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Phylogenetic Relationships of the Genus *Dorcus* and Its Related Genera (Coleoptera, Lucanidae): A Reanalysis of Allozyme Data

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Abstract Six species of the lucanids genus *Dorcus* and its allied genera, two species of genus *Prosopocoilus* and one species of the genus *Prismognatus*, and one outgroup species of the genus *Ceruchus*, from Japan and Taiwan were examined using electrophoretic analyses of 16 enzymes to reanalyze their phylogenetic relationships. From the allozyme variation in 26 genetic loci detected in all species, the NEI's genetic distances between species were calculated, and the dendrogram for the ten species were constructed. The resultant dendrogram indicates that the genus *Prosopocoilus* is more closely related to the genus *Dorcus* than to the genus *Prismognatus*. *Dorcus titanus okinawanus* is clustered with other species of the genus *Dorcus*, and the genus *Dorcus* was monophyletic. In the genus *Dorcus*, *D. r. rectus* and *D. hopei* formed one cluster. This result supports the results of previous DNA analyses (HOSOYA *et al.*, 2002, 2003; HOSOYA & ARAYA, 2005), but not it of former allozymes analysis (MATSUOKA & HOSOYA, 2002).

Introduction

The genus *Dorcus* MACLEAY, 1819 is a fairly large genus, and includes about 140 species (KRAJCIK, 2001). Systematically, the concepts of the genus *Dorcus* and its allied genera such as *Serrognathus* MOTSCHULSKY, 1861 and *Macrodorcas* MOTSCHULSKY, 1861 have changed considerably, and been controversial (HOSOYA *et al*., 2003). In the genus *Dorcus*, some authers, such as DIDIER and SÉGUY (1953), BENESH (1960), NAGAI (1985) and MAES (1992), had recognized many genera, *e.g*., *Serrognathus*, *Macrodorcas*, *Hemisodorcus* THOMSON, 1862, *Ditomoderus* PARRY, 1864, *Metallactulus* RITSEMA, 1885, etc. On the other hand, ARROW (1950) included many genera such as *Prosopocoilus*, *Prismognathus*, *Serrognathus*, *Macrodorcas* and its allied genera into the genus *Dorcus*. *Dorcus* sensu ARROW (1950) was partly accepted by KIKUTA (1986), OKAJIMA and YAMAGUCHI (1988), MIZUNUMA and NAGAI (1994), YOSHIDA (1996), KRAJCIK (2001), FUJIOKA (2002) and FUJITA (2010) and they considered *Serrognathus*, *Macrodorcas* and its allied genera the synonyms of *Dorcus*, but they treated the genus *Prosopocoilus* and the genus *Prismognathus* as varid.

In splitting treatment, the genus *Dorcus* sensu MIZUNUMA and NAGAI (1994) and FUJITA (2010) was taxonomically divided into several groups; seven genera (DIDIER & SÉGUY, 1953), eight genera (BENESH, 1960), four genera (NAGAI, 1985) and six genera (MAES, 1992). In these, three major groups, *Dorcus*, *Serrognathus* and *Macrodorcas*, comprises about 30, 40 and 40 species, respectively (NAGAI, 1985), whereas the other group comprises a few species. In these splitting treatment, *Serrognathus* and *Macrodorcas* were classified into the tribe Dorcini with the genus *Dorcus* (KUROSAWA, 1976, 1985; ISIDA & FUJIOKA, 1988). However, BENESH (1960) and MAES (1992) treated that *Macrodorcas* did not included into the tribe Dorcini, including into Prosopocoilini or Cladognathini with the genus *Prosopocoilus*, the genus *Prismognathus* and its allied genera.

NOMURA and KUROSAWA (NOMURA, 1960) established the new genus *Nipponodorcus*, with *Dorcus rubrofemoratus* and *Dorcus montivagus*, from Japan. This genus has been accepted by some Japanese and Taiwanese authors such as KUROSAWA (1976, 1985), FUJITA (1985), ISIDA and FUJIOKA (1988), ZHANG (1993) and WANG (1994). MAES (1992) considered *Nipponodorcus* synonymous with *Hemisodorcus*, established with *Dorcus nepalensis* in Himarayas. On the other hand, NAGAI (1985) and KRAJCIK (2001) treated *Nipponodorcus* as a synonym of *Macrodorcas*.

In the previous papers, MATSUOKA and his coworker reported to the phylogenetic relationships based on allozyme analysis among six species in the genus *Dorcus* (IGARASHI *et al.*, 1994; MATSUOKA *et al.*, 1998; MATSUOKA & HOSOYA, 2002). As a result, IGARASHI *et al.* (1994) demonstrated that two species of the *Nipponodorcus* group, *D. rubrofemoratus* and *D. montivagus* are closely related to each other. Furthermore, MATSUOKA *et al*. (1998) indicated that *D. rectus* (*Macrodorcas* group) is more closely related to *D. hopei* (*Dorcus* group) than to *D. rubrofemoratus* and *Prosopocoilus inclinatus*. MATSUOKA and HOSOYA (2002) indicated that *D. platymelus* (=*D. titanus*) (*Serrognathus* group) is not clustered with other species of the genus *Dorcus*, thus the genus *Dorcus* is not monophyletic. In addition, *D. rectus* (*Macrodorcas* group) is more closely related to *D. striatipennis* (*Macrodorcas* group) than to *D. hopei* (*Dorcus* group). MATSUOKA and HOSOYA (2002) were detected 34 loci from 17 enzymes and calculated from all loci included in 13 loci which were not detected in one or more species. The calculation method of MATSUOKA and HOSOYA (2002) is not common method and has a problematic.

