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Limnoperna fortunei kikuchii Habe, 1981 (Bivalvia: Mytilidae) is a synonym of *Xenostrobus securis* (Lamarck, 1819): Introduction into Japan from Australia and/or New Zealand

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Abstract: One species and its subspecies of the genus *Limnoperna* are known from Japan: *L. fortunei fortunei* (Dunker, 1856) and *L. fortunei kikuchii* Habe, 1981. The former was reported first in the 1990's in Japanese freshwaters, while the latter was described by Habe (1981) as an endemic subspecies of the species found in brackish waters. According to morphological and isozymatic studies done by Kimura (1994a) and Kimura and Tabe (1997), specimens which have been identified so far in Japan as *L. fortunei kikuchii* are clearly distinguishable from *L. fortunei fortunei*. Deducing from that *L. fortunei kikuchii* shares characteristics in its anatomy and shell morphology with the *Xenostrobus* species, and is probably identical to *X. securis* (Lamarck, 1819), a species that is endemic to the brackish waters of Australia and New Zealand. In order to confirm *L. fortunei kikuchii* is a synonym of *X. securis*, we examined characteristics of shell morphology, anatomy and isozymes of specimens collected from Japan and Western Australia. Specimens from the above two localities shared characteristics relating to shell morphology and anatomy, while they showed genetic variations for 10 loci (in 8 enzymes examined) without allelic substitution between the samples from the two localities. The present study indicates that *L. fortunei kikuchii* should be a junior synonym of *X. securis* and must have been introduced from Australia and/or New Zealand.

Keywords: Mytilidae, *Limnoperna*, *Xenostrobus*, morphology, anatomy, isozyme, introduced species

Introduction

Limnoperna fortunei kikuchii was described by Habe (1981) from Japan as a subspecies of *L. fortunei fortunei* (Dunker, 1856). Presently, *L. fortunei kikuchii* which is the predominant mytilid in intertidal macrobenthic communities in most areas of Japan, has not been reported from areas outside Japan, where it is found in embayment areas, estuaries and brackish waters, *e.g.*, Tokyo Bay to Urado Bay (Kochi Pref.) along the Pacific coast, Seto Inland Sea, and from Dokai Bay (Fukuoka Pref.) to Shinji Lake (Shimane Pref.) along the Japan Sea coast based on Kimura (1994a) compiling updated distributional data in Japan. *Limnoperna fortunei fortunei* has been reported from mainland China, Taiwan, Korea and Thailand based on Kimura (1994b) compiling distributional data in the world, and is known to have been introduced to Hong Kong in 1960's (Morton, 1975), Argentina in 1991 (Darrigran and Pastorino, 1995) and to Japan in 1990's (Kimura, 1994b). In Japan, the species has been reported from Biwa Lake, and also from the lower reaches and tidal areas of Kiso Rivers (Kiso, Ibi, Nagara) (Kimura, 1994b) and Yodo River (Nakai, 1995).

Habe (1981) separated *L. fortunei kikuchii* from *L. fortunei fortunei* based on shell morphology. Some researchers have insisted that this subspecies is clearly distinguishable from *L. fortunei fortunei* by morphological, physiological and genetic characteristics (Kimura, 1994a; Kimura *et al.*, 1995; Ieyama, 1996; Kimura and Tabe, 1997). Furthermore, though *L. fortunei fortunei* mainly inhabits freshwater areas and *L. fortunei kikuchii* mainly inhabits brackish water areas, these two mytilids were found to occur together in a tidal part of the Nagara River, central Japan (Kimura and Tabe, 1997). Thus, the validity of its subspecific status has been questioned. Fukuda (1994) elevated *L. fortunei kikuchii* to *Limnoperna kikuchii* in species rank, while Asakura (1992) considered *L. fortunei kikuchii* to be a synonym of *L. fortunei fortunei*. We wonder if *L. fortunei kikuchii* may be identical with *Xenostrobus securis*, because *L. fortunei kikuchii* has the recurrent loop of the mid-intestine on the right side of the stomach and extensible in- and excurrent siphons which are diagnoses of the genus *Xenostrobus* (Kimura and Shikano, 1996). Furthermore, *L. fortunei kikuchii* shares several morphological characteristics with *X. securis* (as referred in Kimura and Shikano, 1996).

