

Hypothetical Speciation Scenario of Subgenus *Psalidoremus* (Coleoptera: Lucanidae) by Morphological Traits and Geographical Patterns

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ABSTRACT

Psalidoremus is one of the subgenus which consists of five species and eleven subspecies through Taiwan, Japan, Korea and north eastern part of China which present strong endemism to their distribution. While most of advance studies focus on the new species or subspecies from this taxon, this paper suggests paleogeographical assumption and hypothesis of how they diverged from common ancestors. Phylogeographical patterns illustrated by the distribution of five species, which including *Prosopocoilus inclinatus*, *Prosopocoilus hachijoensis*, *Prosopocoilus dissimilis*, *Prosopocoilus pseudodissimilis*, *Prosopocoilus motschulskii* respectively, has been assessed in this research. Speciation history is suggested by morphological tendencies especially in male mandibles with assumption from geographical patterns of under sea level.

Keywords: Lucanidae, *Prosopocoilus*, *Psalidoremus*, Speciation history, Stag beetles

Introduction

Lucanidae is one of the basal clade of Scarabaeoidea (Smith *et al.*, 2006), which consist of about 1,400 species from all around world (Fujita, 2010). Among them, *Prosopocoilus* is one of the biggest genera within Lucanidae. *Psalidoremus* is one of the subgenus which consists of five species and eleven subspecies through East Asia. *Psalidoremus* distributes from Taiwan, Japan, Korea and north eastern part of China confirmed by Japanese and

Chinese entomologists (Fujita, 2010; Huang & Chen, 2013; Mizunuma & Nagai, 1994). Each species does not cover distribution range of other species, which present strong endemism to their distribution. Most of advance studies focus on the new species or subspecies from this taxon (Adachi, 2009; 2014; Fujita, 2009; Matsuoka & Takatoji, 2010; Shimizu & Murayama, 1998; 2004), therefore, this paper suggests paleogeographical assumption and hypothesis of how they diverged from common ancestors. So far, phylogeographical patterns illustrated by the distribution of each species and divergence were assumed by morphological tendencies especially in male mandibles with assumption from geographical patterns of under sea level.

In these processes, three priori assumptions are critical: 1) Currently recognized taxa are monophyletic; 2) diversi-

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fication of each subspecies negligibly small compared to its between-island diversification; 3) recognizable speciation occurred by allopatric speciation. These assumptions are adapted and modified from assumptions of Ota which study on the speciation of Amphibians and Reptiles from Ryukyu Archipelago (Ota, 1998).

Materials and Methods

Study design

This study designed by following process. First of all, distributional data of subgenus *Psalidormus* species has been organized in Table 1.

Data in Table 1 were used in this research with referring global Biodiversity Information Facility (GBIF) and each specimen holding institutions. The distributional data has been referred to occurrence data of the information uploaded to GBIF, and distributional data of key references stag beetle researchers such as Mizunuma, Nagai, Fujita, Huang, and Chen.

After distribution check, morphological data were analyzed by considering male morphology of each species. Especially head structures of male are distinctly differ in each species. Mandibular structure and shape of clypeus is the key morphology to its taxonomy. In mandibular structures, composition of large inner tooth and apical tooth group are considerable. Clypeus shape is organized in three types which considered as gradual changes in speciation process. Female morphology was not analyzed in here because of morphological difference between each species not remarkable as males.

Also, Bathymetric map under sea surface were drawn by author based on open street map to avoid copyright issues. Three bathymetric elevations which respectively 0 m, -750 m, -1,200 m, were used regard species boundary of

distribution.

After all, hypothetical speciation history established based on information as mentioned above.

Materials

Materials used in this research mostly stored in the storage of National Science Museum Korea, National Taiwan Museum, and GBIF occurrence data set (<https://doi.org/10.15468/39omei>).