On the other hand, the author and my coworker reported to the phylogenetic relationships based on DNA analysis in the genus *Dorcus* (HOSOYA *et al*., 2002, 2003; ARAYA & HOSOYA, 2005; HOSOYA & ARAYA, 2005). The results did not supported the allozymic result of MATSUOKA and HOSOYA (2002), and indicated that *D. titanus* (*Serrognathus* group) is clustered with other species of the genus *Dorcus* (HOSOYA *et al*., 2002, 2003; HOSOYA & ARAYA, 2005), and *D. rectus* (*Macrodorcas* group) is more closely related to *D. hopei* (*Dorcus* group) than to *D. striatipennis* (*Macrodorcas* group) (HOSOYA *et al*., 2002, 2003).

In this study, I have attempted to re-examine using allozyme data: 1) the phylogenetic position of *D. titanus*; 2) the phylogenetic relationships among *D. hopei*, *D. rectus* and *D. striatipennis*: 3) the phylogenetic relationships among three genera, *Dorcus*, *Prosopocoilus* and *Prismognathus*: 4) the phylogenetic relationships among six species in the genus *Dorcus*.

Materials and Methods

The taxonomic names followed FUJITA (2010). The allozyme data for *D. hopei binodulosus* (=*D. hopei*) (*Dorcus* group), *D. r. rectus* (=*D. rectus*) (*Macrodorcas* group), *D. s. striatipennis* (=*D. striatipennis*) (*Macrodorcas* group), *D. r. rubrofemoratus* (=*D. rubrofemoratus*) (*Nipponodorcus* group) and *Prosopocoilus i. inclinatus* (=*Pro. inclinatus*) were taken from MATSUOKA and HOSOYA (2002). Furthermore, these five species were analyzed of new enzymes, Fumarase (Fum), and additional samples, five specimens of *D. s. striatipennis*, four of *D. r. rubrofemoratus* and two of *Pro. i. inclinatus*, were used of analysis.

Two species of the genus *Dorcus*, *D. titanus okinawanus* (*Serrognathus* group) (n=2) and *D. m. montivagus* (*Nipponodorcus* group) (n=9), one species of the genus *Prosopocoilus*, *Pro. astacoides blanchardi* (n=7), and one species of the genus *Prismognatus*, *Pri. a. angularis* (n=11), were collected from Japan and Taiwan (see Appendix). I chose *Ceruchus l. lignarius* of the subfamily Ceruchinae belonging to the family Lucanidae as outgroup for phylogenetic analysis. After collection, the whole bodies were stored at −40℃ until analyzed.

Table 1. Enzymes assayed in the electrophoretic study.

Enzyme	Abbreviation	Stain reference
Glycerol-3-phosphate dehydrogenase	G3pdh	AYALA *et al.* (1972)
Formaldehyde dehydrogenase	Fdh	MURPHY *et al.* (1990)
Glucose-6-phosphate dehydrogenase	G6pd	AYALA *et al.* (1974)
Malate dehydrogenase	Mdh	SHAW & PRASAD (1970)
Malate enzyme	Me	AYALA *et al.* (1972)
Octanol dehydrogenase	Odh	AYALA *et al.* (1972)
Sorbitol dehydrogenase	Sdh	SHAW & PRASAD (1970)
Superoxide dismutasa	Sod	AYALA *et al.* (1972)
Fumarase	Fum	SHAW & PRASAD (1970)
Hexokinase	Hk	SHAW & PRASAD (1970)
Phosphoglucomutase	Pgm	SHAW & PRASAD (1970)
Aspartate aminotransferase	Aat	MARCUS (1977)
Acid phosphatase	Acph	AYALA *et al.* (1972)
Alkaline phosphatase	Alk	AYALA *et al.* (1972)
Esterase	Est	SHAW & PRASAD (1970)
Cytosol aminopeptidase	Cap	AYALA *et al.* (1972)

Electrophoresis was performed on 7.5% polyacrylamide gels as described previously (MATSUOKA, 1985). Adult muscle, gut and gonad were separated from the external skeleton and individually homogenized in 5 volumes of 20 mM phophate buffer (pH 7.0) containing 0.1 M KCl and 1 mM EDTA in ice-water bath using a small polyethylene homogenizer of the Potter-Elvehjem type. After centrifugation at 6,100 g for 10 min at 4℃, 0.01–0.1 ml of clear supernatant was used for electrophoretic analyses. Electrode buffer was 0.38 M Glycine-Tris, pH 8.3. After electrophoresis, gels were stained for the following 16 enzymes (Table 1). The loci and alleles were re-estimated all data.

To estimate the genetic variability within and between species, average heterozygosity (H) and genetic distance (D) described by NEI (1972) were calculated from the allele frequency data of the loci detected in all species. The biochemical dendrogram was constructed by same method in MATSUOKA and HOSOYA (2002), using the unweighted pair-group method with arithmetic mean (UPGMA) clustering method (SNEATH & SOKAL, 1973). The confidences levels of each branch were estimated using 1,000 bootstrap replications by resampring loci (FELSENSTEIN, 1985). The dendrogram construction and bootstrap replications were performed using Phylogeny Inference Package (PHYLIP version 3.5c, FELSENSTEIN, 1993).

