**FULL PAPER** *Wildlife Science*

# A morphological analysis of the skull size and shape of Kerivoulinae (Chiroptera: Vespertilionidae) from Vietnam

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(Received 12 May 2015/Accepted 24 August 2015/Published online in J-STAGE 7 September 2015)

ABSTRACT. Southeast Asia is a region of high biodiversity, containing species of plants and animals that are yet to be discovered. In this region, bats of the subfamily Kerivoulinae are widespread and diverse with six species recorded in Vietnam. However, the taxonomy of the Kerivoulinae in Asia is complicated. In our study, we used diagnostic characters and multivariate analysis to determine morphological differences between the genera *Kerivoula* and *Phoniscus*. We showed that the two genera are distinguishable by the size of second upper incisors, the shape of skull, nasal sinus, canines, second upper and lower premolars. In addition, the two genera can be osteometrically separated by measurements of the braincase height, interorbital width and shape of anterior palatal emargination. Our data clearly revealed the morphological variations in the skull shape of *Kerivoula hardwickii* in Vietnam. This suggests a possible separation into three morphotypes, representing cryptic species supported by statistical differences with wide variation in skull shape, size and teeth. These results demonstrated *Kerivoula hardwickii* can be separated three subspecies, and the result will serve as the basis for the future assessment and classification of this group in Southeast Asia.

KEY WORDS: cryptic species, Kerivoulinae, morphological variation, Vietnam, woolly bat

doi: 10.1292/jvms.15-0270; *J. Vet. Med. Sci.* 78(2): 187–198, 2016

Recent studies on Asian bats have indicated that Asia harbors a number of species complexes that present challenges for establishing the taxonomy [6, 18, 47]. This is mainly due to cryptic forms and the limited number of voucher specimens available for morphological comparisons [14]. Since 2000, numerous new species of the family Vespertilionidae have been described in Southeast Asia including some species of Kerivoulinae [5, 6, 17], and undescribed species may yet be common in the natural forest in Southeast Asia [18, 30]. Within the family, one of the taxa with a high number of cryptic forms and an unresolved taxonomy is the subfamily Kerivoulinae [17, 18].

Gray (1842) established the genus *Kerivoula* and has selected *Vespertilio pictus* (Pallas, 1767) as the type species [19]. Subsequently, Miller (1905) has described a new genus and species, *Phoniscus atrox*, and established the subfamily Kerivoulinae [36]. In addition, this author provided the diagnostic characteristics of *Kerivoula* Gray, 1842 and *Phoniscus* Miller, 1905 [36]. The generic rank of *Phoniscus* was recognized by several authors [52, 54], however, it was considered by other scholars to merely be a subgenus of *Kerivoula* [32, 33, 35, 43, 50]. *Phoniscus* can be distinguished from *Kerivoula* based on the following diagnostic characteristics: the upper canine with a well-defined longitudinal groove on the buccal face (versus smoothly rounded in *Kerivoula*), the second upper incisor is much reduced (versus developed in *Kerivoula*), and the anterior part of the rostrum is broader than in *Kerivoula* and anterior palatal emargination is distinctively broader than deep (versus deeper in *Kerivoula*) [9, 23, 52].

In Southeast Asia, the subfamily Kerivoulinae currently contains nine species of *Kerivoula* (including *K. lenis*) and two species of *Phoniscus* [9, 44, 51, 54, 55]. Three new species of *Kerivoula* have recently been described in the region: *K. kachinensis* in Myanmar [5], *K. titania* in Cambodia [6] and *K. krauensis* in Peninsular Malaysia [17]. In addition, *K. titania* was recently recorded from China [58]. Morphological and genetic comparisons suggested that *K. hardwickii* is a species complex, that contains at least three forms [6, 17, 18]. The comparison of braincase height showed that at least two different forms exist: a smaller, flat-headed species, that may be *K. depressa* (Miller, 1906) and a slightly larger dome-skulled taxon, *K. hardwickii* (Horsfield, 1824) [6]. Karyotypes, phylogenetic and morphological studies of *Kerivoula* species in Malaysia indicated that this genus includes three different morphotypes [14]. The morphological analysis of Malaysian *Kerivoula* was done, and as the result, six groupings of *Kerivoula* were identified and *K. papillosa* provided evidence that the species includes two distinctive groups based on size [21]. These studies showed that *Kerivoula* encompasses a group of cryptic species and that the

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diversity of the woolly bats is still underestimated.

In Vietnam, one *Phoniscus* and five *Kerivoula* species have been recorded [6, 8, 22, 34, 51]. Among them, six species have been recorded in Laos [16, 38], five species are known in Thailand [6, 45, 46], and four species have been identified in Cambodia [6, 29, 40]. As the specific content of *K. hardwickii* has been considered as a group of cryptic species [6, 17, 18] and in general, the taxonomy of the Kerivoulinae in Southeast Asia is highly problematic [51], we examined a large number of skulls of Kerivoulinae in Vietnam and used multivariate analysis to investigate the morphological differences of the species within the subfamily.

## MATERIALS AND METHODS

*Morphometric characteristics and measurement*: Skulls of 113 females and 59 males were measured to the nearest 0.01 mm using a digital caliper (Mitutoyo model NTD12-15PMX, Mitutoyo Corp., Kawasaki, Japan) under an SZ40 stereomicroscope (Olympus, Tokyo, Japan). We osteometrically examined 23 cranial and dental measurements (Table 1 and Fig. 1) including the 15 measurements that have been frequently used for taxonomic comparisons between Kerivoulinae species and the other species of bats [4–6, 9, 14, 17, 21–24, 34, 45, 51, 55]. The notation used in describing the first upper and lower incisor is I1/i1, second upper and lower incisor is I2/i2, as for the premolars, first upper/lower premolar is P2/p2, and the second upper/lower premolar is P3/p3, whereas the third upper/lower premolars is P4/p4 [23, 50, 51, 55]. Only fully grown adult specimens were included in this study [34, 41].

Voucher specimens used in this study are deposited in the collection of the Institute of Ecology and Biological Resources (IEBR), Hanoi, Vietnam and the Hungarian Natural History Museum (HNHM), Budapest, Hungary. Registration numbers of each specimen are provided in Appendix 1. We compared 23 original cranial and dental measurements of our collections (Table 1) with previous descriptions and using relevant references [5, 6, 23, 34, 36, 37, 50, 51, 55]. Six species of Kerivoulinae, namely: *K. kachinensis*, *K. hardwickii*, *K. papillosa*, *K. picta*, *K. titania* and *Phoniscus jagorii* were tentatively identified.

The species of Kerivoulinae examined in this study are shown in Table 2. The braincase height can be used as one of the characteristics to separate *Kerivoula* species [5, 6, 9, 51]. The specimens of *K. hardwickii* used in this study originate from various geographical populations. We referred to this characteristic and used the locality data of the specimens to confirm the geographic morphological variations of *K. hardwickii*. Finally, we postulate the three geographic populations in this species [1, 2, 15, 49, 53]. Each population name in the *K. hardwickii* was assigned the locality symbol: the northern (N), the central (C) and the southern (S) populations as arranged in Table 2. The N and S populations originated only from one locality, whereas the C population originated from multiple geographical sites in the center of Vietnam (Table 2 and Fig. 2).

*Statistical analyses*: We calculated the mean values and standard deviations from the 23 craniodental measurements, with the two sexes analyzed separately (Table 3). Measurement data were applied to assess differences of the size and shape within Kerivoulinae. Principal component analysis (PCA) was conducted with the software PAST Statistics [20] to evaluate morphological variations among the six Kerivoulinae populations.

Canonical variate analysis (CVA) was used in Genstat version 10 [39] to confirm the distinctiveness between groups after PCA. For the PCA and CVA, we conducted the two analyses using (1) log-transformed raw data to assess the size [3, 7, 42] and (2) log-transformed standardized data (raw score/geometric mean) to examine the shape [28].

Differences in the craniodental measurements and the mean values of the principal components among populations were examined by one-way analysis of variance (ANOVA), and pairwise comparisons were made with Tukey's test ($P<0.05$) for more than three samples with $F$ and $t$-tests ($P<0.05$) among taxa for comparison between sexes.

## RESULTS

Descriptive statistics of craniodental measurements are presented in Table 3. On the results of the multiple comparisons, one-way ANOVA indicated the greatest length of skull (GTL) was the largest in *K. kachinensis* and *K. papillosa*, which were distinctly separated from the other species of Kerivoulinae. The *P. jagori* and *K. titania* showed intermediate skull size and distinguished them from other species. The N, C, S populations and *K. picta* showed smallest skull size. In females, the GTL values of N, C, S populations and

Appendix 1: Specimens examined for study

*Kerivoula hardwickii*-S (n=18). Female (8): IEBR-M1809, 2378, 2392, 2819, 2907, 2824, 2910, 4410. Male (10): IEBR-M2755, 2808, 2812, 2817, 2821, 2823, 2831, 2931, 4364, 4621.