The present paper indicates that *L. fortunei kikuchii* should be a synonym of *X. securis* (Lamarck, 1819) and must have been introduced in Japan from Australia and/or New Zealand, based on shell morphology, anatomy and isozymatic analysis of specimens of *L. fortunei fortunei* from Japan and Taiwan, *L. fortunei kikuchii* from Japan, *Xenostrobus* specimens from several countries including Western Australia.

Materials and Methods

For descriptions of shell morphology and anatomy, we examined the type specimens of five species (*L. fortunei kikuchii*, *X. securis*, *X. hepaticus* (Gould, 1850), *X. mangle* Ockelmann, 1983 and *X. balani* Ockelmann, 1983) and specimens of *X. inconstans* (Dunker, 1856) and *X. pulex* (Lamarck, 1819) (Table 1). Specimens of *L. fortunei kikuchii* collected from the intertidal zones at five sites in Japan and those of *L. fortunei fortunei* at three sites from freshwater areas in Japan and northern Taiwan were examined (Fig. 1; Table 1). Furthermore, specimens of *X. securis* collected at two sites, i.e., at upstream and downstream sites in an estuarine area of the Swan River, Western Australia (Fig. 1; Table 1), and those of *X. atratus* (Lischke, 1871) and *Xenostrobus* sp. collected from Koajiro Bay in Kanagawa Prefecture, Japan, and Fiji Island were examined (Table 1). The above samples are dried specimens or are fixed in 70% alcohol.

For examination of allometric differences in shell morphology among the three species (*L. fortunei kikuchii*, *L. fortunei fortunei* and *X. securis*), we measured shell length, shell height and shell width to the nearest 0.1 mm. Rates of correct discrimination were calculated by canonical discriminant analysis, and Scheffe's, Kruskal-Wallis and Mann-Whitney's U-tests were done, using the log-transformed data.

For isozymatic analysis, live specimens of *X. securis* were collected at the two sites (the upstream and downstream sites) in the Swan River in July 1996, and those of *L. fortunei kikuchii* were collected at one site in brackish water in Hamana Lake in August 1996 (Fig. 1). All specimens were transported to the laboratory and stored at -20 °C or -80 °C until electrophoretic analysis was done. Mantle tissue extracts of 50 specimens collected at each site were used for electrophoretic analysis using horizontal starch-gel electrophoresis. Procedures of starch-gel electrophoresis were basically according to May *et al.* (1979) and May (1992), while those of staining were according to Harris and Hopkinson (1976) and May (1992). The examined enzymes, their loci and buffer systems used in electrophoresis are shown in Table 2. Identifications of loci, alleles, genetic nomenclature and inscriptions follow Fujio (1984) and Shaklee *et al.* (1990). Alleles were scored as the standard "**100*" allele by arbitrarily designating the most common allele at each locus. The other alleles were assigned as numericals on the basis of the mobility of their products relative to that of the standard allele.

Table 1. Reference specimens. 参照標本. NMHN=Museum National d'Histoire Naturelle, Paris; TMNH=Toyohashi Museum of Natural History; NSMT=National Science Museum Tokyo; USNM=United States National Museum, Washington D.C.; WAM=Western Australian Museum, Perth; ZMC=Zoological Museum, University of Copenhagen. *=holotype, **=paralectotype.