Methods

Habitus photograph were taken by Nikon D7100 Digital Single Lens Reflex Camera (Nikon, Tokyo, Japan) with Tamron 60 mm Macro lens which mounted on Wemacro macro rail set with lighting stands. Photo of each specimen were taken 30 to 40 by each stop and merged together in Zerene Stacker program (Zerene Stacker, Richland, WA, USA) to maximize resolution. Maps of each figure were drawn by author by using PaintTool SAI (Systemax, Port Washington, NY, USA). Male morphological structures labeled as Table 2 for the comparison of each trait. Seven morphological traits have been assessed in the

Table 2. Morphological traits coded in binary notation

Morphological trait	True	False
Basal inner tooth is major inner tooth	1	0
Inner teeth group separated	1	0
Clypeus elongated	1	0
Apice of clypeus separated	1	0
Head procedure flat	1	0
Body surface with matte texture	1	0
Long tarsus	1	0

Table 1. *Psalidoremus* species analyzed in this research

Species	Range	Possible closest relatives
<i>Prosopocoilus inclinatus</i> Motschusky, 1857	Korea (Korean Peninsula, Uleung Is.), Japan (Honshu, Kyushu, Shikoku, Hokkaido, Izu Iss., Yakushima Is., Tanegashima Is., Mishima Is., Ito Is., Kuroshima Is., Kuchinoerabu Is.), Russia (Kunashir Is.), China (Liaoning Province)	<i>P. hachijoensis</i>
<i>Prosopocoilus hachijoensis</i> Nomura, 1960	Japan (Hachijo Is.)	<i>P. inclinatus</i>
<i>Prosopocoilus dissimilis</i> Boileau, 1898	Japan (Tokara Iss., Amami Iss., Okinawa Is.)	<i>P. inclinatus</i>
<i>Prosopocoilus pseudodissimilis</i> Kurosawa, 1976	Japan (Iriomote Is., Ishigaki Is.)	<i>P. motschulskii</i>
<i>Prosopocoilus motschulskii</i> Waterhouse, 1869	Taiwan	<i>P. pseudodissimilis</i>

Distributional data were taken from GBIF (global Biodiversity Information Facility) occurrence data and key references. Is., Island.

IBM SPSS statistics program (ver. 28.0; IBM Co., Armonk, NY, USA) by hierarchical cluster analysis method.

Results

By referring occurrence data of each specimen and dataset, all species of subgenus *Psalidoremus* could be confirmed as endemic to each distribution. The geographical patterns of the *Psalidoremus* species has been displayed on Fig. 1. And brief taxonomic account follows.

Taxonomic accounts

Insecta

Scarabaeoidea

Lucanidae Latreille, 1804

Genus *Prosopocoilus* Westwood, 1845

Subgenus *Psalidoremus* Motschusky, 1862

Species *Prosopocoilus* (*Psalidoremus*) *inclinatus* (Motschusky, 1857)

Species *Prosopocoilus* (*Psalidoremus*) *motschulskii* (Waterhouse, 1869)

Species *Prosopocoilus* (*Psalidoremus*) *dissimilis* (Boileau, 1898)

Species *Prosopocoilus* (*Psalidoremus*) *hachijoensis* Nomura, 1960

Species *Prosopocoilus* (*Psalidoremus*) *pseudodissimilis* Kurosawa, 1976

Prosopocoilus (*Psalidoremus*) *inclinatus* (Motschusky, 1857) (Fig. 1A)

Body length: male 21–72 mm, female 25–42 mm

Distribution: Korea, Japan, China, Russia

Subspecies: This species consist of seven subspecies.



Fig. 1. Geographical patterns of the subgenus *Psalidoremus*. (A) *Prosopocoilus inclinatus*; (B) *Prosopocoilus hachijoensis*; (C) *Prosopocoilus dissimilis*; (D) *Prosopocoilus pseudodissimilis*; (E) *Prosopocoilus motschulskii*.

P. inclinatus inclinatus (Motschusky, 1857) *P. inclinatus mishimauiensis* Shimizu et Murayama, 1998, *P. inclinatus kuchinoerabuensis* Shimizu et Murayama, 1998, *P. inclinatus kuroshimaensis* Shimizu et Murayama, 2004, *P. inclinatus miyakejimaensis* Adachi, 2009, *P. inclinatus mikuraensis* Matsuoka et Takatoji, 2010, *P. inclinatus yakushimaensis* Adachi, 2014.