*K. hardwickii*-N (n=39). Female (21): IEBR-M1950, 2937, 2938, 2940, 2941, 3048, 3933, 4982, 4999, 5003, 5005, 5027, 5485, 5548, 5621, 5635, 5637, T.050412.12, 050412.6, 050412.8, 050412.13, 050412.15. Male (18): IEBR-M2164, 2170, 2937, 3719, 3731, 3737, 4744, 4755, 5023, 5022, 5633, 5634, 5636, T.050412.3, 050412.7, 050412.17.

*K. hardwickii*-C (n=17). Female (n=13): IEBR-M2163, 2168, 2166, 2169, 2217, 3074, 3075, 3286, 3432, 3438, 3590, 3878, 3879, 5057, 5734, IEBR-B240813.6. Male (n=4): IEBR M2166, 2169, 2217, 5734.

*K. kachinensis* (n=38). Female (30): IEBR-M498, 499, 500, 503, 1289, 1365, 1888, 1890, 1913, 1914, 1934, 1949, 1954, 1956, 2568, 2575, 3268, 3271, 3298, 3455, 3585, 3710, 5310, 5337, 5339, 5623, 5626, 5632, IEBR-B310414.14, VN11-1831. Male (8): IEBR-M-900, 1310, 2569, 3265, 5022, LV 05, VN11-0948, 0940.

*K. papillosa* (n=5). Female (3): IEBR-M4620, 4625, 4363. Male (2): IEBR-M4365, 4417.

*K. picta* (n=2). Female (1): IEBR-M12. Male (1): IEBR-M14.

*K. titania* (n=49): Female (35): IEBR-M493, 494, 1314, 1366, 1379, 1380, 1929, 2468, 2470, 2471, 3062, 3064, 3077, 3091, 3179, 3189, 3304, 3305, 3314, 3317, 3903, 4153, 4227, 4622, 4623, 5311, 5312, 5372, 5403, 5404, 5753, VN11-0002, 0939, 0944, 0945. Male (14): IEBR-M490, 502, 3060, 3061, 3301, 3318, 3953, 5359, 5638, NH-2008, T.050412.10, 050412.14, VN11-0044, 1832.

*Phoniscus jagorii* (n=4): Female (2): IEBR-M5418, VN14-0190. Male (2): IEBR-M4458, 5308.

Table 1. List of craniodental measurements used in this study and their abbreviations

| | |
|---|---|
| Cranium | |
| Greatest length of skull, the greatest antero-posterior length of the skull, taken from the most projecting point at each extremity | GTL |
| Condylo-canine length, from an exoccipital condyle to the anterior edge of the anterior canine | CCL |
| Anterior palatal width (least distance between the outer borders of the upper canines) | UCCW |
| Posterior palatal width: greatest width across the outer border first upper premolars from their buccal borders | UP2P2W |
| Posterior palatal width: Greatest width across the outer border second upper premolars from their buccal borders | UP3P3W |
| Greatest width across the outer border third upper premolars from their buccal borders | UP4P4W |
| External palatal width, taken across the outer border of the third upper molar, taken at the widest part. | M3M3W |
| Upper canine-premolar length (from the front of the upper canine to the back of the crown of the posterior third upper premolar) | CP4L |
| Maxillary toothrow length (distance from the front of upper canine to the back of the crown of the third upper molar) | CM3L |
| Molariform toothrow length, from the posterior upper premolar to the last upper molar | P4M3L |
| Palatal width | PALW |
| Palatal length | PBL |
| Width between the cochleae | BasW |
| Interorbital width (least width of the interorbital constriction) | IOW |
| Zygomatic width (greatest width of the skull across the zygomatic arches | ZYW |
| Breadth of braincase at the posterior roots of zygomatic arches | BB |
| Greatest width of the braincase | GBCW |
| Mastoid width (greatest distance across the mastoid region) | MAW |
| Braincase height (from the basisphenoid at the level of the hamular processes to the highest part of the skull) | BCH |
| Mandible | |
| Mandible length (distance from the anterior rim of the alveolus of the first lower incisor to the most posterior part of the condyle) | ML |
| Mandibular tooth row length (distance from the front of the lower canine to the back of the crown of the third lower molar) | cm3L |
| Lower canine-premolar length (distance from the front of the lower canine to the back of the crown of the posterior third lower premolar) | cp4L |
| Least height of the coronoid process (distance from the tip of the coronoid process to the apex of the indentation on the inferior surface of the ramus adjacent to the angular process) | CPH |

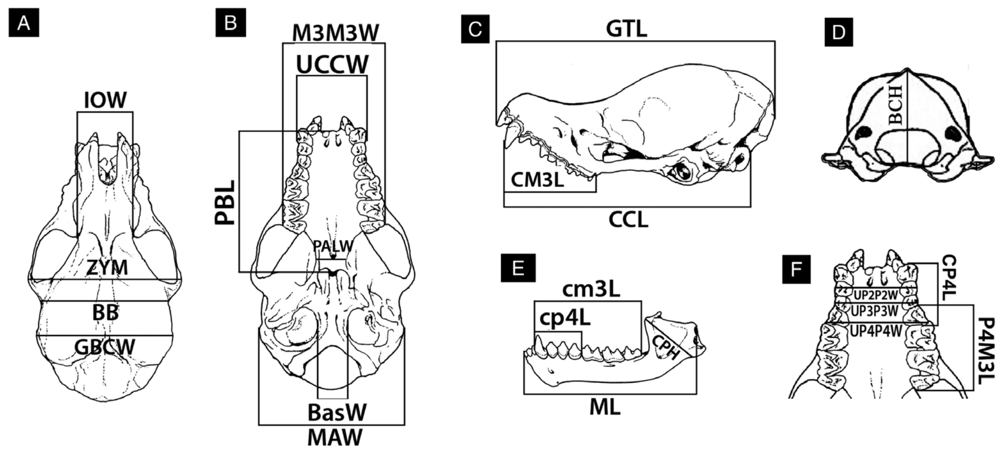


Fig. 1. Dorsal (A), ventral (B), lateral (C) and posterior (D) views of the cranium and mandible (E) and upper (F) dentition showing measurements (see Table 1).

*K. picta* do not overlap, however, in males, N, C populations and *K. picta* do not have overlapping ranges of GTL (Table 3 and Fig. 3) and showed smallest size of skull. In addition, mandibular length (ML) was the greatest in the female of *K. papillasa* and *K. kachinensis* and smallest in the three *K. hardwickii* populations. In the males, ML is the greatest in the *K. papillosa* only. Moreover, *K. kachinensis* and *P. jagori* are overlapped (Fig. 3). However, the S population has greater mean values of GTL and ML than the N and C populations (Fig. 3). Similar trends were also observed in the other measurement, such as CCL, UCCW, UP3P3W, UP4P4W, M3M3W, CP4L, CM3L, BasW, ZYW, BB, MAW and cm3L, in which the largest was found in *K. papillosa* and *K. kachinensis*, medium in *K. titania, P. jagori* and smallest in N, C, S populations (Table 3).

Using one-way ANOVA, the differences in the size clearly separated three groups of Kerivoulinae in both sexes. The factor loadings for PCA of the log-transformed raw data are provided in Table 4. All characteristic factor loadings were positive. PC1 was a size component, which explains

Table 2. Species, sex composition and locality of the specimens used in this study

| Species[a)] | Symbol of species | Sample | | Traditionally-accepted species | Geographic distribution followed [1, 2, 49, 53] |
|---|---|---|---|---|---|
| | | Female | Male | | |
| *Kerivoula kachinenis* | K | 30 | 8 | [5, 51] | Northern, Center and Center highland Plateau. |
| *K. hardwickii*[a)] Northern population | N | 21 | 18 | [8, 23, 34, 50] | The Northern of Vietnam from North Eastern, North Western and Red River Delta |
| *K. hardwickii*[a)] Central population | C | 13 | 4 | [8, 23, 34, 50] | From multiple geographical sites in the center of Vietnam. |
| *K. hardwickii*[a)] Southern population | S | 8 | 10 | [8, 23, 34, 50] | South Eastern and Mekong Delta included Phu Quoc and Condao island. |
| *K. papillosa* | P | 3 | 2 | [8, 23, 34, 50] | Only recorded in the South Eastern and Mekong Delta included Phu Quoc and Condao island. |
| *K. picta* | pi | 1 | 1 | [8, 23, 34, 50] | Widespread species |
| *K. titania* | T | 35 | 14 | [6] | Northern to North Center Coast, South central Coast, Central Highland Plateau |
| *Phoniscus jagorii* | J | 2 | 2 | [8, 23, 34, 50] | Northern and Southern |

a) *K. hardwickii* is separated to three geographic population.