Sp.	Locality	No.	Data	Coll. (Depository)	Dried (D) or alcohol preserved (A) specimens
Limnoperna fortunei kikuchii	Koroen, Hyogo Pref.	1	Mar., 1976	*N. Kikuchi (NSMT Mo58959)	D
	Tokyo Bay	50	Aug. 5, 1996	S. Kimura and T. Kimura (TMNH-MO001932-001981)	D
	Hamana Lake	115	Aug. 13, 1996	S. Kimura and T. Kimura (TMNH-MO001982-002096)	D and A
	Lower site, Nagara River, Gifu Pref.	40	Aug. 5, 1994	S. Kimura and T. Kimura (TMNH-MO002097-002136)	D
	Fukuda River, Hyogo Pref.	30	Aug. 25, 1996	S. Kimura and T. Kimura (TMNH-MO002137-002166)	D
	Hashimoto River, Hagi, Yamaguchi Pref.	50	Jun. 22, 1992	H. Fukuda, Y. F. Ito and I. Kawakami (TMNH-MO002167-002216)	D
Xenostrobus securis	New Holland (Australia)	2	?	**J. B. P. A. de Monet de Lamarck (NMHN)	D
	Upper site, Swan River, WA	111	Jul. 29, 1996	S. Kimura and T. Kimura (TMNH-MO002217-002327)	D and A
	Lower site, Swan River, WA	168	Jul. 29, 1996	S. Kimura and T. Kimura (TMNH-MO002328-002495)	D and A
Xenostrobus sp.	Suva Point, Fiji Is.	2	Jul. 9, 1994	E. Tsuchida (TMNH-MO002496-002497)	A
X. hepaticus	Fiji Is.	1	?	*A. A. Gould (USNM18000)	D
X. inconstans	Oyster Harber, WA	9	Nov. 1961	B. R. Wilson (WAN2589-67)	A
X. pulex	Woodman Point, WA	8	Sep. 7, 1964	B. R. Wilson (WAN846-68)	A
X. atratus	Koajiro Bay, Kanagawa Pref.	4	Jun. 9, 1996	S. Kimura and T. Kimura (TMNH-MO002498-002501)	A
X. mangle	Jeram, W. coast of Malaysia	1	Jun. 19, 1982	*K. W. Ockelmann (ZMC)	A
	Jeram, W. coast of Malaysia	5	Jun. 19, 1982	K. W. Ockelmann (ZMC)	A
X. balani	Ao Nam Bor, Phuket, Thailand	1	Oct. 1974	*K. W. Ockelmann (ZMC)	A
	Ao Nam Bor, Phuket, Thailand	9	Oct, 1974	K. W. Ockelmann (ZMC)	A
L. fortunei fortunei	Upper site, Nagara River, Gifu Pref.	40	Aug. 5, 1994	S. Kimura and T. Kimura (TMNH-MO002502-002541)	D and A
	Hirako, Biwa Lake	104	Nov. 5, 1992	T. Kimura (TMNH-MO002542-002645)	D
	Jyr-Tan dam, Northern Taiwan	56	Jul. 22, 1992	H. Sekiguchi (TMNH-MO002646-002701)	A

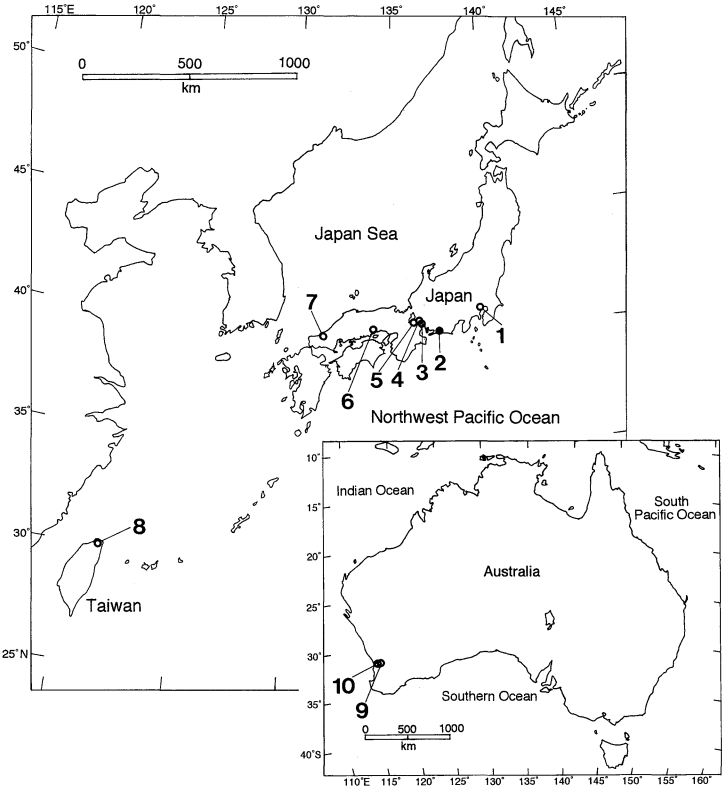

Fig. 1. Location of sampling sites of *Limnoperna fortunei kikuchii*, *L. fortunei fortunei* and *Xenostrobus securis*. コウロエンカワヒバリガイ，カワヒバリガイと *Xenostrobus securis* の採集地点.
1: Tokyo Bay; 2: Hamana Lake; 3: Lower site of Nagara River; 4: Upper site of Nagara River; 5: Biwa Lake; 6: Fukuda River; 7: Hashimoto River; 8: Jyr-Tan; 9: Upper site of Swan River; 10: Lower site of Swan River.