Results

For re-estimated all data, Table 2 shows the allele frequencies for the 26 presumptive loci detected in all species in the 16 enzymes. Table 3 shows the degree of genetic variation in ten lucanids species. The number of alleles per locus was in the range of 1.4–2.3, with a mean of 1.8, the proportion of polymorphic loci (P), in the range of 38.5–84.6%, with a mean of 62.3%, expected average heterozygosity per locus (H), in the range of 21.2–37.8%, with a mean of 28.7%.

To quantify the degree of genetic differentiation between the ten lucanids species, I calculated the genetic distance (D) between each species from 26 loci detected in all species of the allele frequencies data in Table 2. Table 4 shows the matrices of D values between all pairs of ten

Table 2. Allele frequencies at 26 genetic loci detected in all 10 lucanids species.

Locus	*Allele*	*Dto*	*Dhb*	*Drere*	*Dss*	*Druru*	*Dmm*	*Proii*	*Proab*	*Priaa*	*Cll*
G3pdh-2 (α-Gpdh)	a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.80	0.00
	b	0.00	0.00	0.07	0.78	0.00	0.00	1.00	1.00	0.20	0.00
	c	1.00	1.00	0.93	0.22	1.00	1.00	0.00	0.00	0.00	1.00
		(2)	(2)	(7)	(9)	(9)	(9)	(8)	(7)	(10)	(6)
Fdh-3 (Fdh-2)	a	0.00	0.00	0.50	0.61	0.00	0.00	0.00	0.00	0.19	1.00
	b	1.00	0.00	0.50	0.28	0.17	0.11	0.00	0.00	0.75	0.00
	c	0.00	0.00	0.00	0.11	0.83	0.89	1.00	1.00	0.00	0.00
	d	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00
		(2)	(1)	(2)	(9)	(6)	(9)	(5)	(7)	(8)	(5)
G6pd-1 (G6pd)	a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.82	0.00
	b	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.18	0.00
	c	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00
	d	0.00	0.00	0.00	0.89	0.00	0.00	0.00	0.00	0.00	0.83
	e	1.00	1.00	0.83	0.00	1.00	1.00	0.75	1.00	0.00	0.00
	f	0.00	0.00	0.17	0.00	0.00	0.00	0.13	0.00	0.00	0.17
		(2)	(2)	(6)	(9)	(10)	(9)	(8)	(7)	(11)	(6)
Mdh-2	a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00
	b	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.50
	c	0.75	0.25	1.00	1.00	1.00	1.00	1.00	1.00	0.63	0.50
	d	0.25	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		(2)	(2)	(3)	(9)	(10)	(9)	(4)	(7)	(8)	(1)
Mdh-3	a	0.00	0.75	0.86	0.94	0.80	1.00	1.00	1.00	1.00	1.00
	b	1.00	0.25	0.14	0.06	0.20	0.00	0.00	0.00	0.00	0.00
		(2)	(2)	(7)	(9)	(10)	(1)	(8)	(6)	(5)	(6)
Me-1 (Me)	a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30
	b	0.75	0.00	0.29	0.80	0.40	0.33	0.44	0.57	0.30	0.70
	c	0.25	1.00	0.71	0.20	0.60	0.67	0.56	0.43	0.10	0.00
	d	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.60	0.00
		(2)	(2)	(7)	(5)	(10)	(9)	(8)	(7)	(10)	(5)
Odh-2 (Odh-1)	a	1.00	0.00	0.00	0.00	1.00	0.40	1.00	0.00	0.11	0.00
	b	0.00	0.00	0.00	0.44	0.00	0.00	0.00	0.86	0.28	1.00
	c	0.00	1.00	1.00	0.56	0.00	0.60	0.00	0.14	0.61	0.00
		(1)	(1)	(5)	(8)	(2)	(5)	(1)	(7)	(9)	(1)
Odh-3 (Odh-2)	a	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.00	0.00	1.00
	b	0.00	0.00	0.75	0.13	0.00	0.00	0.00	0.00	0.00	0.00
	c	1.00	0.00	0.00	0.13	0.00	0.00	0.00	0.14	1.00	0.00
	d	0.00	1.00	0.25	0.44	1.00	1.00	1.00	0.86	0.00	0.00
	e	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00
		(2)	(2)	(6)	(8)	(12)	(9)	(8)	(7)	(1)	(6)
Sdh	a	0.00	0.00	0.00	0.00	0.00	0.83	0.00	0.00	0.00	0.60
	b	0.00	0.00	1.00	0.81	1.00	0.00	0.06	0.00	0.56	0.00
	c	1.00	1.00	0.00	0.19	0.00	0.17	0.94	1.00	0.17	0.00
	d	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.40
	e	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00
		(2)	(1)	(7)	(8)	(10)	(9)	(8)	(7)	(9)	(5)
Sod-2 (Sod-1)	a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	b	0.00	0.00	0.00	0.14	0.08	0.29	0.00	0.00	0.55	0.00
	c	0.00	1.00	0.75	0.79	0.92	0.50	0.36	0.00	0.18	0.00
	d	0.50	0.00	0.25	0.07	0.00	0.21	0.50	0.50	0.18	0.00
	e	0.50	0.00	0.00	0.00	0.00	0.00	0.14	0.50	0.09	0.00
		(2)	(2)	(6)	(7)	(6)	(7)	(7)	(7)	(11)	(6)

Table 2. Continued.