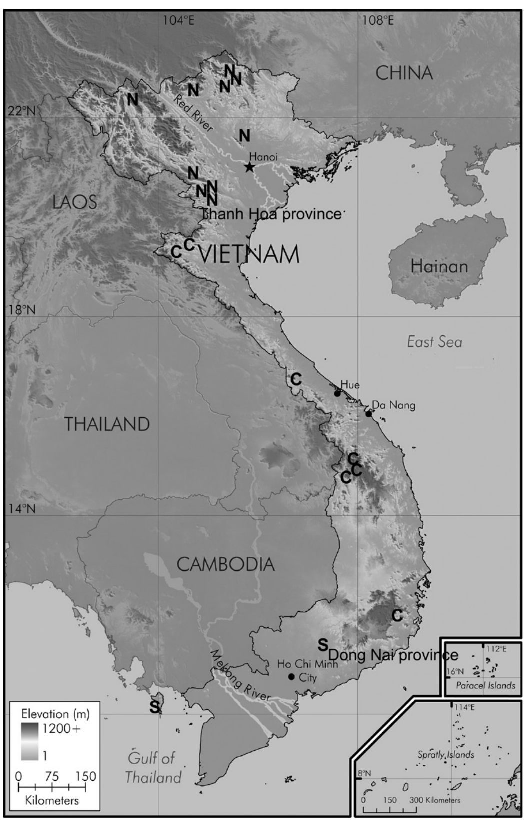


Fig. 2. Map showing specimen localities of three *K. hardwickii* populations from Vietnam. N: northern populations. S: southern populations. C: widely distributed populations, from multiple geographical sites in central of Vietnam. Symbols are explained in Table 2.

the 83.10% total variance in the males and 86.05% total variance in females. The high factor loadings of the both sexes are demonstrated by the following measurements: CCL, UCCW, UP2P2W, UP3P3W, CP4L, CM3L, P4M3L, PBL, BasW, ZYW, ML, cm3L, cp4L and CPH (Table 4). The PC1 scores indicated that Kerivoulinae is divided into three groups (Tukey's test, $P<0.05$) (Fig. 4). In the females (Fig. 5), higher factor loadings in the PC1 indicated the larger size in *K. papillosa* (mean: 1.649, range: 1.474~1.791), which overlapped with *K. kachinensis* (1.308, 0.892~1.918), but were significantly larger than the other populations of Kerivoulinae ($P<0.05$). The medium-sized species, such as *P. jagori* (0.583~0.784), were larger than *K. titania* (PC1 mean: −0.026; range: −0.389~0.319) and significantly larger than the small-sized group that included *K. picta* (−0.746) and *K. hardwickii* populations (−1.046; −1.470~ –0.641) ($P<0.05$).

In males (Fig. 5), the species of the largest size is *K. papillosa* (range: 2.151~2.283), which is larger than *K. kachinensis* (mean: 1.577, range: 1.260~1.987) ($P<0.05$). The species of medium size was *P. jagori* (1.498~1.628), which is larger than *K. titania* (0.316, 0.093~0.499) ($P<0.05$), and both *P. jagori* and *K. titania* were significantly larger than the other small-sized *K. hardwickii* populations (−0.751, −1.592~0.096) ($P<0.05$) and *K. picta* (−0.102).

In addition, the statistic results in both sexes indicated that the PC1 mean score of the S population (female: −0.916 and male: −0.400) was larger than that of the N (female: −1.051 and male: −0.892) and C (female: −1.119 and male: 0.950) populations.

Using log-transformed standardized data in the PCA, PCs 1, 2 and 3 were interpreted as shape components (Table 4 and Fig. 6). In females, PC1 explained 30.13% of the variance. The data show the highest factor loading for IOW, followed by BCH, GBCW and PALW in negative axes; BasW and cp4L in positive axes in Table 4. PC2 explained 18.75% of the variance, with the highest factor loading for BCH, followed by cp4L in negative axes; PALW and BasW in positive axes. PC3 showed CPH, PALW and UCCW in positive axes; BasW in the negative axes, which was the highest factor loading of 13.89% of the variance. In the plots for PC1 and 2 scores of the both sexes, *K. kachinensis*, *K. papillosa* and *K. picta* formed a separated two-dimensional space from the plots of the other species, with almost no overlap ($P<0.05$) (Fig. 6). In males, 25.48% of the variance could be explained using PC1, with the highest factor loading for BCH followed by CP4L and IOW in positive axes;

Table 3. Minimum, maximum, mean values (mm) and standard deviations for craniometric measurement in various populations of Kerivoulinae in Vietnam

