lampung	-1.488048	0.2610459144
Kutai – Martabe	1.03196138	0.63438944	Kutai – Martabe	-1.882248	0.1794070958
Kutai – Riau	0.17313939	0.90566896	Kutai – Riau	-1.630074	0.2706001031
Kutai – Nunukan	0.96754363	0.58322660	Kutai – Nunukan	1.630074	0.2405334250
Lampung – Martabe	1.84341819	0.27412550	Lampung – Martabe	0.000000	1.00000000000
Lampung – Riau	0.87588160	0.57164161	Lampung – Riau	0.000000	1.00000000000
Lampung - Nunukan	1.67028584	0.28458847	Lampung - Nunukan	3.260149	0.0046768555
Martabe – Riau	-0.97161017	0.63237591	Martabe - Riau	0.000000	1.00000000000
Martabe – Nunukan	0.09956429	0.92069024	Martabe – Nunukan	4.395984	0.0001157857
Nunukan – Riau	-0.88817094	0.60487884	Nunukan – Riau	-3.644957	0.0018720528

**Table 4.** Contd.

<b>Infralabial</b>	<b>Z</b>	<b>P.adj</b>	<b>Tubercle post cloaca</b>	<b>Z</b>	<b>P.adj</b>
Java – Kerinci	-2.3910922	0.11758834	Java – Kerinci	2.5173879	0.04965601
Java – Kutai	-0.8818600	0.61037718	Java - Kutai	2.1330294	0.11522809
Java – Lampung	-2.3742384	0.09232227	Java – Lampung	0.8295114	0.65716279
Java – Martabe	0.2539041	0.79956964	Java – Martabe	-0.7841682	0.56823565
Java – Riau	-0.3068924	0.83881214	Java – Riau	2.5173879	0.06207001
Java – Nunukan	-1.6278641	0.27182848	Java – Nunukan	1.4917854	0.35635795
Kerinci – Kutai	0.9634662	0.58679881	Kerinci – Kutai	0.0000000	1.000000000
Kerinci – Lampung	-0.2932289	0.80781459	Kerinci – Lampung	-1.0976604	0.51994629
Kerinci – Martabe	2.4747159	0.28001861	Kerinci – Martabe	-2.9601699	0.03228429
Kerinci – Riau	1.6626162	0.28916783	Kerinci – Riau	0.0000000	1.000000000
Kerinci – Nunukan	0.6088454	0.75967770	Kerinci – Nunukan	-0.8181477	0.57858197
Kutai – Lampung	-1.1472004	0.58636387	Kutai – Lampung	-1.0020222	0.55358248
Kutai – Martabe	1.0067051	0.59960059	Kutai – Martabe	-2.5349381	0.07872705
Kutai – Riau	0.5236230	0.78820982	Kutai – Riau	0.0000000	1.000000000
Kutai – Nunukan	-0.4188984	0.78783882	Kutai – Nunukan	-0.7317736	0.57355543
Lampung – Martabe	2.4578116	0.14677580	Lampung – Martabe	-1.2674690	0.47830447
Lampung – Riau	1.7803180	0.31510050	Lampung – Riau	1.0976604	0.57194092
Lampung - Nunukan	0.8377967	0.60321732	Lampung - Nunukan	0.3658868	0.83352448
Martabe - Riau	-0.4695253	0.78897522	Martabe - Riau	2.9601699	0.06456858
Martabe – Nunukan	-1.7404208	0.28624808	Martabe – Nunukan	1.9734466	0.14533411
Nunukan – Riau	1.0537709	0.61317446	Nunukan – Riau	0.8181477	0.61990925
<b>Enlarged median subcaudal</b>	<b>Z</b>	<b>P.adj</b>	<b>Enlarged post cloacal scales</b>	<b>Z</b>	<b>P.adj</b>
Java – Kerinci	0.000000	1.0000000000	Java – Kerinci	0.000000	1.00000000000
Java - Kutai	3.679465	0.004908202	Java - Kutai	0.000000	1.00000000000
Java – Lampung	0.000000	1.0000000000	Java – Lampung	0.000000	1.00000000000
Java – Martabe	0.000000	1.0000000000	Java – Martabe	-4.459790	0.0001722842
Java – Riau	0.000000	1.0000000000	Java – Riau	0.000000	1.00000000000
Java – Nunukan	0.000000	1.0000000000	Java – Nunukan	-3.181580	0.0153797960
Kerinci – Kutai	3.098387	0.008172250	Kerinci – Kutai	0.000000	1.00000000000
Kerinci – Lampung	0.000000	1.0000000000	Kerinci – Lampung	0.000000	1.00000000000
Kerinci – Martabe	0.000000	1.0000000000	Kerinci – Martabe	-3.060970	0.0115825990
Kerinci – Riau	0.000000	1.0000000000	Kerinci – Riau	0.000000	1.00000000000
Kerinci – Nunukan	0.000000	1.0000000000	Kerinci – Nunukan	-2.538023	0.0292637106
Kutai – Lampung	-2.828427	0.016372072	Kutai – Lampung	0.000000	1.00000000000
Kutai – Martabe	-3.577709	0.003639503	Kutai – Martabe	-2.621258	0.0306620401
Kutai – Riau	-3.098387	0.013620416	Kutai – Riau	0.000000	1.00000000000
Kutai – Nunukan	-3.098387	0.010215312	Kutai – Nunukan	-2.270076	0.0487261938
Lampung – Martabe	0.000000	1.0000000000	Lampung – Martabe	-2.621258	0.0367944481
Lampung – Riau	0.000000	1.0000000000	Lampung – Riau	0.000000	1.00000000000
Lampung - Nunukan	0.000000	1.0000000000	Lampung - Nunukan	-2.270076	0.0541402153
Martabe - Riau	0.000000	1.0000000000	Martabe - Riau	3.060970	0.0154434653
Martabe – Nunukan	0.000000	1.0000000000	Martabe – Nunukan	0.000000	1.00000000000
Nunukan – Riau	0.000000	1.0000000000	Nunukan – Riau	2.538023	0.0334442407