Locus	*Allele*	*Dto*	*Dhb*	*Drere*	*Dss*	*Druru*	*Dmm*	*Proii*	*Proab*	*Priaa*	*Cll*
Sod-3 (Sod-2)	a	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00
	b	0.00	0.00	0.21	0.11	0.38	0.43	0.00	0.00	0.00	0.00
	c	0.50	1.00	0.71	0.72	0.38	0.57	0.69	0.93	0.00	0.67
	d	0.50	0.00	0.07	0.17	0.00	0.00	0.31	0.07	0.00	0.33
	e	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
		(2)	(2)	(7)	(9)	(8)	(7)	(8)	(7)	(11)	(6)
Fum	a	0.25	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00
	b	0.75	0.00	0.14	0.50	0.63	0.43	0.00	0.00	0.00	0.00
	c	0.00	1.00	0.64	0.50	0.13	0.57	0.00	0.00	0.00	0.00
	d	0.00	0.00	0.21	0.00	0.00	0.00	1.00	1.00	1.00	1.00
		(2)	(2)	(7)	(5)	(8)	(7)	(8)	(7)	(11)	(6)
Hk	a	0.00	0.00	0.00	0.00	0.00	0.00	0.30	1.00	0.00	1.00
	b	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00
	c	0.00	0.00	0.00	0.00	0.17	0.50	0.20	0.00	0.00	0.00
	d	0.00	0.00	0.00	0.06	0.67	0.50	0.50	0.00	0.00	0.00
	e	0.50	1.00	1.00	0.11	0.17	0.00	0.00	0.00	0.91	0.00
	f	0.50	0.00	0.00	0.78	0.00	0.00	0.00	0.00	0.09	0.00
		(2)	(2)	(5)	(9)	(6)	(4)	(5)	(7)	(11)	(1)
Pgm-2	a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	b	0.00	0.00	0.17	0.00	0.00	0.00	0.06	0.14	0.00	0.00
	c	1.00	1.00	0.83	1.00	1.00	0.22	0.94	0.86	0.00	0.00
	d	0.00	0.00	0.00	0.00	0.00	0.78	0.00	0.00	1.00	0.00
		(2)	(2)	(6)	(9)	(8)	(9)	(8)	(7)	(11)	(6)
Aat-2	a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
	b	0.00	0.25	0.33	0.21	0.00	0.00	0.00	0.00	0.00	0.75
	c	1.00	0.75	0.67	0.79	0.89	0.00	0.83	0.86	1.00	0.00
	d	0.00	0.00	0.00	0.00	0.11	1.00	0.17	0.14	0.00	0.00
		(2)	(2)	(6)	(7)	(9)	(9)	(6)	(7)	(6)	(4)
Acph-1	a	0.00	0.00	0.00	0.40	0.00	0.00	0.00	0.17	0.75	0.60
	b	1.00	1.00	1.00	0.60	1.00	1.00	1.00	0.83	0.25	0.40
		(1)	(2)	(6)	(5)	(8)	(8)	(8)	(6)	(2)	(5)
Acph-2	a	0.25	0.00	0.00	0.29	0.75	0.75	0.83	0.30	0.88	0.00
	b	0.00	0.50	0.00	0.14	0.13	0.00	0.00	0.70	0.13	0.50
	c	0.00	0.00	0.70	0.36	0.13	0.25	0.17	0.00	0.00	0.30
	d	0.75	0.50	0.30	0.21	0.00	0.00	0.00	0.00	0.00	0.20
		(2)	(2)	(5)	(7)	(4)	(8)	(3)	(5)	(4)	(5)
Alk-1 (Alk)	a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
	b	0.00	0.25	0.00	0.17	0.11	0.89	0.00	0.00	0.36	0.00
	c	1.00	0.75	0.67	0.78	0.67	0.00	0.44	0.00	0.64	0.75
	d	0.00	0.00	0.17	0.06	0.22	0.11	0.56	1.00	0.00	0.00
	e	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		(2)	(2)	(6)	(9)	(9)	(9)	(8)	(7)	(11)	(6)
Est-1	a	0.25	0.25	0.43	0.17	0.00	0.17	0.25	0.57	0.79	0.17
	b	0.75	0.75	0.57	0.83	1.00	0.83	0.75	0.43	0.21	0.83
		(2)	(2)	(7)	(6)	(3)	(3)	(6)	(7)	(7)	(6)
Est-2	a	0.50	0.50	0.10	0.19	0.14	0.44	0.19	0.07	0.95	0.58
	b	0.50	0.50	0.60	0.69	0.23	0.39	0.44	0.29	0.05	0.42
	c	0.00	0.00	0.30	0.13	0.64	0.17	0.38	0.64	0.00	0.00
		(2)	(2)	(5)	(8)	(11)	(9)	(8)	(7)	(11)	(6)
Est-3	a	1.00	0.00	0.38	0.44	0.72	0.81	0.31	0.64	0.00	0.20
	b	0.00	1.00	0.63	0.56	0.28	0.19	0.69	0.36	0.95	0.80
	c	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00
		(2)	(2)	(4)	(8)	(9)	(8)	(8)	(7)	(10)	(5)

Table 2. Continued.

