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First Report of Two Phylogenetically Distant Lucanid Taxa, *Platycerus hongwonpyoi* Imura et Choe and *Prismognathus dauricus* (Motschulsky) (Coleoptera, Lucanidae) in South Korea, Sharing the Same Lineage of Yeast Symbionts

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Abstract It is known that the closely related symbiotic yeasts inhabit beetles of the genus *Platycerus* Geoffroy in Korea and Japan, and they are distant from those of *Prismognathus angularis angularis* Waterhouse in Japan. In this study, we found that *Prismognathus dauricus* (Motschulsky) and *Platycerus hongwonpyoi hongwonpyoi* Imura et Choe in South Korea share the same lineage of yeast symbionts. This is the first study to report that phylogenetically distant lucanid taxa share the same lineage of yeasts.

Key words: COI gene, IGS region, ITS region, phylogenetic analysis

Introduction

Yeast symbionts are often associated with xylophagous insects and are believed to assist them in degrading wood components like hemicellulose (Suh *et al*., 2003, 2006; Jeffries *et al*., 2007; Urbina & Blackwell, 2012; Tanahashi & Fremlin, 2013; Urbina *et al*., 2013). Stag beetles (Coleoptera, Lucanidae) normally feed on decayed wood at the larval stage and adult females retain yeast symbionts in the mycangia inside the tip of their abdomen (Tanahashi *et al*., 2010; Hawes, 2013). Those feeding on white rot wood possess *Scheffersomyces* yeast, a group of xylose-fermenting yeasts (Tanahashi *et al*., 2010, 2017; Hawes, 2013; Tanahashi & Fremlin, 2013). The genetic lineages of the yeast symbionts correspond to their host taxa (i.e., species or genus). For example, the two species of the same genus share closely related yeast symbionts between Europe and Japan [*Lucanus cervus* (Linnaeus, 1758) and *L. maculifemoratus* Motschulsky, 1861: Tanahashi *et al*., 2017; *Dorcus parallelipipedus* (Linnaeus, 1758) and *D. hopei binodulosus* Waterhouse, 1874: Tanahashi *et al*., 2017, Kubota *et al*. unpublished data].

The same phenomenon was also recognized among the populations within each of species in Japan, e.g., *D. rectus rectus* (Motschulsky, 1857), *D. striatipennis striatipennis* (Motschulsky, 1861), and *D. rubrofemoratus rubrofemoratus* (Vollenhoven, 1865) (Tanahashi *et al*., 2010; Kubota unpublished data). Tanahashi and Hawes (2016) believe that adult females are more likely to transmit the *Scheffersomyces* yeast symbionts to their larvae through the oviposition process.

The genus *Platycerus* Geoffroy, 1762 is a group of small stag beetles comprising more than 30 species in East Asia (Imura, 2010; Kubota *et al*., 2011). Ten and one *Platycerus* species are known in Japan and Korea, respectively. The formers are all endemic to Japan, but the latter, *Platycerus hongwonpyoi* Imura et Choe, 1989 is not only distributed in Korea but also in eastern to central China (Imura, 2010; Kubota *et al*., 2011).

To detect the phylogenetic divergence of the *Platycerus* yeast symbionts, Tanahashi *et al*.

(2017) analyzed two regions of nuclear DNA of *Pl. delicatulus delicatulus* Lewis, 1883 and *Pl. acuticollis* Y. Kurosawa, 1969 from Japan and seven females of *Pl. hongwonpyoi hongwonpyoi* Imura et Choe, 1989 from South Korea. One genetic region they analyzed was the internal transcribed spacer (ITS) region (ITS1 and ITS2), consisting of the continuous sequence of the 18S ribosomal RNA (rRNA) gene (18S rRNA), the 5.8S rRNA gene (5.8S rRNA), and the 26S rRNA gene (26S rRNA) (2931 bp). The other was the intergenic spacer (IGS) region, including 26S rRNA, IGS1, the 5S rRNA gene (5S rRNA), IGS2, and 18S rRNA (> 2000 bp).

There was no variation in the ITS region among yeast symbionts of *Platycerus*. The yeasts of *Prismognathus angularis angularis* Waterhouse, 1874 in Japan were phylogenetically related to those of *Platycerus* (Tanahashi *et al*., 2017). In the IGS region, where the sequence is more variable, the yeasts from Japanese *Platycerus* species were monophyletic and the sister group to those from Korean *Pl. h. hongwonpyoi*. Both were distant to the yeasts of *Pr. a. angularis*, although they are all phylogenetically related to *Scheffersomyces segobiensis* (Tanahashi *et al*., 2017). For the host beetle phylogeny, Japanese and Korean *Platycerus* are sister to each other, and they were distant to *Pr. a. angularis* (Kubota *et al*., 2011).