Results

1. Shell morphology of *Limnoperna fortunei kikuchii*

Differences in characteristics of shell morphology were not detectable among specimens of *L. fortunei kikuchii* which were collected at the five sites from Japan. *L. fortunei kikuchii* has a shell thickness almost the same as in *L. fortunei fortunei*, the shell being rounded-triangular in a lateral view, and height near 2/3 of total shell length (P1. 1, figs. 1, 2). The anterior margin of the shell is narrowly rounded, the antero-dorsal margin being straight or gently curved, and the ventral margin being straight but often arcuate in larger specimens. The umbones, being close to terminal in position, are prominent and are moderately elevated. The external surface of the shell is smooth in juveniles, while in adults it has usually slight but well-defined commarginal sculpture. The periostracum is smooth and reddish brown in adults, while in juveniles it is smooth with reddish variegations or black zig-zag patterns (P1. 1, fig. 13). The interior wall of the shell is pale blue-iridescent on the antero-ventral side and purple-iridescent on the postero-dorsal side. The muscle scars and pallial line are distinct in adults. The posterior byssal retractor scar is narrow, being not separated (Fig. 2). The ligament is half of the total shell length. The byssal hair is sometimes on the shell. The byssus threads are numerous, very fine and silky with a pale brownish-yellow color.

Table 2. Enzyme examined, their loci and buffer systems used in electrophoresis.
使用した酵素，遺伝子座，緩衝液.

Enzyme	Number	Locus	Buffer
Aspartate aminotransferase	2.6.1.1	*AAT**	1
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*G3PDH**	2
Glucose-6-phosphate isomerase	5.3.1.9	*GPI**	2
Isocitrate dehydrogenase ($NADP^+$)	1.1.1.42	*IDHP-1**	2
		*IDHP-2**	2
Malate dehydrogenase	1.1.1.37	*MDH-1**	2
		*MDH-2**	2
Tripeptide aminopeptidase	3.4.-.-	*PEPB**	1
Phosphogluconate dehydrogenase	1.1.1.44	*PGDH**	2
Superoxide dismutase	1.15.1.1	*SOD**	1

Buffer: 1 = a Tris-boric acid-EDTA buffer (pH 8.5) described by Markert and Faulhazber (1965)
Buffer: 2 = an amin (n-(3-aminopropyl)-morpholine) citrate buffer (pH 6.5) described by Clayton and Tretiak (1972)

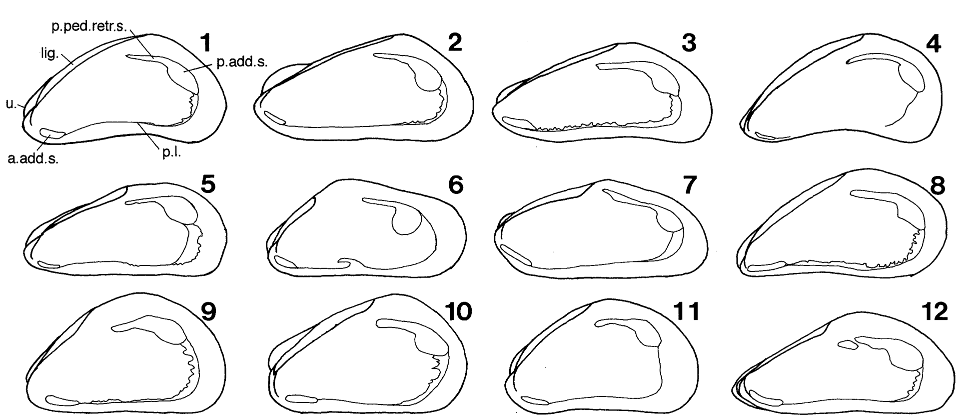

Fig. 2. Interior walls of left shell valves of *Limnoperna fortunei kikuchii*, *L. fortunei fortunei* and *Xenostrobus* species. コウロエンカワヒバリガイ，カワヒバリガイとクログチガイ属各種の左殻内側.

a.add.s.: anterior adductor scar 前閉殻筋痕; lig.: ligament 靱帯; p.add.s.: posterior adductor scar 後閉殻筋痕; p.bys.retr.s.: posterior byssal retractor scar 後足糸牽引筋痕; p.l.: pallial line 外套膜線; u.: umbo 殻頂.