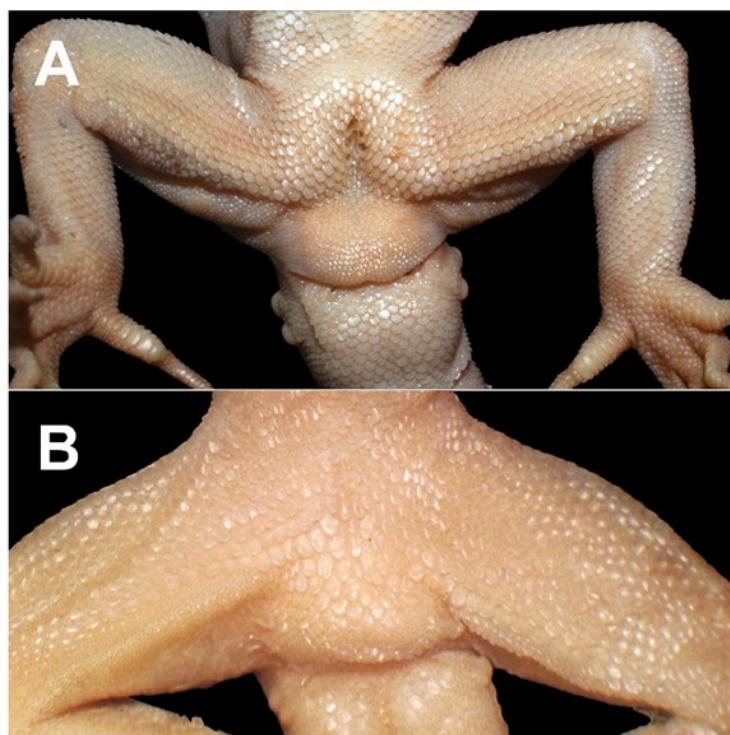
**Table 5.** Morphometric (in mm) and meristic characters of OTUs examined in this study. The number of precloacal pores not given for specimen with precloacal and femoral pores in a continuous series.