On the other hand, for the genus *Prismognathus* Motschulsky, 1860, no yeast symbiont sequence has been known except for those from one *Pr. a. angularis*, which were treated as the outgroup of the yeast symbionts of *Platycerus* (Tanahashi *et al*., 2017). Since *Prismognathus* species are sometimes collected with *Platycerus* species from the host wood both in Korea and Japan (Kubota & Zhu, private observation), they seem to be adapted to almost the same climate and similar host wood decay type. The species belonging to *Prismognathus* are distributed widely in East Asia (Huang & Chen, 2017). Is the phylogenetic relationship between yeast symbionts of *Platycerus* and *Prismognathus* in Japan observed also in the Korean Peninsula or China? For understanding the evolutionary relationship between stag beetles and their yeast symbionts in East Asia, it is useful to detect and compare the DNA sequences of yeast symbionts of the Asian continental *Prismognathus* species with those of Japanese *Prismognathus* and East Asian *Platycerus*.

Between 2017 and 2018, we examined a female *Pr. dauricus* (Motschulsky, 1860) from South Korea and a female *Pr. a. angularis* from Japan to classify their yeast symbionts and obtained results that differed from those of Tanahashi *et al*. (2017). *Prismognathus angularis* is distributed in most areas of Japan (Hokkaido, Honshu, Shikoku, Kyushu, and their surrounding islands), and *Pr. dauricus* is distributed in most area of Korea, Tsushima Island (Japan), north-eastern China, and eastern Siberia (Russia). No other *Prismognathus* species is known in Japan and Korea (Huang & Chen, 2017). Here we report our findings and discuss the importance of understanding the evolutionary relationships between beetles in these taxa and their yeast symbionts.

Materials and Methods

Insect samples and isolated yeast strains in this study are shown in Table 1. These samples were collected at sites 3 and 9 (Fig. 1). *Prismognathus dauricus* is sympatric with *Platycerus hongwonpyoi hongwonpyoi* at Site 3 (Birosa). An adult female *Pr. dauricus* (22 mm in body length) was collected on the forest floor on 27 July, 2017 and was brought to the laboratory of Kangwon National University in a plastic container. A female *Pr. angularis angularis* was collected from the wood as the third instar larva on 21 April, 2018 and was brought to the laboratory of the University of Tokyo and reared in the wood from which it was collected until dissection after the emergence. Other collection site profiles are shown in Table 2.

Adult females were dissected and the yeast symbionts were extracted from their mycangia fol-

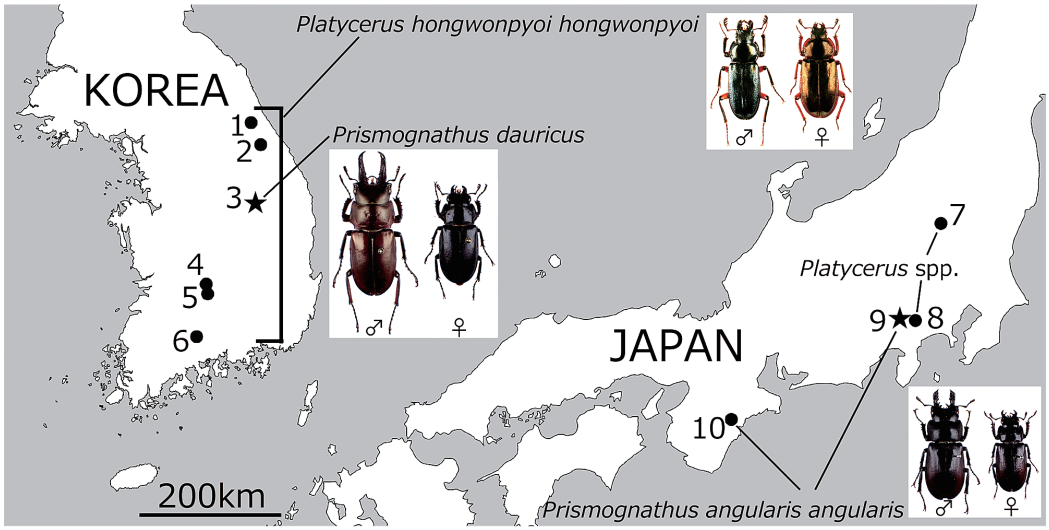

Fig. 1. Sampling sites. Black stars and circles indicate the sampling sites in this study (Sites 7–10) and in Tanahashi *et al*. (2017) (Sites 1–6), respectively. Habitus of *Platycerus hongwonpyoi hongwonpyoi*, *Prismognathus dauricus*, and *Prismognathus angularis angularis* are also shown.

lowing the methods described by Tanahashi *et al*. (2017). Four colonies per female were selected, and nucleic acid solutions were prepared following the methods of Tanahashi *et al*. (2017). Genomic DNA was also extracted from the muscle tissues of adult females using the Wizard Genomic DNA Purification Kit (Promega, Madison, WI, USA).