Locus	*Allele*	*Dto*	*Dhb*	*Drere*	*Dss*	*Druru*	*Dmm*	*Proii*	*Proab*	*Priaa*	*Cll*
Est-5	a	0.00	0.00	0.14	0.17	0.22	0.00	0.88	0.67	0.00	0.70
	b	1.00	1.00	0.71	0.83	0.33	0.06	0.00	0.08	1.00	0.30
	c	0.00	0.00	0.14	0.00	0.44	0.44	0.13	0.25	0.00	0.00
	d	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00
		(1)	(2)	(7)	(6)	(9)	(8)	(4)	(6)	(8)	(5)
Cap-1 (Lap-1)	a	0.00	1.00	0.67	1.00	0.67	0.50	0.17	0.00	0.28	0.42
	b	1.00	0.00	0.33	0.00	0.33	0.00	0.00	0.00	0.06	0.58
	c	0.00	0.00	0.00	0.00	0.00	0.50	0.83	1.00	0.67	0.00
		(1)	(1)	(3)	(4)	(3)	(4)	(3)	(1)	(9)	(6)
Cap-2 (Lap-2)	a	1.00	0.50	0.42	1.00	1.00	1.00	0.00	0.86	0.11	0.00
	b	0.00	0.50	0.58	0.00	0.00	0.00	1.00	0.14	0.89	1.00
		(1)	(2)	(6)	(6)	(6)	(9)	(2)	(7)	(9)	(4)
Cap-3 (Lap-3)	a	0.50	0.00	0.30	0.67	0.06	0.50	0.00	0.86	0.43	0.58
	b	0.50	0.75	0.70	0.22	0.56	0.00	0.88	0.07	0.00	0.42
	c	0.00	0.25	0.00	0.11	0.39	0.50	0.13	0.07	0.57	0.00
		(2)	(2)	(5)	(9)	(9)	(8)	(8)	(7)	(7)	(6)
Cap-4 (Lap-4)	a	0.00	0.00	0.30	0.88	0.00	0.00	0.00	0.00	0.50	0.33
	b	0.00	0.75	0.20	0.13	0.33	0.71	0.00	0.00	0.50	0.00
	c	1.00	0.25	0.50	0.00	0.67	0.29	1.00	1.00	0.00	0.67
		(1)	(2)	(5)	(4)	(3)	(7)	(3)	(3)	(6)	(3)

The locus names in parentheses show its in MATSUOKA and HOSOYA (2002). Alleles are correspondingly lettered from "a", this being the allele of the lowest electrophoretic mobility. Numbers of sampled for each locus are in parentheses.

Dto=*D. titanus okinawanus*; *Dhb*=*D. hopei binodulosus*; *Drere*=*D. r. rectus*; *Dss*=*D. s. striatipennis*; *Druru*=*D. r. rubrofemoratus*; *Dmm*=*D. m. montivagus*; *Proii*=*Pro. i. inclinatus*; *Proab*=*Pro. astacoides blanchardi*; *Priaa*=*Pri. a. angularis*; *Cll*=*C. l. lignarius.*

Table 3. Genetic variation at 26 genetic loci in 10 lucanids species.

Parameter	*Dto*	*Dhb*	*Drere*	*Dss*	*Druru*	*Dmm*	*Proii*	*Proab*	*Priaa*	*Cll*
No. of alleles per locus	1.4	1.4	2.0	2.3	1.9	1.8	1.8	1.7	2.1	1.7
Proportion of polymorphic loci: *P* (%)	38.5	38.5	80.8	84.6	61.5	69.2	61.5	57.7	69.2	61.5
Expected average heterozygosity per locus: *H* (%)	22.4	21.2	37.8	36.6	29.3	31.7	25.1	21.8	30.2	31.1

lucanids species.

To clarify their genetic differentiation and phylogenetic relationships, the dendrogram for ten species was constructed from the NEI's genetic distance matrix of Table 4 by using the UPGMA clustering method. Figure 1 shows the phylogenetic tree of ten lucanids species. In the resultant tree, the genera *Dorcus* and *Prosopocoilus* were closely related to each other in the three genera, *Dorcus*, *Prosopocoilus* and *Prismognatus*. This clade was supported by bootstrap proportions (BP) of 65%. The genus *Dorcus* was monophyletic, but not strongly supported (BP$<$50%), and *D. titanus okinawanus* (*Serrognathus* group) was firstly diverged in the genus *Dorcus*. The remaining *Dorcus* species were divided into two clusters; 1) *D. r. rubrofemoratus* and *D. m. montivagus* (*Nipponodorcus* group) (BP=51%); 2) *D. hopei binodulosus* (*Dorcus* group), *D. r. rectus* (*Macrodorcas* group) and *D. s. striatipennis* (*Macrodorcas* group) (BP $<$ 50%). Further, the later cluster was split into two subclusters, *D. hopei binodulosus* (*Dorcus* group) and *D. r. rectus*

Table 4. NEI's (1972) genetic distance based on 26 genetic loci between 10 lucanids species.