	OTU	<i>C. marmoratus</i> (n=11)	<i>C. lateralis</i> (n=8)	<i>C. malayensis</i> (n=8)	<i>C. marmoratus</i> Nunukan (n=3)	<i>C. consobrinus</i> (n=5)	<i>C. marmoratus</i> Kerinci (n=3)	<i>C. marmoratus</i> Riau (n=3)	<i>C. marmoratus</i> Martabe (n=8)	<i>C. marmoratus</i> Lampung (n=2)	<i>C. marmoratus</i> Kutai (n=2)
SVL	73.7±7.5 (59.6-85.2)	74.7±11.2 (57.6-88.9)	85.9±8.4 (68.6-95.1)	58.1±6.61 (50.5-62.3)	80.1±30.2 (42.5-118.6)	69.4±4.8 (65.2-74.8)	60.9±6.5 (53.6-66.2)	57.4±5.0 (50.5-62.9)	53.6±2.7 (51.7-55.6)	68.7±1.5 (67.6-69.8)	
TL/SVL	0.822±0.214 (0.450-1.003)	0.970±0.207 (0.502-1.173)	1.008±0.368 (0.278-1.331)	1.064±0.102 (0.952-1.154)	1.038±0.233 (0.781-1.352)	1.026±0.116 (0.894-1.115)	1.214±0.083 (1.118-1.274)	0.900±0.419 (0.126-1.351)	0.747±0.077 (0.692-0.802)	1.219±0.203 (1.075-1.363)	
AGL/SVL	0.473±0.062 (0.385-0.630)	0.457±0.045 (0.402-0.544)	0.428±0.023 (0.383-0.453)	0.449±0.036 (0.407-0.477)	0.413±0.017 (0.390-0.435)	0.427±0.033 (0.406-0.466)	0.433±0.030 (0.401-0.462)	0.423±0.024 (0.377-0.449)	0.423±0.024 (0.421-0.426)	0.396±0.022 (0.380-0.412)	
HeadL/SVL	0.277±0.016 (0.260-0.316)	0.288±0.016 (0.273-0.320)	0.278±0.016 (0.266-0.318)	0.261±0.009 (0.251-0.269)	0.273±0.021 (0.238-0.289)	0.259±0.003 (0.255-0.262)	0.254±0.008 (0.248-0.264)	0.279±0.015 (0.263-0.308)	0.256±0.017 (0.244-0.268)	0.264±0.020 (0.250-0.273)	
HeadW/SVL	0.187±0.011 (0.170-0.215)	0.191±0.029 (0.151-0.250)	0.162±0.011 (0.139-0.174)	0.163±0.005 (0.157-0.168)	0.174±0.007 (0.166-0.183)	0.166±0.016 (0.150-0.183)	0.151±0.016 (0.132-0.161)	0.156±0.007 (0.148-0.168)	0.161±0.007 (0.156-0.167)	0.160±0.008 (0.153-0.166)	
HeadD/SVL	0.119±0.005 (0.110-0.130)	0.112±0.013 (0.094-0.134)	0.096±0.009 (0.081-0.109)	0.104±0.005 (0.100-0.110)	0.112±0.010 (0.103-0.128)	0.100±0.014 (0.086-0.114)	0.102±0.010 (0.091-0.111)	0.105±0.006 (0.104-0.114)	0.105±0.006 (0.100-0.109)	0.098±0.004 (0.094-0.101)	
EyeS/SVL	0.118±0.007 (0.107-0.129)	0.123±0.004 (0.116-0.128)	0.111±0.003 (0.106-0.116)	0.107±0.001 (0.105-0.109)	0.112±0.009 (0.096-0.120)	0.107±0.009 (0.099-0.117)	0.112±0.003 (0.108-0.115)	0.113±0.010 (0.103-0.135)	0.110±0.007 (0.108-0.112)	0.110±0.008 (0.097-0.113)	
EyeD/SVL	0.055±0.004 (0.051-0.065)	0.057±0.007 (0.045-0.067)	0.070±0.011 (0.059-0.089)	0.066±0.010 (0.057-0.077)	0.068±0.007 (0.059-0.075)	0.049±0.007 (0.048-0.052)	0.053±0.004 (0.048-0.057)	0.065±0.019 (0.049-0.111)	0.067±0.003 (0.049-0.114)	0.067±0.007 (0.094-0.101)	
SnEye/SVL	0.081±0.005 (0.074-0.090)	0.091±0.009 (0.079-0.106)	0.078±0.006 (0.069-0.090)	0.083±0.002 (0.081-0.085)	0.082±0.009 (0.070-0.092)	0.069±0.002 (0.068-0.072)	0.076±0.016 (0.057-0.088)	0.079±0.009 (0.069-0.100)	0.080±0.001 (0.079-0.081)	0.071±0.008 (0.065-0.077)	
EarEye/SVL	0.088±0.006 (0.076-0.100)	0.094±0.007 (0.086-0.110)	0.088±0.022 (0.065-0.138)	0.093±0.004 (0.089-0.099)	0.087±0.002 (0.0827-0.090)	0.091±0.011 (0.083-0.104)	0.083±0.008 (0.074-0.090)	0.083±0.007 (0.071-0.095)	0.077±0.002 (0.075-0.079)	0.086±0.009 (0.079-0.093)	
IO/SVL	0.051±0.003 (0.046-0.056)	0.041±0.008 (0.024-0.050)	0.034±0.001 (0.032-0.037)	0.033±0.002 (0.030-0.035)	0.054±0.017 (0.036-0.080)	0.041±0.006 (0.036-0.049)	0.034±0.004 (0.029-0.038)	0.032±0.004 (0.027-0.040)	0.040±0.001 (0.039-0.041)	0.034±0.008 (0.028-0.040)	
Supralabial	8-11	10-12	12-13	10-11	8-12	10-13	11-12	10-12	12-13	11-12	
Infralabial	9-11	9-11	absent	absent	8-14	10-12	9-10	8-10	11	10	
Tubercle on brachium	present	present	absent	absent	absent	absent	absent	absent	absent	absent	
Tubercle on antebrachium	present	present	absent	present	present	Absent	present	present	present	present	
Tubercl on hindlimbs	present	present	present	present	present	present	present	present	present	present	
Tubercl on ventrolateral fold	absent	present	present	present	absent	absent	absent	absent	absent	absent	
DT	14-23	17-22	16-18	14-20	18-25	22-25	19-24	18-19	20-24	27	
PVT	24-33	22-30	24-32	26-32	27-33	31-33	31-36	28	28	27	