The yeast ITS region (including 18S rRNA, ITS1, 5.8S rRNA, ITS2, and 26S rRNA) (primers NS1 and NL4; White *et al*., 1990) and IGS region (including 26S rRNA, IGS1, 5S rRNA, IGS2, and 18S rRNA) (primers IGS1 and IGS4; Tanahashi *et al*., 2017) were amplified by polymerase chain reaction (PCR) at 95℃ for 3 min followed by 35 cycles of 95℃ for 45 s and 52℃ for 45 s, and 72℃ for 1.5 min for ITS or 2 min 15 s for IGS, with a final extension at 72℃ for 5 min. Mitochondrial cytochrome oxidase subunit I (COI) (primers C1-J-2183 and L2-N-3014; Simon *et al*., 1994) of the host beetles was amplified by PCR at 94℃ for 3 min followed by 30 cycles of 94℃ for 1 min, 48℃ for 1 min, and 72℃ for 1 min, with a final extension at 72℃ for 7 min.

The PCR products were purified using the Illustra ExoStar clean-up kit (GE Healthcare, Buckinghamshire, UK). The Dye terminator cycle sequencing reactions were performed using the ABI Big Dye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, Foster City, CA, USA) and electrophoresed using an ABI 3130xl Genetic Analyzer (Applied Biosystems). For the cycle sequencing reactions, the following primers were used: NS7 and ITS5 for ITS (White *et al*., 1990); IGS1, IGS2, IGS3, IGS4, IGS7i, and IGS8i for IGS (Tanahashi *et al*., 2017); and C1-J-2183 and L2-N-3014 for COI.

The sequence data were deposited in the DNA Data Bank of Japan (DDBJ) under accession numbers LC492883–LC492884 for the ITS region (651–652bp), LC492885– LC492886 for the IGS region (2193–2194bp), and LC492881–LC492882 for the COI gene (784bp). The voucher specimens of *Pr. dauricus* and *Pr. a. angularis* were deposited at Kangwon National University and Laboratory of Forest Zoology, the University of Tokyo, respectively.

We used most sequence data for ITS, IGS, and COI from Tanahashi *et al*. (2017) (see accession no. of GenBank in Figs. 2–4). For ITS, IGS, and COI, a haplotype matrix was constructed using the

Table 1. Insect samples and isolated yeast strains in this study.

Country	Site number	Collection site	Insect		Yeast		
			Species	DDBJ accession number	Strain	DDBJ accession number	
				COI		ITS	IGS
South Korea	3	Gyeonsangbuk-do (Birosa)	*Prismognathus dauricus*	LC492881	YC019.4	LC492883	LC492885
Japan	9	Kanagawa (Mt. Mikuniyama)	*Prismognathus angularis angularis*	LC492882	YC021.5	LC492884	LC492886

Table 2. Collection site profiles.

Site number	Country	Locality	Altitude (m)
1	South Korea	Gangwon Province I (Mt. Hangeryeoung)	950
2		Gangwon Prov. II (Mt. Jengoge Pass)	650
3		Gyeonsangbuk Prov. (Birosa)	600
4		Jeollabuk Prov. I (Mt. Deogyusan)	1,600
5		Jeollabuk Prov. II (Mt. Jeoksangsan)	500
6		Jeollanam Prov. (Mt. Nogodan)	1,430
7	Japan	Tochigi Prefecture (Nikko)	1,280
8		Kanagawa Pref. (Mt. Kanyudoyama)	1,400
9		Kanagawa Pref. (Mt. Mikuniyama)	1,280
10		Mie Pref. (Mt. Odaigaharayama)	1,520

Data from Tanahashi *et al*. (2017) except for Sites 3, 9.

DnaSP ver. 5.10.01 software package (Librado & Rozas, 2009). Aligned haplotype sequences were used to construct phylogenetic trees based on maximum likelihood (ML) and Bayesian inference (BI) methods. An ML tree was constructed using PhyML ver. 3.0 (Guindon & Gascuel, 2003), under the best-fit substitution model selected using jModelTest ver. 2.1.7 (Darriba *et al*., 2012) based on the Bayesian information criterion (BIC). Confidence at each node was assessed by 100 bootstrap replications.