| Character | *K. kachinensis* | | *K. papillosa* | | *K. picta* | | *K. titania* | | *Phoniscus jagorii* | | *K. hardwickii*-N | | *K. hardwickii*-C | | *K. hardwickii*-S | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ♀ (30) | ♂ (8) | ♀ (3) | ♂ (2) | ♀ (1) | ♂ (1) | ♀ (35) | ♂ (14) | ♀ (2) | ♂ (2) | ♀ (21) | ♂ (18) | ♀ (13) | ♂ (4) | ♀ (8) | ♂ (10) |
| GL | 17.17–18.42 | 16.76–17.69 | 17.15–17.85 | 17.26–17.51 | 15.23 | 14.98 | 15.22–16.35 | 15.26–15.98 | 16.71–17.02 | 16.56–16.84 | 13.63–14.56 | 13.38–14.62 | 13.74–14.60 | 13.72–14.01 | 13.89–15.00 | 13.89–15.26 |
| | 17.81 ± 0.32 | 18.28 ± 0.37 | 17.44 ± 0.37 | | | | 15.79 ± 0.26 | 15.57 ± 0.20 | | | 13.63 ± 0.21 | 13.99 ± 0.32 | 14.19 ± 0.24 | 13.89 ± 0.12 | 14.55 ± 0.42 | 14.53 ± 0.37 |
| CCL | 15.23–16.44 | 15.08–15.79 | 15.52–15.91 | 15.34–15.53 | 13.07 | 13.04 | 13.33–14.18 | 13.10–13.92 | 14.76–15.26 | 14.64–14.81 | 11.94–12.98 | 11.88–12.81 | 12.19–12.88 | 11.98–12.26 | 12.16–13.15 | 12.17–13.22 |
| | 15.87 ± 0.31 | 15.41 ± 0.24 | 15.67 ± 0.21 | | | | 13.82 ± 0.24 | 13.54 ± 0.21 | | | 12.62 ± 0.22 | 12.34 ± 0.29 | 12.52 ± 0.18 | 12.11 ± 0.14 | 12.70 ± 0.37 | 12.69 ± 0.31 |
| UCCW | 4.13–4.66 | 3.88–4.52 | 4.50–4.70 | 4.57–4.72 | 3.32 | 3.33 | 3.30–3.77 | 3.37–3.67 | 3.60–3.63 | 3.50–3.73 | 3.17–3.58 | 3.00–3.56 | 3.24–3.50 | 3.11–3.35 | 3.37–3.62 | 3.32–3.68 |
| | 4.35 ± 0.13 | 4.23 ± 0.21 | 4.62 ± 0.11 | | | | 3.55 ± 0.11 | 3.53 ± 0.08 | | | 3.36 ± 0.11 | 3.28 ± 0.17 | 3.42 ± 0.12 | 3.22 ± 0.11 | 3.45 ± 0.11 | 3.47 ± 0.13 |
| UP2P2W | 4.19–4.82 | 3.94–4.55 | 4.42–4.67 | 4.33–4.44 | 3.12 | 3.28 | 3.55–3.92 | 3.54–3.78 | 3.59–3.75 | 3.67–3.61 | 3.20–3.61 | 3.08–3.62 | 3.28–3.55 | 3.17–3.37 | 3.37–3.62 | 3.39–3.68 |
| | 4.41 ± 0.13 | 4.23 ± 0.21 | 4.56 ± 0.13 | | | | 3.72 ± 0.10 | 3.66 ± 0.07 | | | 3.45 ± 0.10 | 3.35 ± 0.16 | 3.41 ± 0.09 | 3.26 ± 0.08 | 3.50 ± 0.10 | 3.52 ± 0.09 |
| UP3P3W | 4.14–4.82 | 3.81–4.43 | 4.39–4.61 | 4.36–4.41 | 3.25 | 3.38 | 3.65–3.99 | 3.65–3.88 | 3.63–3.84 | 3.74–3.69 | 3.28–3.68 | 3.16–3.58 | 3.33–3.64 | 3.19–3.44 | 3.48–3.69 | 3.49–3.65 |
| | 4.38 ± 0.14 | 4.19 ± 0.20 | 4.53 ± 0.12 | | | | 3.81 ± 0.08 | 3.75 ± 0.07 | | | 3.50 ± 0.11 | 3.38 ± 0.13 | 3.48 ± 0.11 | 3.31 ± 0.10 | 3.57 ± 0.09 | 3.57 ± 0.06 |
| UP4P4W | 4.39–5.75 | 4.85–5.49 | 5.42–5.57 | 5.31–5.34 | 4.34 | 4.34 | 4.45–4.84 | 4.48–4.78 | 4.37–4.77 | 4.52–4.58 | 4.05–4.56 | 3.94–4.57 | 4.10–4.48 | 4.01–4.27 | 4.25–4.47 | 4.27–4.60 |
| | 5.36 ± 0.22 | 5.14 ± 0.19 | 5.52 ± 0.09 | | | | 4.66 ± 0.10 | 4.60 ± 0.09 | | | 4.33 ± 0.13 | 4.21 ± 0.19 | 4.23 ± 0.14 | 4.13 ± 0.13 | 4.34 ± 0.10 | 4.44 ± 0.12 |
| M3M3W | 6.18–6.94 | 5.87–6.61 | 6.45–6.77 | 6.37–6.37 | 5.48 | 5.72 | 5.39–5.88 | 5.38–5.69 | 5.50–5.68 | 5.65–5.70 | 4.85–5.33 | 4.76–5.48 | 5.01–5.79 | 4.96–5.23 | 5.12–5.39 | 5.01–5.34 |
| | 6.46 ± 0.18 | 6.21 ± 0.24 | 6.58 ± 0.17 | | | | 5.67 ± 0.12 | 5.54 ± 0.09 | | | 5.15 ± 0.12 | 5.04 ± 0.19 | 5.19 ± 0.22 | 5.14 ± 0.12 | 5.22 ± 0.13 | 5.25 ± 0.12 |
| CP4L | 3.19–3.65 | 3.07–3.42 | 3.53–3.57 | 3.49–3.60 | 2.96 | 2.88 | 2.88–3.19 | 2.86–3.06 | 3.63–3.74 | 3.74–3.75 | 2.51–2.89 | 2.43–2.84 | 2.46–2.80 | 2.41–2.70 | 2.47–2.79 | 2.51–2.86 |
| | 3.40 ± 0.12 | 3.22 ± 0.12 | 3.55 ± 0.02 | | | | 3.05 ± 0.07 | 2.98 ± 0.05 | | | 2.64 ± 0.10 | 2.62 ± 0.12 | 2.61 ± 0.09 | 2.55 ± 0.13 | 2.67 ± 0.14 | 2.73 ± 0.10 |
| CM3L | 6.54–7.28 | 6.53–6.89 | 7.02–7.34 | 7.07–7.18 | 5.78 | 5.81 | 5.78–6.26 | 5.81–6.12 | 6.44–6.65 | 6.57–6.60 | 5.03–5.50 | 4.96–5.56 | 5.14–5.43 | 4.94–5.25 | 5.06–5.62 | 5.26–5.76 |
| | 6.86 ± 0.17 | 6.71 ± 0.12 | 7.21 ± 0.17 | | | | 6.07 ± 0.10 | 5.97 ± 0.08 | | | 5.27 ± 0.13 | 5.22 ± 0.18 | 5.30 ± 0.09 | 5.15 ± 0.14 | 5.45 ± 0.21 | 5.51 ± 0.13 |
| P4M3L | 4.18–4.80 | 4.61–4.50 | 4.53–4.68 | 4.58–4.62 | 3.76 | 3.77 | 3.06–4.18 | 3.82–3.98 | 3.67–400 | 3.89–3.93 | 2.64–3.65 | 3.27–3.69 | 3.34–3.62 | 3.21–3.55 | 3.24–3.86 | 3.52–3.81 |
| | 4.49 ± 0.13 | 4.32 ± 0.29 | 4.62 ± 0.08 | | | | 3.97 ± 0.24 | 3.90 ± 0.06 | | | 3.46 ± 0.21 | 3.46 ± 0.12 | 3.53 ± 0.09 | 3.43 ± 0.15 | 3.63 ± 0.20 | 3.68 ± 0.11 |
| PALW | 1.92–2.32 | 1.91–2.13 | 1.76–1.95 | 1.78–1.81 | 1.96 | 1.98 | 1.52–2.00 | 1.67–1.89 | 1.94–2.11 | 1.77–2.00 | 1.63–1.98 | 1.53–1.87 | 1.66–1.89 | 1.61–1.74 | 1.63–1.89 | 1.53–1.75 |
| | 2.12 ± 0.12 | 2.02 ± 0.09 | 1.85 ± 0.10 | | | | 1.79 ± 0.11 | 1.77 ± 0.07 | | | 1.78 ± 0.08 | 1.70 ± 0.10 | 1.78 ± 0.08 | 1.71 ± 0.02 | 1.75 ± 0.09 | 1.66 ± 0.07 |
| PBL | 6.67–7.85 | 6.68–7.43 | 7.40–7.83 | 7.26–7.54 | 6.46 | 6.99 | 5.88–6.90 | 5.96–6.67 | 6.55–6.68 | 7.15–7.44 | 5.35–6.08 | 5.13–5.87 | 5.32–6.71 | 5.40–6.12 | 5.79–6.08 | 5.63–6.11 |
| | 7.31 ± 0.24 | 7.14 ± 0.30 | 7.62 ± 0.22 | | | | 6.42 ± 0.27 | 6.38 ± 0.20 | | | 5.69 ± 0.21 | 5.65 ± 0.20 | 5.71 ± 0.16 | 5.69 ± 0.25 | 5.89 ± 0.17 | 5.90 ± 0.17 |
| BasW | 1.65–2.31 | 1.70–1.90 | 1.82–2.09 | 1.86–1.89 | 1.29 | 1.4 | 1.49–1.91 | 1.53–1.83 | 1.52–1.59 | 1.68–1.71 | 1.40–1.73 | 1.31–1.59 | 1.25–1.70 | 1.38–1.58 | 1.32–1.58 | 1.34–1.49 |
| | 1.93 ± 0.15 | 1.81 ± 0.07 | 1.93 ± 0.14 | | | | 1.74 ± 0.11 | 1.68 ± 0.10 | | | 1.57 ± 0.09 | 1.48 ± 0.07 | 1.44 ± 0.13 | 1.47 ± 0.10 | 1.43 ± 0.08 | 1.41 ± 0.05 |
| IOW | 3.34–3.94 | 3.44–3.75 | 3.37–3.59 | 3.38–3.39 | 3.43 | 3.38 | 3.26–3.65 | 3.28–3.64 | 4.37–4.48 | 4.29–4.49 | 3.11–3.57 | 2.94–3.53 | 3.20–3.60 | 3.03–3.31 | 3.20–3.28 | 3.23–3.48 |
| | 3.63 ± 0.15 | 3.61 ± 0.09 | 3.45 ± 0.12 | | | | 3.45 ± 0.09 | 3.41 ± 0.11 | | | 3.32 ± 0.12 | 3.24 ± 0.14 | 3.29 ± 0.11 | 3.21 ± 0.13 | 3.24 ± 0.03 | 3.38 ± 0.08 |
| ZYW | 10.03–11.29 | 9.52–10.58 | 10.78–11.19 | 10.70–10.70 | 8.77 | 9.03 | 9.00–9.77 | 8.72–9.38 | 9.60–9.66 | 10.17–10.21 | 7.93–8.78 | 7.29–8.89 | 7.74–8.58 | 8.11–8.50 | 8.36–8.94 | 8.33–9.04 |
| | 10.54 ± 0.26 | 10.19 ± 0.39 | 10.95 ± 0.21 | | | | 9.30 ± 0.18 | 9.08 ± 0.20 | | | 8.37 ± 0.23 | 8.16 ± 0.38 | 8.27 ± 0.25 | 8.35 ± 0.17 | 8.61 ± 0.28 | 8.64 ± 0.23 |
| BCH | 5.21–5.88 | 5.28–5.78 | 6.63–6.88 | 6.69–6.76 | 5.22 | 5.7 | 5.04–5.83 | 5.15–5.70 | 7.14–7.15 | 7.54–7.65 | 4.40–5.41 | 4.37–5.60 | 5.07–5.48 | 5.15–5.55 | 4.89–6.28 | 5.67–6.04 |
| | 5.55 ± 0.17 | 5.56 ± 0.19 | 6.87 ± 0.24 | | | | 5.48 | 5.47 ± 0.16 | | | 4.78 ± 0.33 | 4.85 ± 0.32 | 5.24 ± 0.13 | 5.36 ± 0.17 | 5.62 ± 0.55 | 5.87 ± 0.14 |
| GBCW | 7.77–8.75 | 7.94–8.27 | 8.00–8.22 | 8.10–8.11 | 6.74 | 6.95 | 7.37–8.03 | 7.54–7.98 | 7.87–8.03 | 7.87–8.00 | 6.80–7.47 | 6.94–7.45 | 6.88–7.44 | 7.00–7.29 | 7.06–7.37 | 6.95–7.70 |
| | 8.23 ± 0.22 | 8.21 ± 0.16 | 8.08 ± 0.12 | | | | 7.75 ± 0.16 | 7.74 ± 0.14 | | | 7.21 ± 0.15 | 7.12 ± 0.14 | 7.21 ± 0.17 | 7.14 ± 0.12 | 7.16 ± 0.10 | 7.15 ± 0.22 |
| BB | 7.53–8.42 | 7.24–7.97 | 7.61–8.11 | 7.86–7.95 | 6.58 | 6.87 | 6.86–7.59 | 6.86–7.46 | 7.73–7.75 | 7.84–7.95 | 6.35–6.95 | 6.09–6.96 | 6.26–6.80 | 6.44–6.74 | 6.49–6.88 | 6.41–7.08 |
| | 7.88 ± 0.23 | 7.70 ± 0.25 | 7.78 ± 0.29 | | | | 7.15 ± 0.17 | 7.15 ± 0.20 | | | 6.68 ± 0.14 | 6.52 ± 0.26 | 6.54 ± 0.16 | 6.58 ± 0.12 | 6.62 ± 0.12 | 6.67 ± 0.20 |
| MAW | 8.15–9.12 | 8.20–8.84 | 8.60–8.88 | 8.64–8.64 | 7.69 | 7.86 | 7.61–8.27 | 7.57–8.09 | 8.35–8.42 | 8.44–8.58 | 7.18–7.61 | 6.82–7.47 | 6.97–7.57 | 7.05–7.50 | 7.19–7.58 | 7.18–7.86 |
| | 8.72 ± 0.24 | 8.43 ± 0.21 | 8.77 ± 0.15 | | | | 7.97 ± 0.17 | 7.85 ± 0.16 | | | 7.43 ± 0.12 | 7.24 ± 0.18 | 7.35 ± 0.18 | 7.27 ± 0.19 | 7.36 ± 0.17 | 7.37 ± 0.21 |
| ML | 11.82–12.81 | 11.47–12.20 | 12.47–12.82 | 12.36–12.53 | 10.47 | 10.54 | 10.19–11.00 | 9.89–10.77 | 11.75–11.85 | 11.51–11.78 | 9.13–9.91 | 8.80–9.67 | 9.02–9.55 | 8.75–9.34 | 9.14–10.00 | 9.09–10.13 |
| | 12.28 ± 0.24 | 11.88 ± 0.24 | 12.62 ± 0.18 | | | | 10.55 ± 0.24 | 10.31 ± 0.22 | | | 9.48 ± 0.24 | 9.19 ± 0.23 | 9.33 ± 0.15 | 9.08 ± 0.28 | 9.63 ± 0.30 | 9.62 ± 0.27 |
| cp4L | 3.07–3.47 | 3.03–3.31 | 3.54–3.68 | 3.50–3.60 | 2.7 | 2.56 | 2.71–3.07 | 2.75–3.01 | 3.64–3.65 | 3.63–3.74 | 2.33–2.81 | 2.15–2.62 | 2.35–2.64 | 2.25–2.41 | 2.35–2.63 | 2.49–2.71 |
| | 3.33 ± 0.09 | 3.19 ± 0.10 | 3.61 ± 0.07 | | | | 2.92 ± 0.07 | 2.85 ± 0.07 | | | 2.47 ± 0.12 | 2.41 ± 0.13 | 2.44 ± 0.09 | 2.34 ± 0.07 | 2.52 ± 0.08 | 2.56 ± 0.06 |
| cm3L | 7.07–7.77 | 6.75–7.46 | 7.76–7.96 | 7.69–7.87 | 6 | 6.22 | 6.28–6.76 | 6.19–6.61 | 7.00–7.49 | 7.17 | 5.42–5.89 | 5.25–5.98 | 5.50–5.83 | 5.13–5.59 | 5.30–6.04 | 5.64–6.08 |
| | 7.38 ± 0.18 | 7.15 ± 0.21 | 7.88 ± 0.11 | | | | 6.52 ± 0.11 | 6.39 ± 0.12 | | | 5.62 ± 0.14 | 5.56 ± 0.20 | 5.65 ± 0.10 | 5.45 ± 0.22 | 5.76 ± 0.26 | 5.85 ± 0.13 |
| CPH | 3.37–4.12 | 3.43–4.00 | 4.17–4.60 | 4.16–4.55 | 2.89 | 2.8 | 2.86–3.43 | 2.86–3.22 | 3.65–3.68 | 3.82–3.88 | 2.79–3.27 | 2.68–3.15 | 2.60–3.17 | 2.75–2.88 | 2.95–3.03 | 2.75–3.12 |
| | 3.86 ± 0.18 | 3.63 ± 0.18 | 4.37 ± 0.22 | | | | 3.10 ± 0.13 | 3.02 ± 0.13 | | | 2.98 ± 0.12 | 2.88 ± 0.15 | 2.89 ± 0.14 | 2.83 ± 0.06 | 2.98 ± 0.06 | 2.93 ± 0.13 |