Species	1	2	3	4	5	6	7	8	9	10
1. *D. titanus okinawanus*										
2. *D. hopei binodulosus*	0.595									
3. *D. r. rectus*	0.491	0.255								
4. *D. s. striatipennis*	0.580	0.477	0.287							
5. *D. r. rubrofemoratus*	0.413	0.450	0.313	0.390						
6. *D. m. montivagus*	0.747	0.550	0.534	0.595	0.283					
7. *Pro. i. inclinatus*	0.653	0.605	0.539	0.635	0.348	0.546				
8. *Pro. astacoides blanchardi*	0.680	0.762	0.670	0.602	0.527	0.564	0.214			
9. *Pri. a. angularis*	0.957	0.848	0.691	0.689	1.031	0.970	0.841	0.941		
10. *C. l. lignarius*	1.050	0.975	0.715	0.657	1.052	1.099	0.802	0.789	0.902	

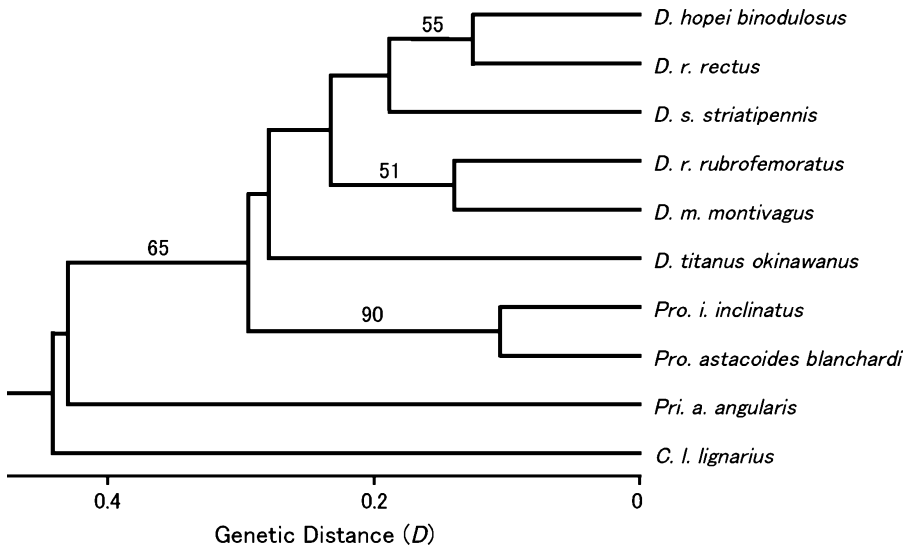

Fig. 1. The dendrogram showing the phylogenetic relationships among ten lucanid species. It was constructed from NEI's (1972) genetic distance based on 26 genetic loci by using the UPGMA clustering method. Bootstrap propotions (BP) of more than 50% are given for each branch.

(*Macrodorcas* group) (BP＝55%), and *D. s. striatipennis* (*Macrodorcas* group).

Discussion

In this study, genetic distance (*D*) was calculated from the allele frequency data of the loci detected in all species, and the loci which were not detected in one or more species were excluded from the calculation. On the other hand, MATSUOKA and HOSOYA (2002) were calculated from all loci included in its which was not detected in one or more species. The calculation method of MATSUOKA and HOSOYA (2002) is not common method and has a problematic. Furthermore, in the re-estimated the loci and alleles, it was found that the some estimate of the allele in the loci, *e.g.*, Fdh-3, G6pd-1, Sod-2 and Cap-2 (show the locus name in this study), was not accurate in MATSUOKA and HOSOYA (2002), and revised them in this study. The present result contradicts

its of MATSUOKA and HOSOYA (2002). However, this result agrees with those of other phylogenitic analyses (*e.g.*, HOSOYA *et al*., 2002, 2003; HOSOYA & ARAYA, 2005).

In this study, it is suggested that *D. titanus okinawanus* (*Serrognathus* group) is clustered with other species of the genus *Dorcus*, and the genus *Dorcus* was monophyletic. This result contradicts the result of MATSUOKA and HOSOYA (2002) based on allozyme electrophoresis that *D. platymelus* (=*D. titanus*) is not clustered with other species of the genus *Dorcus*, and the genus *Dorcus* is not monophyletic. However, the present result agrees with those of HOSOYA *et al*. (2002) using random amplified polymorphic DNA (RAPD), HOSOYA *et al*. (2003) using mitochondrial cytochrome oxidase subunit I (COI) gene sequences, and HOSOYA and ARAYA (2005) using mitochondrial 16S ribosomal RNA (16S rRNA) gene sequences.

Dorcus r. rectus and *D. s. striatipennis* were originally described as belonging to the genus *Macrodorcas*. The result of present analyses indicates *D. r. rectus* and *D. s. striatipennis* is clustered into the genus *Dorcus* cluster, and this result contradicts the opinions that *Macrodorcas* belongs to the tribe Prosopocoilini (BENESH, 1960) or to the tribe Cladognathini (MAES, 1992). The present result also agrees with those of HOSOYA *et al*. (2002) using RAPD, MATSUOKA and HOSOYA (2002) based on allozyme electrophoresis, HOSOYA *et al*. (2003) using COI gene sequences, and HOSOYA and ARAYA (2005) using 16S rRNA gene sequences.