BI trees were constructed using three runs in MrBayes ver. 3.2.6 (Ronquist & Huelsenbeck, 2003) under the best-fit substitution model selected by jModelTest ver. 2.1.7 for 200 million generations (sample freq = 20,000) and 2,500 samples burn-in, using Tracer ver. 1.5.0 (Rambaut & Drummond, 2009) to examine convergence towards highly effective sample sizes.

Results

Yeast colony formation units (CFU: inferred cell number of yeasts in a mycangium, see Tana-

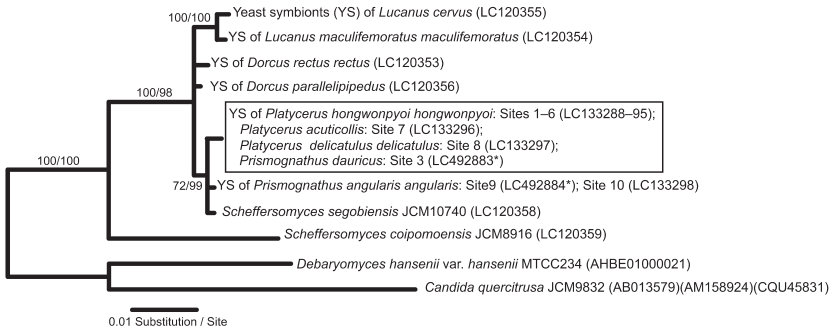

Fig. 2. Bayesian inference (BI) tree of yeasts based on the internal transcribed spacer (ITS) region. Numbers near the branches indicate posterior probabilities in the BI tree (>50%)/bootstrap probabilities in the maximum likelihood tree (>50%). Asterisks after the accession numbers in parentheses indicate the sequences determined in this study. A dashed box indicates a haplotype shared by more than one species of host stag beetles.

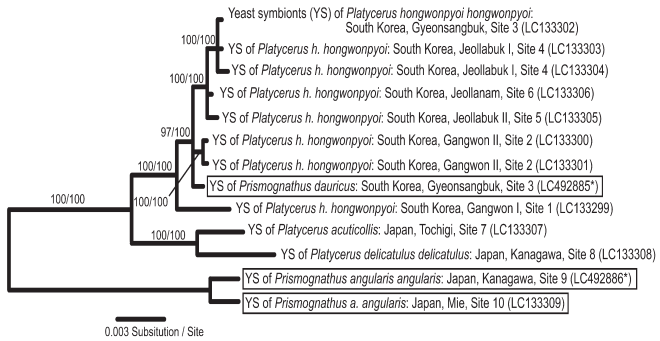

Fig. 3. Bayesian inference (BI) tree of yeasts based on the intergenic spacer (IGS) region. Numbers near the branches indicate posterior probabilities in the BI tree (>50%)/bootstrap probabilities in the maximum likelihood tree (>50%). Asterisks after the accession numbers in parentheses indicate the sequences determined in this study. Boxes indicate the yeast symbionts of *Prismognathus* species.

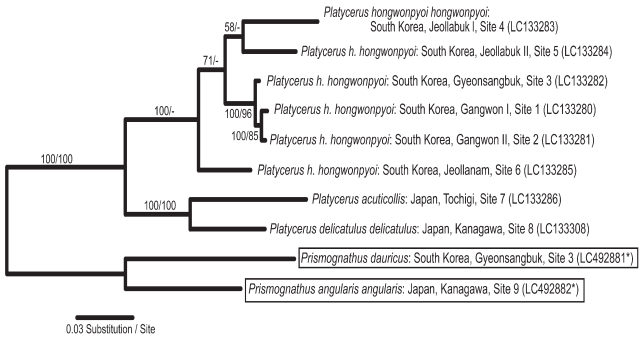

Fig. 4. Bayesian inference (BI) tree of host stag beetles based on the cytochrome oxidase subunit I (COI) gene. Numbers near the branches indicate posterior probabilities in the BI tree (>50%)/bootstrap probabilities in the maximum likelihood tree (>50%). Asterisks after the accession numbers in parentheses indicate the sequences determined in this study. Boxes indicate *Prismognathus* species.

Table 3. Best fit model selected by jModelTest.

Region		ML tree	BI tree
Yeast	ITS	HKY+I	HKY+I
	IGS	HKY	HKY
Host	COI	TN93 +G+I	HKY+I

HASHI *et al*., 2017) were ca. 2×10^4 and 1×10^3 for *Prismognathus dauricus* and *Pr. angularis angularis*, respectively. Four colonies from each female exhibited the same sequences for both ITS and IGS.