Values are given as mean (if n≥3), SD (if n≥3) in below row and minimum–maximum (Min-max) in upper row.

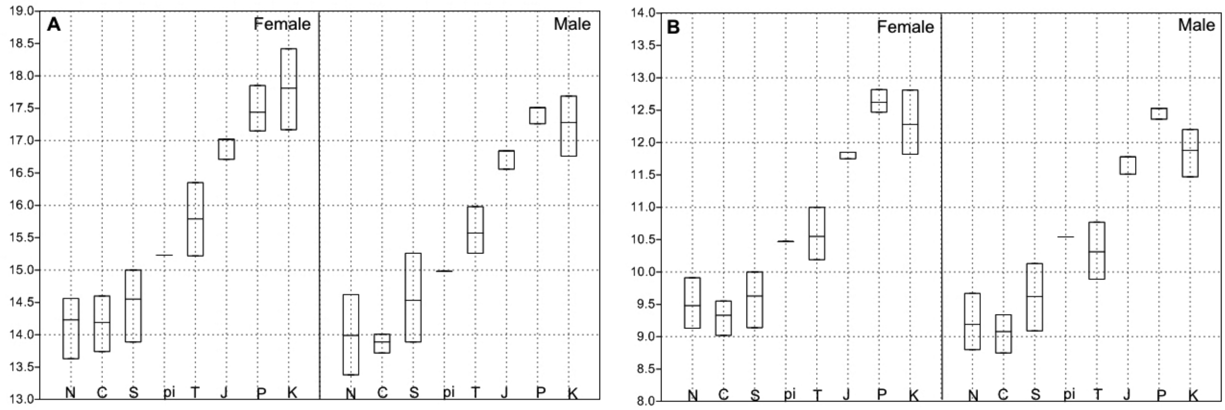


Fig. 3. Range (minimum value to maximum value in boxplots) (mm) and mean value (in horizontal bar) (mm) of greatest length of the skull (A) and mandible length (B). The line the top and bottom of boxplot: maximum and minimum values. The horizontal line within the boxes indicated medium value. Symbols are explained in Table 2.

Table 4. Character factor loadings for principal components analysis of the log-transformed raw data (PCs 1) and log-transformed standardized data (PCs 1, 2 and 3) of Kerivoulinae populations from Vietnam

| Measurement | Raw data | | Standardized data | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Female | Male | Female | | | Male | | |
| | PC 1 | PC 1 | PC1 | PC2 | PC3 | PC1 | PC2 | PC3 |
| GTL | 0.198 | 0.196 | –0.024 | 0.001 | –0.015 | –0.027 | –0.029 | 0.074 |
| CCL | **0.206** | **0.203** | 0.008 | 0.023 | 0.031 | –0.063 | 0.014 | 0.074 |
| UCCW | **0.240** | **0.238** | **0.178** | 0.097 | **0.301** | –0.114 | 0.177 | **–0.454** |
| UP2P2W | **0.229** | **0.212** | 0.150 | 0.109 | 0.133 | **–0.159** | 0.054 | **–0.352** |
| UP3P3W | **0.208** | **0.200** | 0.069 | 0.076 | 0.054 | –0.106 | 0.011 | –0.246 |
| UP4P4W | 0.196 | 0.183 | 0.047 | 0.103 | 0.137 | –0.099 | –0.058 | –0.298 |
| M3M3W | 0.203 | 0.187 | 0.039 | 0.064 | 0.056 | –0.077 | –0.085 | –0.154 |
| CP4L | **0.239** | **0.242** | 0.079 | **–0.242** | –0.076 | **0.216** | 0.175 | 0.250 |
| CM3L | **0.238** | **0.248** | 0.117 | –0.154 | –0.041 | 0.024 | 0.195 | 0.086 |
| P4M3L | **0.226** | **0.207** | 0.121 | –0.131 | –0.108 | –0.042 | 0.079 | –0.057 |
| PALW | 0.148 | 0.129 | **–0.247** | **0.470** | **0.309** | **–0.312** | **–0.396** | –0.062 |
| PBL | **0.223** | **0.226** | 0.109 | –0.032 | 0.017 | 0.030 | 0.073 | 0.231 |
| BasW | **0.230** | **0.209** | **0.242** | **0.316** | **–0.752** | **–0.327** | 0.027 | **0.494** |
| IOW | 0.090 | 0.114 | **–0.521** | 0.081 | –0.023 | **0.191** | **–0.470** | 0.113 |
| ZYW | **0.213** | **0.215** | 0.040 | –0.009 | –0.006 | 0.009 | 0.037 | –0.087 |
| BB | 0.158 | 0.170 | –0.169 | 0.117 | –0.092 | 0.007 | –0.184 | 0.060 |
| GBCW | 0.122 | 0.131 | **–0.286** | 0.132 | –0.177 | –0.105 | **–0.290** | 0.106 |
| MAW | 0.152 | 0.151 | –0.183 | 0.101 | –0.110 | –0.018 | –0.218 | 0.097 |
| BCH | 0.117 | 0.171 | **–0.472** | **–0.567** | –0.028 | **0.785** | –0.168 | –0.135 |
| ML | **0.239** | **0.242** | 0.118 | –0.062 | 0.064 | 0.025 | 0.163 | 0.113 |
| cm3L | **0.249** | **0.257** | 0.149 | –0.206 | –0.049 | 0.050 | **0.242** | 0.161 |
| cp4L | **0.283** | **0.296** | **0.217** | **–0.344** | 0.023 | 0.029 | **0.368** | 0.065 |
| CPH | **0.260** | **0.260** | **0.219** | 0.058 | **0.353** | 0.082 | **0.282** | –0.081 |
| Eigenvalue | 0.039 | 0.032 | 0.003 | 0.002 | 0.001 | 0.002 | 0.002 | 0.001 |
| % variance | 86.05 | 83.1 | 30.13 | 18.75 | 13.89 | 25.48 | 23.62 | 12.25 |

Boldface numerals: High factor loading.