Prosopocoilus (*Psalidoremus*) *hachijoensis* Nomura, 1960 (Fig. 1B)

Body length: male 24–59 mm, female 26–38 mm

Distribution: Japan (Hachijo Island [Is.])

Subspecies: This species does not have subspecies.

Prosopocoilus (*Psalidoremus*) *dissimilis* (Boileau, 1898) (Fig. 1C)

Body length: male 26–79 mm, female 25–40 mm

Distribution: Japan (Okinawa Iss., Amami Iss., Tokara Iss.)

Subspecies: This species consist of seven subspecies. *P. dissimilis* (Boileau, 1898), *P. dissimilis elegans* (Inahara, 1958), *P. dissimilis okinawanus* Nomura, 1962, *P. dissimilis makinoi* Ichikawa et Fujita, 1985, *P. dissimilis okinoerabuensis* Ichikawa et Fujita, 1985, *P. dissimilis kumejimaensis* Ichikawa et Fujita, 1985, *P. dissimilis hayashii* Fujita, 2009.

Prosopocoilus (*Psalidoremus*) *pseudodissimilis* Kurosawa, 1976 (Fig. 1D)

Body length: male 28–63 mm, female 25–36 mm

Distribution: Japan (Yaeyama Iss.)

Subspecies: This species does not have subspecies.

Prosopocoilus (*Psalidoremus*) *motschulskii* (Waterhouse, 1869) (Fig. 1E)

Body length: male 24–60 mm, female 25–36 mm

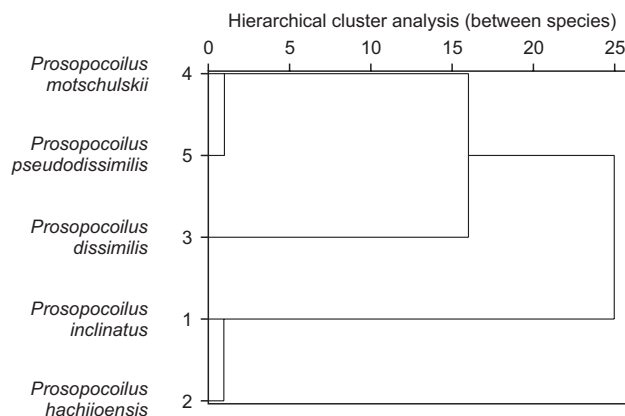


Fig. 2. Dendrogram of hierarchical cluster analysis in SPSS (ver. 28.0; IBM Co., Armonk, NY, USA) between species based on seven morphological traits. x-axis value means rescaled distance cluster combine.

Distribution: Taiwan Is.

Subspecies: This species does not have subspecies.

And seven morphological traits in Table 2 coded by binary notation and run through the SPSS hierarchical cluster analysis method and results are displayed in dendrogram in Fig. 2. In this analysis, common ancestor divided into two clades from *inclinatus-hachijoensis* cluster and others divided for later also divided into *dissimilis* and *motschulskii* - *pseudodissimilis* cluster and for the last *motschulskii* and *pseudodissimilis* divided in each area. But morphological characters not strong enough to assume speciation history of this subgenus, so geographical assessment also performed to provide strong hypothesis.



Fig. 3. Sea elevation map of present sea level. A-D indicates border of each species (Scale bar: 200 km).



Fig. 4. Sea elevation map of sea level -750 m below surface. A-D indicates border of each species (Scale bar: 200 km).

By considering ecological niche of the family Lucanidae, stag beetles not able to move across the sea surface. This provide strong barrier to the gene flow, which enables to proceed to speciation process by allopatric speciation. Also bathymetric elevation maps of distribution range at present sea level in Fig. 3, -750 m under sea surface in Fig. 4, -1,200 m under sea surface were displayed in Fig. 5. This provides strong evidence of the allopatric speciation of the subgenus *Psalidoremus*. Because of border of species almost identical to the land isolation gap appear on the bathymetric elevation maps in Figs. 3-5.