The best-fit models for phylogenetic analyses are shown in Table 2. The topologies of ML and BI trees were the same for ITS and IGS and were similar for COI.

For the ITS region, the yeasts from the two *Pr. a. angularis* female s from Japan shared identical sequences. In contrast, the yeasts from the Korean *Pr. dauricus* exhibited one nucleotide substitution and one insertion. The latter sequences were identical to the sequences from the Korean and Japanese *Platycerus* species. Besides, they were phylogenetically distant from the sequences of yeasts from all other lucanid taxa (Fig. 2).

For the IGS region, the yeast sequences from the two *Pr. a. angularis* females formed a monophyletic clade that was distant from those of all *Platycerus* species and *Pr. dauricus*. The yeast sequences from *Pr. dauricus* were situated in the same clade as the yeast sequences from the Korean *Pl. hongwonpyoi hongwonpyoi* (Fig. 3).

For the host beetle COI, the species belonging to the genus *Prismognathus* composed a different clade from that of *Platycerus* (Fig. 4).

Discussion

It has been reported that yeast symbionts in mycangia can be matched to their corresponding host stag beetle taxa according to the sequences of their ITS and IGS regions (TANAHASHI *et al*., 2010, 2017; TANAHASHI & HAWES, 2016). The result of this study was based on only one female of *Prismognathus dauricus*, and we cannot deny the possibility of an unusual combination between this female and its yeast symbionts. However, these previous studies suggest that the combination between a stag beetle taxon and its yeast symbionts is robust, even if the yeast symbionts may have free-living stages, or other insects may bring them by chance.

The yeast symbionts of *Platycerus* and *Prismognathus* are most related to *Scheffersomyces segobiensis* of all the described yeast species (TANAHASHI *et al*., 2017). However, host stag beetle taxa usually correspond to the fine lineages of the yeast symbionts in their mycangia (TANAHASHI *et al*., 2010, 2017).

In this study, *Pr. dauricus* and *Platycerus hongwonpyoi hongwonpyoi* from South Korea were found to share yeast symbionts from the same lineage (Figs. 2 & 3). However, looking very finely, the phylogenies of *Pl. h. hongwonpyoi* populations and their yeast symbionts were not completely the same (Figs. 3 & 4). A likely reason is that the frequent gene flow of *Pl. h. hongwonpyoi* by secondary contact results in the co-existence of host beetles derived from some local populations (ZHU *et al*., 2019). By the same reason, the yeasts from *Pr. dauricus* collected in Site 3 may be genetically a little different from those from *Pl. h. hongwonpyoi* in the same site analyzed by TANAHASHI *et al*. (2017).

This is the first study to report that phylogenetically distant lucanid taxa (KUBOTA *et al*., 2011)

share yeasts of the same lineage, which was not observed in TANAHASHI *et al*. (2017). We have observed that *Pr*. *dauricus* and *Pl*. *h*. *hongwonpyoi* prefer similar temperate deciduous broad-leaved forests and similar white rot wood. This may cause horizontal transmission of yeast symbionts between the two species via host wood or cannibalism. On the other hand, in Japan, *Prismognathus* and *Platycerus* possess different clades of yeasts (Figs. 2–4), although they also prefer similar habitats. One of the possible reasons is that *Pr*. *angularis* dispersed to Japan earlier than *Platycerus*, and the yeast symbionts of *Pr*. *angularis* has been specialized to this host species. An alternative reason is the transmission of the yeast symbionts from *Platycerus* to *Prismognathus* in Korea.

These results are relevant for the study of co-evolution between stag beetles and their yeast symbionts. To further explore these relationships, more beetle samples must be examined. In future studies, we would like to focus on regions in China, which is home to many species of *Prismognathus* and *Platycerus*.

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要　　約

朱　雪姣・張　太雄・久保田耕平：同系統の共生酵母を共有する系統的に遠縁なクワガタムシ分類群の初報告―韓国産チョウセンルリクワガタとキンオニクワガタ（鞘翅目クワガタムシ科）．――――韓国および日本産ルリクワガタ属には非常に近縁な共生酵母が存在し，日本産オニクワガタ *Prismognathus angularis angularis* WATERHOUSE の共生酵母とは系統的に異なることが知られている．本研究では韓国産チョウセンルリクワガタ *Platycerus hongwonpyoi hongwonpyoi* IMURA et CHOE とキンオニクワガタ *Prismognathus dauricus* (MOTSCHULSKY) が同系統の共生酵母を共有していることが見いだされた．これは系統的に遠縁なクワガタムシ分類群が同系統の酵母を共有していることの初の報告である．

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