BasW, PALW and UP2P2W in negative axes in Table 4. PC2 explained 23.62% of the variance with high negative factor loadings for IOW, PALW and GBCW; cm3L, cp4L and CPH in positive axes. PC3 accounted for 12.25% of the variance, with the highest factor loadings for BasW in positive axes; UCCW and UP2P2W in negative axes in Table 4. Above results revealed that the overlap in N, C and S populations of *K. hardwickii*, in which the skull shape of C population overlapped a part of the N and S populations from females, but the S population was separated from the N and C popula-

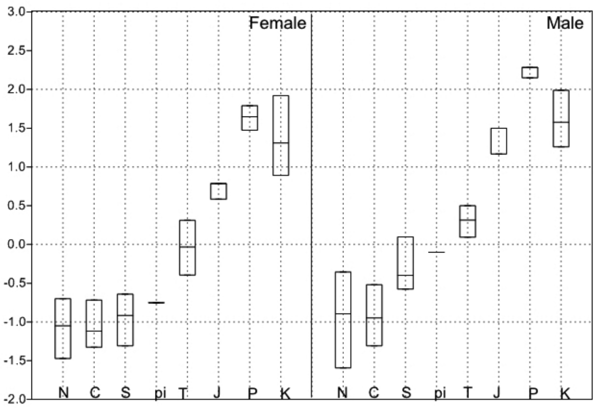


Fig. 4. Range (minimum value to maximum value in boxplots) and mean value (in horizontal bar) of PC1 scores of log-transformed raw data of Kerivoulinae populations from Vietnam. The line the top and bottom of boxplot: maximum and minimum values. The horizontal line within the boxes indicated medium value. Symbols are explained in Table 2.

tions in the males (*P*<0.05) (Fig. 6).

Results of CVA are shown in Table 5. In log-transformed raw data, the CVA for females and males clearly separated the Kerivoulinae populations into the different groups (Fig. 7). In the CVA of characteristics of females, the first canonical variable indicated the largest (positive and negative) coefficients of the discriminate function to be ZYW, followed by UP2P2W, GBCW, UP4P4W, UCCW, cm3L, MAW and IOW with percentage variation of 38.83%. The CCL, GTL, GBCW, BCH, CM3L and cm3L were higher (positive and negative) coefficients of the discriminate function in the second canonical variate of 38.07% (Table 5). Furthermore, the CVA for the characteristics of males separated the Kerivoulinae populations into the different groups. The first canonical variate had the highest (positive and negative) coefficients of the discriminate function with GBCW, UP3P3W, UP4P4W, CP4L, CM3L, BCH, GTL and IOW at 56.07% of the percentage variation. The CM3L, CCL, CP4L and IOW were the highest (positive and negative) coefficients of the discriminate functions in the second canonical variate of 22.24% (Table 5 and Fig. 7).

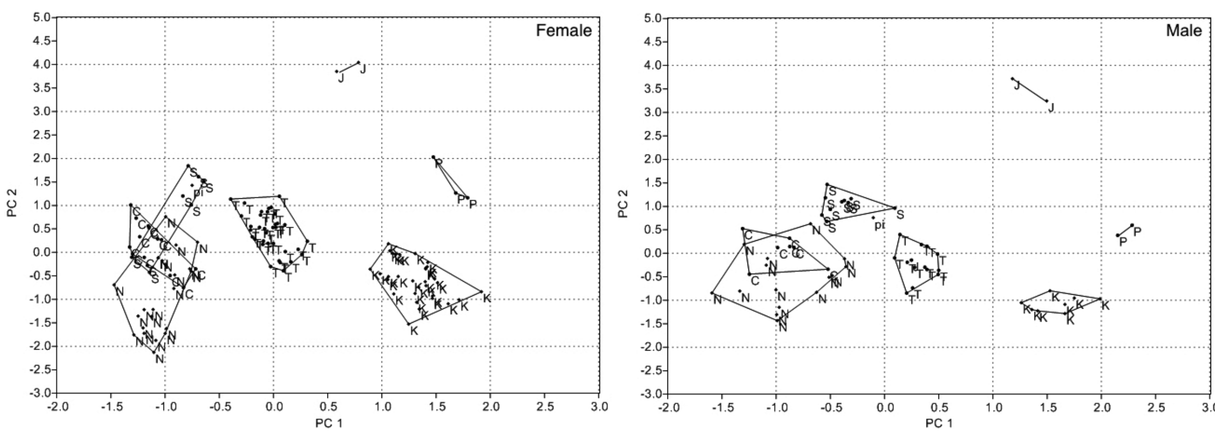


Fig. 5. Scatterplots of scores of the first principal component axes based on log-transformed raw data indicated the significant differences of the size of the females and the males of Kerivoulinae populations from Vietnam. Symbols are explained in Table 2.

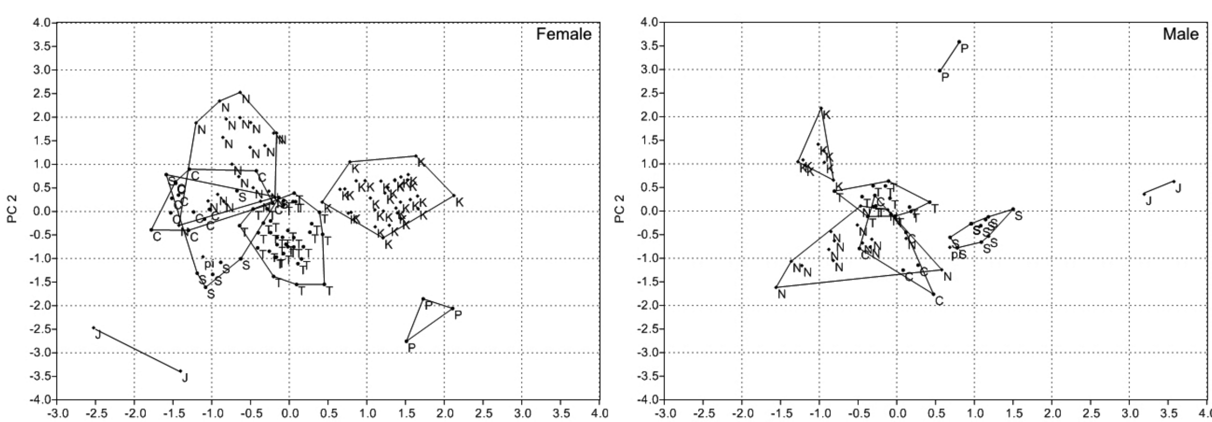


Fig. 6. Scatterplots of scores of the first and second principal component axes based on log-transformed standardized data for females and males of Kerivoulinae populations from Vietnam. Symbols are explained in Table 2.

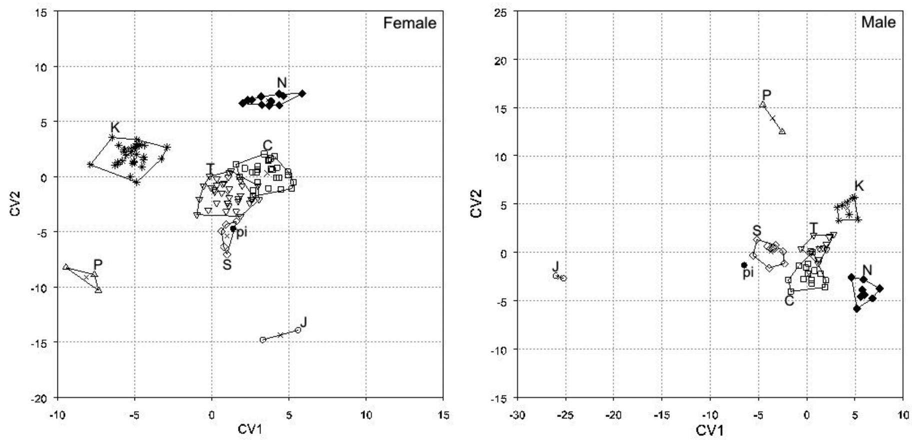


Fig. 7. The visualized results of the canonical variate analysis among Kerivoulinae populations and included three populations of *K. hardwickii*. Scattergrams showing the individual scores on the discriminant axes 1 (horizontal) and 2 (vertical). The locality symbols are explained in Table 2. Female) the first function comprises 38.83% of the variance and the second function 38.07%. Male) the first function comprises 56.07% of the variance and the second function 22.24%.