Morphologically, *D. r. rectus* and *D. s. striatipennis* has been considered closely related, and belonged to the genus or subgenus *Macrodorcas* (BENESH, 1960; NOMURA, 1960; KUROSAWA, 1976, 1985; FUJITA, 1985; NAGAI, 1985; ISIDA & FUJIOKA, 1988; MAES, 1992; ZHANG, 1993; WANG, 1994). MATSUOKA and HOSOYA (2002) also indicated that *D. rectus* and *D. striatipennis* were the most closely related to each other. However, this result suggested that non-monophyly of the *Macrodorcas*, and *D. r. rectus* and *D. hopei* (*Dorcus* group) formed one cluster. Such result was also suggested by HOSOYA *et al*. (2002) using RAPD and HOSOYA *et al*. (2003) using COI gene sequences. Forthermore, closer relationship between *D. r. rectus* and *D. hopei* is also supported by the observed possible hybridazation between them both in the field and laboratory breeding (*e.g.*, SAKAINO & KAWADA, 1982; ARAMAKI & YOSHITAKE, 1989; HORIE, 1992).

In the tree, the genus *Nipponodorcus* (*D. rubrofemoratus* and *D. montivagus*) sensu NOMURA (1960), KUROSAWA (1976, 1985), FUJITA (1985) and ISIDA and FUJIOKA (1988) formed one cluster in the genus *Dorcus*. This result was already demonstrated by IGARASHI *et al*. (1994) based on allozyme electrophoresis, HOSOYA *et al*. (2002) using RAPD, and HOSOYA *et al*. (2003) using COI gene sequences.

The phylogenetic relationship among the four clusters, *D. rectus* and *D. hopei*, *D. striatipennis*, *D. rubrofemoratus* and *D. montivagus*, and *D. titanus* were not clearly resolved in the results of three molecular methods, HOSOYA *et al*. (2002) using RAPD, HOSOYA *et al*. (2003) using COI gene sequences and this study based on allozyme electrophoresis.

In this study, it is suggested that the genera *Prosopocoilus* and *Prismognatus* belonging to the tribe Prosopocoilini (BENESH, 1960) or to the tribe Cladognathini (MAES, 1992) did not formed one cluster, and the genus *Prosopocoilus* was clustered with the genus *Dorcus*. The result also agrees with those of HOSOYA and ARAYA (2005) using 16S rRNA gene sequences.

Appendix

Localities, collection data and size of samples used in this study, including reanalysis samples taken from MATSUOKA and HOSOYA (2002), were given below.

D. titanus okinawanus: Kunigami, Okinawa Pref., IX–1998 (n=2). *D. hopei binodulosus*:

Fukuoka Pref. (n＝2). *D. r. rectus*: Aomori Pref., 14–VIII–1988 (n＝1); Hiraka, Aomori Pref., 9–VIII–1991 (n＝1); Meya, Aomori Pref., 30–VII–1992 (n＝2); Aomori Pref., 20–VII–1992 (n＝1); Meya, Aomori Pref., 4–VII–1994 (n＝1); Aomori Pref., (n＝1). *D. s. striatipennis*: Hakkouda, Aomori Pref., 14–VIII–1991 (n＝1); Mt. Iwaki, Aomori Pref., 7–VI–1994 (n＝1); Meya, Aomori Pref., 3–VII–1994 (n＝1); Meya, Aomori Pref., 21–VII–1994 (n＝1); Meya, Aomori Pref., 3–VII–1995 (n＝1); Mt. Iwaki, Aomori Pref., 8–VII–1995 (n＝1); Tennôzawa, Aomori Pref., 15–VIII–1995 (n＝1); Tsutanuma woodland pass, Aomori Pref., 8–IX–1995 (n＝1); Aomori Pref. (n＝1). *D. r. rubrofemoratus*: Akaishigawa, Aomori Pref., 14–VIII–1988 (n＝3); Hakkouda, Aomori Pref., 9–VIII–1991 (n＝1); Kousei woodland pass, Aomori Pref., 16–IX–1991 (n＝1); Ikarigaseki, Aomori Pref., 12–VII–1992 (n＝1); Jogakura, Aomori Pref., 12–VII–1992 (n＝1); Kuroishi, Aomori Pref., IX–1992 (n＝1); Iwaki, Aomori Pref., 13–IV–1993 (n＝1); Hisayoshi, Aomori Pref., 8–VIII–1995 (n＝1); Yunosawa, Aomori Pref., 13–VIII–1995 (n＝1); Aomori Pref., (n＝1). *D. m. montivagus*: Aomori Pref., 14–VIII–1988 (n＝1); Aonizawa, Aomori Pref., 27–VIII–1992 (n＝2); Aonizawa, Aomori Pref., 28–VIII–1992 (n＝1); Aonizawa, Aomori Pref., 29–VIII–1992 (n＝1); Tsutanuma woodland pass, Aomori Pref., 3–IX–1995 (n＝1); Hisayoshi, Aomori Pref., 4–IX–1995 (n＝1); Tsutanuma woodland pass, Aomori Pref., 8–IX–1995 (n＝1); Aomori Pref., (n＝1). *Pro. i. inclinatus*: Akaishigawa, Aomori Pref., 14–VIII–1988 (n＝3); Aomori Pref., 22–VIII–1988 (n＝1); Hiraka, Aomori Pref., 9–VIII–1991 (n＝1); Meya, Aomori Pref., 20–VII–1992 (n＝1); Hisayoshi, Aomori Pref., 8–VIII–1995 (n＝1); Hisayoshi, Aomori Pref., 23–VIII–1995 (n＝1). *Pro. astacoides blanchardi*: Puli, Nantou Hsien, Taiwan, 19–VIII–1995 (n＝7). *Pri. a. angularis*: Aomori Pref., 8–VIII–1988 (n＝1); Lake Jûniko, Aomori Pref., 21–IV–1991 (n＝1); Kousei woodland pass, Aomori Pref., 16–IX–1991 (n＝1); Meya, Aomori Pref., 3–VIII–1994 (n＝1); Meya, Aomori Pref., 4–VIII–1994 (n＝1); Hisayoshi, Aomori Pref., 20–VIII–1995 (n＝3); Yachi, Aomori Pref., 22–VIII–1995 (n＝2); Hisayoshi, Aomori Pref., 23–VIII–1995 (n＝1). *C. l. lignarius*: Hiraka, Aomori Pref., 29–IV–1988 (n＝2); Hiraka, Aomori Pref., 1–XII– 1991 (n＝2); Kodomari, Aomori Pref., 1–XII–1991 (n＝2).