Table 5. Contd.

	OTU					
Character	<i>C. marmoratus</i> (n=11)	<i>C. lateralis</i> (n=8)	<i>C. malayanus</i> (n=8)	<i>C. marmoratus</i> Nunukan (n=3)	<i>C. consobrinus</i> (n=5)	<i>C. marmoratus</i> Kerinci (n=3)
VS	39–47	51–60	34–53	35–42	44–48	28–46
EPS	present	present	absent	present	present	40–43
EFS	present	present	absent	present	present	30–40
PP	-	7–10	6–10	8–10	present	30
EPFS	yes	no	no	No	present	48–49
PFP	45–52	0	0	0	present	absent
Pectoacal	groove	groove	pit	pit	present	present
depression					present	present
Tubercle post	1–2	2–3	1–3	0–3	1	0
cloacal					1	0
Enlarged median sub-caudal	absent	absent	present	absent	absent	absent
Enlarged post cloacal scales	absent	present	present	absent	absent	absent
Subdigital lamella 4 <sup>th</sup> toe	19–24	21–22	18–26	17–19	23–27	20–24
						22–23
						19–22
						21–23
						20–23

*Cyrtodactylus marmoratus* from Martabe differs from the other OTUs by its unique combination of characters such as the absence of tubercle on the upper arm, presence of tubercles along ventrolateral folds, and presence of EPFS. As the result of our statistical analysis, *C. marmoratus* from Martabe (Sumatra) is differ with *C. marmoratus* from Java. The *C. marmoratus* from Martabe can be distinguished from Java specimens by combination characters: more supralabial (10-12 vs 8-11), presence of tubercle on ventrolateral fold (vs absent), more number of paravertebral tubercle (31-36 vs 24-33), precloacal depression in groove form (vs pit), and presence of enlarged post cloacal scales (vs absent) (Figure 4).



**Figure 4.** Comparison of precloacal region. **A** *C. marmoratus* from Java, **B** *C. marmoratus* from Martabe

## Discussion

We assigned that specimens *C. marmoratus* from Kerinci belong to *C. semicinctus* described by [Harvey et al. \(2015\)](#). It is based on similarity in its morphology including fewer supralabial (10-13 vs 10-15), presence of tubercles on antebrachium, absence of tubercle on brachium, matching the number of paravertebral tubercles (27-33 vs 24-27), number of ventral scales (28-46 vs 33-44), number of precloacofemoral pores (35-45 vs 36-38), number of the lamella under the fourth toe (20-24 vs 19-22). This assignment is also supported by the similarity of the collected specimens with the type locality of *C. semicinctus*.

*Cyrtodactylus semicinctus*, *C. marmoratus* from Nunukan and *C. marmoratus* from Riau are grouped on the *C. marmoratus* from Martabe in all PC. The overlapping of *C. marmoratus* from Lampung, *C. marmoratus* from Riau, *C. marmoratus* from Nunukan and *C. marmoratus* from Kutai may be due to small

samples size. According to Rogell et al. (2020), this phenomenon can lead to an erroneous taxonomic conclusion. The position of these OTUs can be evident when the sample sizes for each OTU are sufficiently large, as suggested by Chan & Grismer (2021). Although *C. marmoratus* from Nunukan are overlapping within Martabe group, these species are distinct species according to Riyanto et al. 2021. *Cyrtodactylus marmoratus* from Nunukan is described as a new species namely *C. hamidi*. These species are closely related to morphological characters within *C. matsuii*.