Table 5. Coefficients of the discriminate function for canonical variate analysis of the log-transformed standardized data (CVs 1, 2) of Kerivoulinae populations from Vietnam

| Measurement | Female | | Male | |
|---|---|---|---|---|
| | CV1 | CV2 | CV1 | CV2 |
| GTL | –28.86 | **31.89** | **–63.97** | –28.74 |
| CCL | –11.13 | **75.16** | **44.39** | **–123.73** |
| UCCW | **–37.66** | 24.71 | **–37.19** | –9.15 |
| UP2P2W | **–43.14** | 15.7 | 6.83 | 36.7 |
| UP3P3W | 25.18 | 4.7 | **81.54** | 23.02 |
| UP4P4W | **37.14** | –4.43 | **72.36** | –27.49 |
| M3M3W | –16.31 | –3.07 | 17.32 | 15.29 |
| CP4L | 6.64 | 1.2 | **–79.95** | **–70.96** |
| CM3L | 4.66 | **–61.35** | **–71.45** | **54.04** |
| P4M3L | –12.48 | 7.08 | 28.07 | –2.9 |
| PALW | 3.98 | 2.56 | 20.7 | –27.23 |
| PBL | –6.86 | 17.15 | –3.28 | 27.22 |
| BasW | –1.02 | 5.27 | 17.9 | –1.65 |
| IOW | **31.15** | –8.32 | **–63.66** | **–54.01** |
| ZYW | **–45.55** | –20.96 | –9.02 | 16.78 |
| BB | 15.46 | –6.28 | –4.56 | –48.76 |
| GBCW | **40.45** | **59.09** | **99.94** | 15.23 |
| MAW | **29.03** | 27.16 | –2.33 | –17.18 |
| BCH | 15.63 | **–82.15** | **–67.17** | 7.76 |
| ML | –14.01 | **–28.12** | 34.27 | 53.76 |
| cm3L | **–37.64** | **–37.51** | **34.91** | 11.6 |
| cp4L | –10.46 | –19.71 | 13.55 | 39.16 |
| CPH | –19.18 | 0.45 | –11.53 | 31.77 |
| Percentage variation | 38.83 | 38.07 | 56.07 | 22.24 |

Boldface numerals: High (positive and negative) coefficients of the discriminate function.

The results from both PCA with higher positive and negative factor loadings and CVA with higher coefficients of the discriminate function of CCL, UCCW, UP2P2W, UP3P3W, CP4L, CM3L, IOW, GBCW, BCH and cm3L (Tables 4 and 5) indicated clear differences between *Phoniscus* and *Kerivoula* and among *Kerivoula* populations (Figs. 6 and 7).

We focused on the high factor loadings and higher coefficients of the discriminate function of UCCW, UP3P3W, IOW, GBCW and BCH used ratio comparisons of BCH and GBCW, IOW and GBCW and UCCW and UP3P3W to assess differences in the shape of neurocranium, interorbital region and rostrum between *Kerivoula* and *Phoniscus* (Fig. 8). The results clearly showed that BCH and IOW are the effective diagnostic characteristics to reveal significant differences between populations. The skull of *Phoniscus* was considerably more dome-shaped and slightly inflated anteriorly with a braincase height over 89.04% of the greatest width of the braincase (BCH/GBCWx100) compared with the genus *Kerivoula* (Fig. 8A) and the interorbital width over 54.90% of the greatest width of the braincase (IOW/GBCWx100) (versus narrower and slender in *Kerivoula*) (Fig. 8B). The ratio of the upper canine distance (UCCW) and second upper premolar distance (UP3P3W) is 98.94%–99.73% in *Phoniscus*; however, it is <98.80% in medium-sized and small-sized *Kerivoula* species and over 100% in large-sized species of *Kerivoula* and *K. picta* (Fig. 8C). This result indicated that the anterior part of the palatal bones is parallel in *Phoniscus*, whereas they are anteriorly narrowed in *K. tinania*, N, C and S populations and anteriorly extended in *K. picta*, *K.papillosa* and *K. kachinensis* (Fig. 8C). The characters for CCL, CM3L, CP4L and cm3L also indicated the significant difference of the teeth, in which the second upper incisors are much reduced (versus developed in *Kerivoula*), and the canines, second upper and lower premolars are narrow in *Phoniscus* (versus broader in *Kerivoula*). The genus *Phoniscus* is clearly separated from *Kerivoula* by significant differences in the dome-shaped skull, the shape of the nasal sinus and second upper and lower premolars.

The high factor loadings of PCA and the coefficients of the discriminate functions of CVA for CM3L and CP4L (Tables 4 and 5) showed significant variation of N, C and S

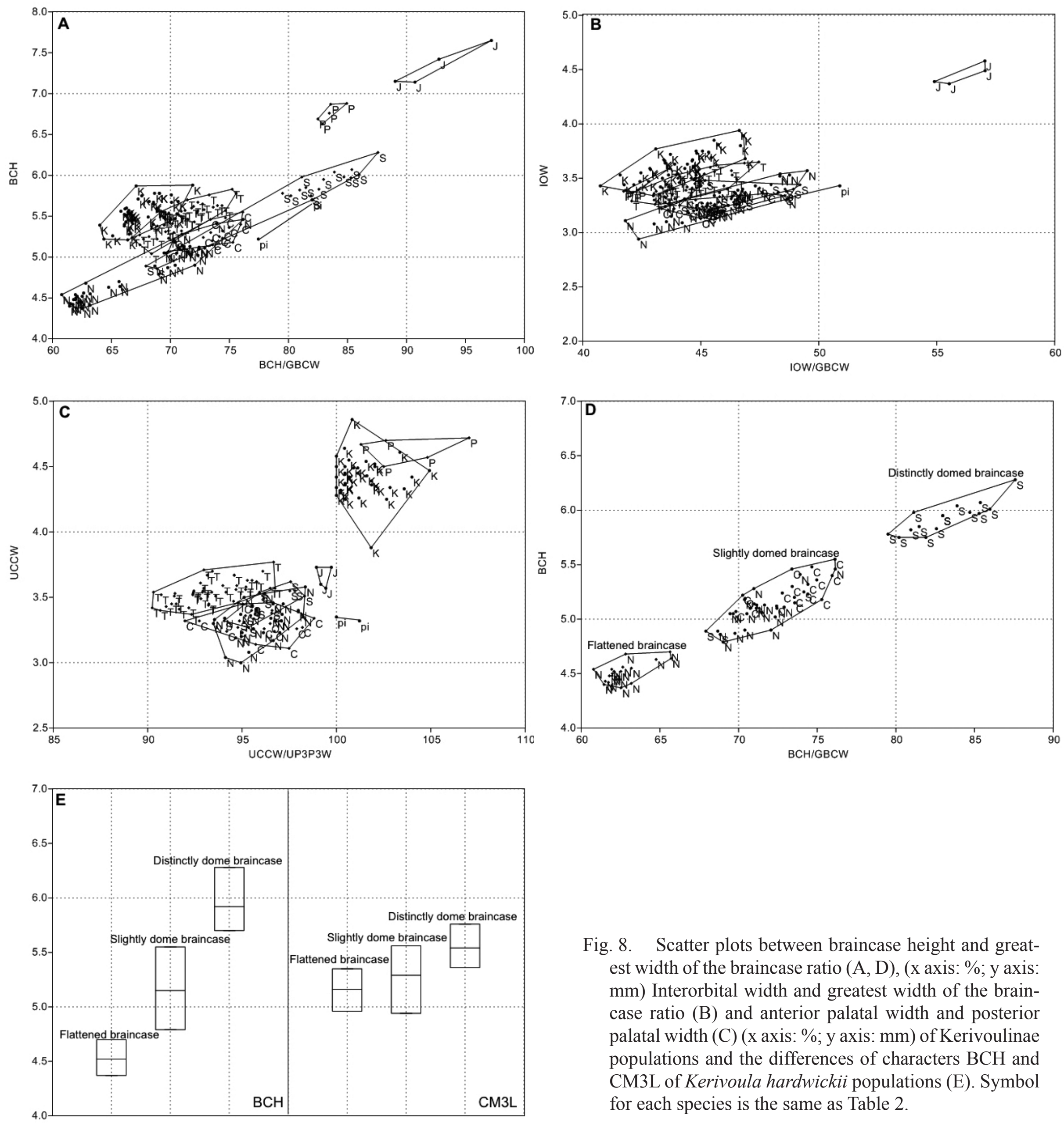


Fig. 8. Scatter plots between braincase height and greatest width of the braincase ratio (A, D), (x axis: %; y axis: mm) Interorbital width and greatest width of the braincase ratio (B) and anterior palatal width and posterior palatal width (C) (x axis: %; y axis: mm) of Kerivoulinae populations and the differences of characters BCH and CM3L of *Kerivoula hardwickii* populations (E). Symbol for each species is the same as Table 2.

populations. The character for BCH showed the variation in size and shape of skull within *K. hardwickii* populations. The ratio of braincase height and greatest width of the braincase of S (67.92% <BCH/GBCWx100 <80.91%) and N (60.78% <BCH/GBCWx100 <77.89%) populations showed a higher variation than C population (69.83% <BCH/GBCWx100 <76.13%) (Fig. 8A). Therefore, based on braincase shape of the *K. hardwickii* populations in Vietnam could be divided into three forms: the flattened braincase form containing the specimens from multiple sites in northern provinces, the slightly domed braincase form comprising the specimens from C and some specimens from multiple sites in northern provinces as well as one site (Dong Nai province) from southern provinces and the distinctly domed braincase form consisting of the specimens from only in southern provinces (Figs. 2 and 8D).