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要　　約

細谷忠嗣：クワガタ属 *Dorcus*（コウチュウ目クワガタムシ科）とその近縁属の系統関係：アロザイムデータの再解析．—— DNA を用いた系統解析の結果と矛盾が生じているアロザイムデータについて再解析を行った．クワガタ属 *Dorcus* 6 種とその近縁属ノコギリクワガタ属 *Prosopocoilus* 2 種とオニクワガタ属 *Prismognatus* 1 種，それに外群としてツヤハダクワガタ属 *Ceruchus* 1 種について，松岡・細谷 (2002) のアロザイムデータと追加のデータを合わせて再解析を行った．その結果，クワガタ属 *Dorcus* とノコギリクワガタ属 *Prosopocoilus* が組み，ヒラタクワガタ *D. titanus* はクワガタ属 *Dorcus* の系統群に含まれ，クワガタ属 *Dorcus* は単系統群となった．また，コクワガタ *D. rectus* はスジクワガタ *D. striatipennis* ではなくオオクワガタ *D. hopei* と系統群を形成した．これらの結果は，松岡・細谷 (2002) のアロザイムによる結果と異なるものであったが，従来の DNA 分析の結果とは良く一致するものであった．

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Records of the Exotic and Pest Beetle *Oryctes rhinoceros* (Coleoptera, Scarabaeidae, Dynastinae) from Takara Island in the Tokara Islands

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The coconut rhinoceros beetle, *Oryctes rhinoceros* (LINNAEUS) is widely distributed in tropical and subtropical region of Asia, and has been known as an important pest. Its adults seriously damage coconut or other useful palms by tunneling into the growing point, destroying leaf tissue and sucking the juice from the macerated tissue (ARROW, 1925; RITCHER, 1958; BEDFORD, 1980). In addition, they also damage sago palm, screw pine, banana, sugar cane, etc (ARROW, 1925; RITCHER, 1958; SATO & IMURE, 2003).

The first invasion to Japan by this beetle was recorded in Ishigaki Island in Yaeyama Islands, in 1921 (SONAN, 1922), and its distribution spread gradually. This beetle has been expanded and established in the Ryukyu archipelago: Kita-daito Island in 1960, Iriomote Island in 1967, Yonaguni Island in 1972, Okinawa Island in 1975, Miyako Island in 1983, Okinoerabu Island in 1987, Yoron Island in 1988, Amami-Ôshima Island and Tokunoshima Island in 1991, Kikai Island in 1997, etc (SATO & IMURE, 2003). This beetle is sometimes collected at harbor in Kyushu Island of Kagoshima Prefecture, but not established (SATO & IMURE, 2003).

In the Tokara Islands, this beetle was first collected in Takara Island, in 2009 (K. YOSHIDA, personal communication), but not reported a paper. In this paper, I reported newly record of *O. rhinoceros* in Takara Island, the Tokara Islands.

Oryctes rhinoceros (LINNAEUS, 1758)

Specimens examined. 1♂, the street in front of the Takarajima primary and junior high school, Takara Island, Tokara Islands, Kagoshima pref., Japan, by light-trap, 21–VII–2011, T. HOSOYA leg.; 1♂, the thermal power station, Takara Island, Tokara Islands, Kagoshima pref., Japan, by the light of power station, but dead specimen, 21–VII–2011, T. HOSOYA leg.

OSHIRO and OKUSHIMA (1980) suggested that *O. rhinoceros* has immigrated to the islands in Okinawa Prefecture, almost certainly by adhering to the host plants. It is suggest that this beetle adhered with the host plant would be transported from Amami-Ôshima Island to Takara Island by the ferry Toshima.

The additional collections in this study suggest that *O. rhinoceros* might be established in Takara Island. *Pandanus odoratissimus* naturally grows in Takara Island and other islands of the Tokara Islands. In addition, this beetle also breeds in decaying organic materials like compost, sawdust heaps, heaps of cattledung and bagasse (BEDFORD, 1980; OSHIRO & OKUSHIMA, 1980). The cattle breeding are one of the main industries in the Tokara Islands. Therefor, it is possible that this beetle breeds in heaps of cattle-dung in Takara Island. We must be careful to the distribution expansion and establishment of *O. rhinoceros* in the Tokara Islands.

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