After all, subgenus *Psalidoremus* is allopatric group



Fig. 5. Sea elevation map of sea level -1,200 m below surface. A-D indicates border of each species (Scale bar: 200 km).

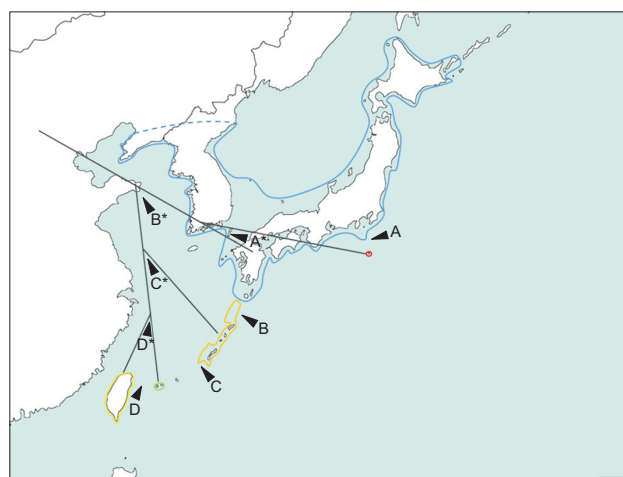


Fig. 6. Pictorial speciation scenario of the subgenus *Psalidoremus* by each geographical gap A-D and speciation point provided in each gap marked with asterisk * (Scale bar: 200 km).

which sharing common ancestor in monophyletic clade. And their speciation scenario could be assumed by referring those morphological characters and bathymetric elevation and result as follows.

Hypothetical speciation scenario

First, common ancestor divided into *inclinatus* group and *dissimilis* group by Tokara Gap (marked as B in Fig. 6). Second, *dissimilis* group divided into two groups by *dissimilis* and *motschulskii* - *pseudodissimilis* cluster by Kerama Gap (marked as C in Fig. 6). Third, *inclinatus* - *hachijo* cluster and *motschulskii* - *pseudodissimilis* divided into each species level respectively by Hachijo Gap (marked as A in Fig. 6), and Taiwan Gap (marked as D in Fig. 6). This scenario has been pictorialized in Fig. 6 to enhance visibility of concept.

Discussion

This research has been performed to establish hypothesis of how *Psalidoremus* species gone through the speciation from their common ancestors. And this is first attempt to provide visible clearance between *Psalidoremus* species and geographical data. Also Pictorial speciation scenario provides good visual agenda for other researchers.

The hypothesis in this here are supported by following references especially Ota (1998) which studied geographic pattern of amphibian and reptiles of Ryukyu archipelago has become good foundation of this article, and other taxonomic articles such as Fujita (2010) and Tsuchiya (2010), Tsuchiya (2017) provided numerous figures which in real sized magnification. Also, Tojo *et al.* (2017) provides strong evidence of deep straits provides similar difference in damselfly group, *Repidolestis* spp. Near Okinawa and Taiwan region.

Also this hypothesis could be disturbed by dispersal by typhoon as described in Osozawa *et al.* (2021) in case of Cicada species which distributes in Japan. Transportation by typhoon model was not considered in this article. Because of Lucanidae in general is not attempt to fly in raining day and also not good fliers as well.

In the result, most significant part is that the Hachijo gap is deep in substance, but the difference between *P. inclinatus* and *P. hachijoensis* not significant, also exposed in dendrogram. However, by consider in subspecies level, most closest relative is *P. inclinatus miyakejimaensis* which provides tendencies of intermediate tendencies in gradually from main island of Japan to Hachijo island. These tendencies should be study in advance in further researches. Also in subspecies level study must be performed to provide tendencies infraspecific level. Especially author noticed strong tendencies infraspecific difference in *P. dissimilis*, This tendencies would be the next research

subject.

The scenario has been established in this research limited by the restriction of the morphological traits that useful in morphological identification and geographical patterns of each species. Therefore, research including DNA of each species and subspecies is demanded for more robust foundation of evidence.

Conflict of Interest

The authors declare that they have no competing interests.

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