We used two characters BCH and CM3L from the both sexes to compare the differences of *K. hardwickii* populations. The result indicated the significant difference of character BCH ($P<0.05$), which slightly domed braincase comprising of N, C and S populations (4.79 mm <BCH <5.60 mm, 67.92% <BCH/GBCWx100 <76.16%) larger than flattened braincase of N population (4.37 mm <BCH <4.70 mm, 60.78% <BCH/GBCWx100 <65.72%), but smaller than distinctly domed braincase of S population (5.70 mm <BCH, 79.50% <BCH/GBCWx100) (Fig. 8D and 8E). The character CM3L also indicated distinctly domed braincase of S population (5.36 mm <CM3L) significant larger than flattened braincase of N population (CM3L <5.35 mm) ($P$<0.05) (Fig. 8E). The result also pointed out the significant differences in the size related to the difference in the shape of second upper and lower premolars of *K. hardwickii* populations (Table 6).

## DISCUSSION

Multivariate analysis of skull size and shape is one of the most important methods to establish taxonomy of bats, particularly for species complexes, subspecies and cryptic species, or to assess the geographical variations in the Southeast Asian region, where few taxonomical investigations have been carried out [10–13, 21, 48]. In Vietnam, five *Kerivoula* species and *P. jagorii* were recorded recently [6, 8, 22, 34, 51]. In this study, we used *P. jagorii* as an active representative of the genus *Phoniscus* for comparison with the genus *Kerivoula*. Our analysis first time indicated that *P. jagorii* is a medium-sized species of Kerivoulinae, but larger than the medium-sized species (*K. tinania* and *K. picta*) by measurement CCL is announced in the first time ($P$<0.05); however, *P. jagorii* overlapped with large-sized species, *K. kachinensis*. PC1 of log-transformed data showed high factor loadings as CCL, UCCW, UP1P1W, UP2P2W, UP4P4W, M3M3W, CP4L, CM3L, P4M3L, PBL, BasW, cm3L and cp4L indicated the significant differences between *Phoniscus* and *Kerivoula*, which are mainly related to the rostrum, palatal bones, size of second upper incisors, first and second upper and lower premolars. The factor loading of PCA for PBL also showed significant differences in anterior palatal emargination that has been indicated by some previous studies [23, 37]. Our results pointed out that the anterior palatal emargination in *Kerivoula* is distinctively deeper than in *Phoniscus.* Although DNA analysis did not support the phylogenetic separation between *Kerivoula* and *Phoniscus* [18], the present morphological data, demonstrated that the *Kerivoula* and *Phoniscus* are clearly distinguished from each other and represent two separated genera.

PCs 1 and 2 from log-transformed standardized data and the CVA result showed high factor loadings and larger (positive and negative) coefficients of the discriminate function from both analyses to be CCL, UCCW, UP2P2W, CP4L, CM3L, IOW, GBCW, BCH, cm3L, cp4L and CPH (Tables 4 and 5). We confirmed the high factor loadings of CP4L and cp4L, and larger and smaller coefficients of the discriminate function of CM3L, CP4L and cm3L demonstrated that the length of the first and second upper premolars was pointed, trenchant and the shape is elongated in *Phoniscus*, whereas ovate and circular in the *Kerivoula* species. CVA results showed larger (positive in female and negative in male) coefficients of the second discriminate function for GTL and CCL, can be related with significant difference of the shape of second upper incisor, which Hill (1965) has shown that the second upper incisor is much more reduced in *Phoniscus*, whereas more massive in *Kerivoula* [23]. The larger coefficients of the discriminate functions for GBCW also indicated the braincase width is domed in *Kerivoula* (versus flattened in *Phoniscus*). We suggest that the development of the second upper incisors, shape of canines, second upper and lower premolars, interobital region and shape of skull are considered to be the generic characteristics between *Phoniscus* and *Kerivoula*.

The *K. hardwickii* (Horsfield, 1824) was originally described from Java [27]. Recent studies suggested that *K. hardwickii* is a complex of cryptic species [6, 17, 18] and is widely distributed from Southern India to Nepal and from Southern China to Southeast Asia [4, 9, 16–18, 23, 25–27, 31–34, 38, 40, 44, 55–57]. Members of this complex are common and widely distributed species throughout Vietnam [9, 34].

PCA results showed the *K. hardwickii* N, C and S populations overlapped in the size measurements and had large variation in the skull shape. However, the CVA result indicated the clear separation among the N, C and S (Fig. 7). Our results first indicated important measurements, such as CP4L, CM3L and BCH (Tables 4 and 5), showed a statistically significant variation in teeth, skull size and shape among the three populations of *K. hardwickii* (Figs. 5 and 6), and the variation in the species composition is broadly correlated with the topography, habitat complexity and climate condition in Vietnam [2, 49]. Averyanov *et al*. (2003) have provided a phylogeographic review of eastern Indochina [1], and Fooden (1996) suggested that a zoogeographic barrier formerly extended from east to west across Vietnam at ca. 14–17° N [15]. Our results support the hypothesis that the Annamite mountain chains act as a geographical barrier at ca. 14–17° N and the difference of the habitat and climate influence the morphological characteristics separating *K. hardwickii* populations.

The N and S populations may represent two distinct taxa. The C population shows variation in skull shape and is widely distributed from northern to southern of Vietnam, because this is an area with much faunal overlap of the Lower Mekong Watershed area and the Central Highlands area [2, 49, 53]. Furthermore, we suggest that the Thanh Hoa and Dong Nai provinces (Fig. 2) are the transition zones for the N population, with the Annamite mountains and S population, with the Central Highlands to the Mekong Delta [2, 15, 49, 53] comprising an area of morphological differentiation, observed on the basis of the differences in skull shape among the N, C and S populations. In conclusion, both areas contain specimens with a wide variation in skull shape.

Furthermore, we also suggest that the measurements, such as CM3L and CP4L, may be related to the difference in the shape of the first and second upper premolars and BCH related to the significant difference in the size and shape of skull among the *K. hardwickii* populations, and these differences may be due to the variation of habitats. Finally, our results, based on mutivariate analysis, demonstrate for the first time that significant differences in morphological characteristics indicate the presence of cryptic taxa of *Kerivoula* in Vietnam, which the results clearly showed the separation of three forms. This result will be the basis for a reassessment and reclassification of this group in Vietnam and Asia in the near future.

Table 6. Differences in size of braincase high and maxillary toothrow length and shape of first (P2) and second upper premolars (P3) of *K. hardwickii* populations

| Character | N flattened braincase | N, C and S slightly domed braincase | S distincly domed braincase |
|---|---|---|---|
| Size of P2, P3 | Small, P2>P3 | Small, P2>P3 | Large, P2=P3 |
| Shape of P2, P3 | Circular | Circular or ovate | Ovate |
| P2 | Inner circular | Inner circular or oval | Inner oval |
| | Outnet circular | Outer slightly traight | Outer oval |
| P3 | Inner circular | Inner circular | Inner oval |
| | Outer circular | Outer slightly circular | Outer circular |
| Transverse diameters P2, P3 | Equal their longitudinal diameters | Equal, exceeding their longitudinal diameters | Exceeding their longitudinal diameters |
| BCH (mm) | Less 4.7 | 4.89–5.60 | Over 5.7 |
| CM3L (mm) | Less 5.36 | 4.90–5.60 | Over 5.36 |

ACKNOWLEDGMENTS. We are grateful to the director, Department of Vertebrate Zoology and Nguyen Quang Truong, Vu Dinh Thong and Vuong Tan Tu from IEBR, Bui Tuan Hai from Vietnam National Museum of Nature, Hoang Trung Thanh from Hanoi University of Science, Nguyen Vu Khoi and Thomas O'Shea from Wildlife-at-Risk, Ministry of Agriculture and all the staff of nature reserve and national park from Vietnam for their support for our field survey and specimens. Thanks to Gabor Csorba from the Hungarian Natural History Museum for providing access to the specimens and for accommodating our bats specimens in the collection of his museum; Eleanor Jane Sterling (New York) and Kevin Koy (Berkeley) for providing the map. This study was partially supported by JSPS RONPAKU Program ID No. VAST-11125 and JSPS AA Science Platform Program (2012–2014, 2014–2016). We also would like to thank two reviewers and editor for useful comments on the earlier version of the manuscript.

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