In this paper, we reported that *C. marmoratus* from Martabe has morphological variations compared to *C. marmoratus* from Java. In concordant, the comparison between *C. marmoratus* from Martabe and *C. agamensis* resulted that it has still unique morphological variations. *Cyrtodactylus marmoratus* from Martabe is easily distinguished from *C. agamensis* by fewer supralabial (10-12 vs 10-13), fewer infralabial (8-10 vs 9-12), widely dorsal tubercles (19-24 vs 17-21), fewer ventral scales (30-40 vs 50-67), a lower subdigital lamella on 4th toe (19-22 vs 21-26) (Milto & Bezman-Moseyko 2021).

*Cyrtodactylus marmoratus* group is a unique species regarding phylogenetic relationship and a gap-wide distribution (Riyanto et al. 2022). This group consists of four species, including *C. marmoratus*, *C. semiadii*, *C. papuensis* and *C. papeda* (Riyanto et al. 2022). *Cyrtodactylus marmoratus* group has potentially several undescribed species from Sumatra and Java (O'Connell et al 2019; Grismer et al. 2021). According to Riyanto et al. (2022) which stated that *C. marmoratus* is restricted to Java. It is indicated that specimens of *C. marmoratus* outside of Java island potential as a distinct species. Integrative taxonomic studies are needed to reveal hidden diversity on *C. marmoratus* and explain of phylogenetic relationship of this group.

## CONCLUSION

The morphometric and meristic study of the *C. marmoratus* from Sumatra and Kalimantan revealed one suspected undescribed species, *C. marmoratus* from Martabe. Further study on molecular analysis is an ongoing issue to better understand phylogeny and reveal the taxonomic status of *Cyrtodactylus* in Sumatra and Kalimantan. The diagnostic characteristics to determine specimens to be *C. marmoratus* are the absence of tubercle on the upper arms, absence of enlarged median subcaudal, absence of tubercle on ventrolateral fold, vary in arrangement of precloaco femoral pores, absence of enlarged post cloacal scales, and presence of groove precloacal depression in male.

## AUTHORS CONTRIBUTION

M.A.F. designed and conducted the research, analysed and interpretation the data, and wrote the draft of manuscript. A.R. designed the research, analysed and interpretation the data, reviewed the draft of manuscript, and supervised all the process. N.K. designed the research, reviewed the draft of manuscript, and supervised all the process.

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## CONFLICT OF INTEREST

The authors declare there is no competing interest.

## REFERENCES

- Bauer, A.M. et al., 2010. *Cyrtodactylus dumnnuii* (Squamata: Gekkonidae), a new cave-dwelling gecko from Chiang Mai Province, Thailand. *Zootaxa*, 2570, pp. 41– 50. doi: 10.11646/zootaxa.2570.1.2.
- Chan, K.O. & Grismer, L.L., 2021. Correcting for Body Size Variation in Morphometric Analysis. *bioRxiv*. doi: 10.1101/2021.05.17.444580.
- Davis, H.R., 2019. Uncovering karst endemism within Borneo: two new *Cyrtodactylus* species from Sarawak, Malaysia. *Zootaxa*, 4614(2), pp. 331-352. doi: 10.11646/zootaxa.4614.2.4.
- Davis, H.R., 2021. Genetically diverse yet morphologically conserved: Hidden diversity revealed among Bornean geckos (Gekkonidae:*Cyrtodactylus*). *Journal of Zoological Systematic and Evolutionary Research*, 00, pp.1-23. doi: 10.1111/jzs.12470.
- Dring, J.C.M., 1979. Amphibians and reptiles from Northern Trengganu, Malaysia, with descriptions of two new geckos: *Cnemaspis* and *Cyrtodactylus*. *Bulletin of the British Museum (Natural History) Zoology*, 34(5), pp. 181-241
- Gray, J.E., 1827. A synopsis of the genera of saurian reptiles in which some new genera are indicated, and the others reviewed by actual examination. *Philosophical Magazine*. 2(2), pp. 54–58.
- Grismer, L.L., 2012. *Cyrtodactylus majulah*, A new species of bent-toed gecko (Reptilia: Squamata: Gekkonidae) from Singapore and the Riau archipelago. *The Raffles Bulletin of Zoology*, 60(2), pp. 487-499.
- Grismer, L.L. et al., 2020. Two new species of *Cyrtodactylus* Gray, 1827 (Squamata: Gekkonidae) from a karstic archipelago in the Salween Basin of southern Myanmar (Burma). *Zootaxa*, 4718, pp. 151–183. doi: 10.11646/zootaxa.4718.2.1.
- Grismer, L.L. et al., 2021. Phylogenetic partitioning of the third-largest vertebrate genus in the world, *Cyrtodactylus* Gray, 1827 (Reptilia; Squamata; Gekkonidae) and its relevance to taxonomy and conservation. *Vertebrate Zoology*, 71, pp 101-154. doi: 10.3897/vz.71.e59307.

- Harvey, M.B. et al., 2015. Two new species of *Cyrtodactylus* from the Southern Bukit Barisan Range of Sumatra and an estimation of their phylogeny. *Zootaxa*, 4020(3), pp. 495–516. doi: 10.11646/zootaxa.4020.3.5.
- Hikida, T., 1990. Bornean gekkonid lizards of the genus *Cyrtodactylus* (Lacertidae: Gekkonidae) with descriptions of three new species. *Japanese Journal of Herpetology*, 13(3), pp. 91–207.
- Mecke, S. et al., 2016a. Redescription of *Cyrtodactylus fumosus* (Muller, 1895) (Reptilia: Squamata: Gekkonidae), with a revised identification key to the bent-toed geckos of Sulawesi. *Acta Herpetologica*, 11(2), pp. 151-160. doi: 10.13128/Acta\_Herpetol-17874.
- Mecke, S. et al., 2016b. Historical considerations and comments on the type series of *Cyrtodactylus marmoratus* Gray, 1831, with an updated comparative table for the bent-toed geckos of the Sunda Island and Sulawesi. *Zootaxa*, 4175(4), pp. 353–365. doi: 10.11646/zootaxa.4175.4.5.
- Milto, K.D.& Bezman-Moseyko, O.S., 2021. Herpetofauna of the Maninjau caldera, West Sumatra, Indonesia, with special account to geckos. *Proceedings of the Zoological Institute RAS*, 325(4), pp. 430-446. doi: 10.31610/trudyzin/2021.325.4.430.
- O'Connell, K.A. et al., 2019. Diversification of bent-toed geckos (*Cyrtodactylus*) on Sumatra and west Java. *Molecular Phylogenetics and Evolution*, 134, pp. 1–11. doi: 10.1016/j.ympev.2019.01.021.
- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for statistical computing. Vienna. Austria. <https://www.R-project.org/>.
- Riyanto, A. et al., 2020. Taxonomic evaluation of two similar bent-toed geckos (Squamata: Gekkonidae: *Cyrtodactylus* Gray, 1827) from East Java, Indonesia, *Zootaxa*, 4830(1), pp.186–196. doi: 10.11646/zootaxa.4830.1.8.
- Riyanto, A. et al., 2021. Another new-bent toed gecko, genus *Cyrtodactylus* Gray 1837 (Squamata: Gekkonidae), from Borneo. *Zootaxa*, 5026(2), pp. 286-300.
- Riyanto, A. et al., 2022. A new bent-toed gecko of the *Cyrtodactylus marmoratus* group (Reptilia: Gekkonidae) from Obi island, Indonesia. *Herpetologica*, 78(1), pp. 30-39. doi: 10.11646/zootaxa.5026.2.8.
- Rogell, B. et al., 2020. Controlling for body size leads to inferential biases in the biological sciences, *Evolution Letters*, 4(1), pp.73–82. doi: 10.1002/evl3.151.
- Uetz, P. et al., 2021. 'Diversity of the genus *Cyrtodactylus*', in *Reptile Database*, viewed 13 June 2021 from <http://www.reptile-database.org>
- Wood, P.L. et al., 2012. Phylogeny of bent toed geckos (*Cyrtodactylus*) reveals a west to east pattern of diversification. *Molecular Phylogenetic and Evolution*, 65, pp. 992-1003. doi: 10.1016/j.ympev.2012.08.025.
- Zar, J.H., 2010. *Biostatistical Analysis*, 5th edition. Prentice Hall Inc., USA.