1: *L. fortunei kikuchii* from Hamana Lake; 2: *L. fortunei kikuchii* (Holotype) from Koroen; 3: *X. securis* from Swan River, WA; 4: *X. securis* (Paralectotype) from Australia,; 5: *Xenostrobus* sp. from Fiji Is.; 6: *X. hepaticus* (Holotype) from Fiji Is.; 7: *X. inconstans* from Oyster Harbor, WA; 8: *X. pulex* from Woodman point, WA; 9: *X. atratus* from Koajiro Bay; 10: *X. balani* (Holotype) from Ao Nam Bor, Phuket; 11: *X. mangle* (Holotype) from Jeram, W. coast of Malaysia; 12: *L. fortunei fortunei* from Nagara River.

2. Allometric comparisons of shells of *Limnoperna fortunei kikuchii*, *L. fortunei fortunei* and *Xenostrobus securis*

Data for shell length (SL), shell height (SH), shell width (SW) and ratios of each (SH/SL, SW/SL, SH/SW) are shown in Table 3 for *L. fortunei kikuchii*, *L. fortunei fortunei* and *X. securis*. Significant differences were detected statistically for ratios of SH/SL, SW/SL and SH/SW among specimens of *L. fortunei kikuchii* collected at the five sites in Japan (Kruskal-Wallis test, $H = 80.1 - 228.4$, $p < 0.01$). The rate of correct discrimination using SL, SH and SW was 50.2 %. Significant differences were detected for the ratios of SW/SL and SH/SW among specimens of *L.*

Table 3. Morphometric measurements (mean ± SD) of *Limnoperna fortunei kikuchii*, *Xenostrobus securis* and *L. fortunei fortunei*.
コウロエンカワヒバリガイ，*Xenostrobus securis*, カワヒバリガイの形態平均値.

Sp.	Sampling sites	No.	SL	SH	SW	SH/SL	SW/SL	SH/SW
L. fortunei kikuchii	Tokyo Bay	50	21.99 ± 3.54	10.14 ± 1.42	7.90 ± 1.34	0.46 ± 0.02	0.36 ± 0.02	1.29 ± 0.09
	Hamana Lake	115	18.67 ± 7.16	9.22 ± 3.32	7.11 ± 2.72	0.74 ± 0.07	0.63 ± 0.12	1.26 ± 0.59
	Nagara River	40	21.08 ± 2.47	11.82 ± 1.59	9.46 ± 1.05	0.56 ± 0.04	0.45 ± 0.03	1.25 ± 0.12
	Fukuda River	29	19.15 ± 4.96	10.74 ± 2.43	8.45 ± 1.97	0.56 ± 0.04	0.44 ± 0.04	1.27 ± 0.08
	Hashimoto River	50	16.35 ± 2.26	8.35 ± 1.13	6.38 ± 0.94	0.51 ± 0.03	0.39 ± 0.02	1.32 ± 0.11
X. securis	Upper site, Swan R.	111	14.56 ± 10.12	7.11 ± 4.64	5.30 ± 3.66	0.51 ± 0.04	0.37 ± 0.03	1.40 ± 0.12
	Lower site, Swan R.	168	11.56 ± 5.07	5.89 ± 2.38	4.96 ± 2.26	0.52 ± 0.04	0.43 ± 0.06	1.24 ± 0.25
L. fortunei fortunei	Nagara River	40	24.75 ± 2.76	10.92 ± 1.00	9.40 ± 1.21	0.44 ± 0.03	0.38 ± 0.03	1.17 ± 0.11
	Biwa Lake	104	19.45 ± 7.09	8.63 ± 2.93	7.90 ± 2.99	0.46 ± 0.05	0.40 ± 0.04	1.15 ± 0.20
	Taiwan	56	27.68 ± 3.30	12.75 ± 1.44	10.52 ± 1.25	0.46 ± 0.04	0.38 ± 0.03	1.22 ± 0.12

SL = shell length (mm), SH = shell height (mm), SW = shell width (mm)

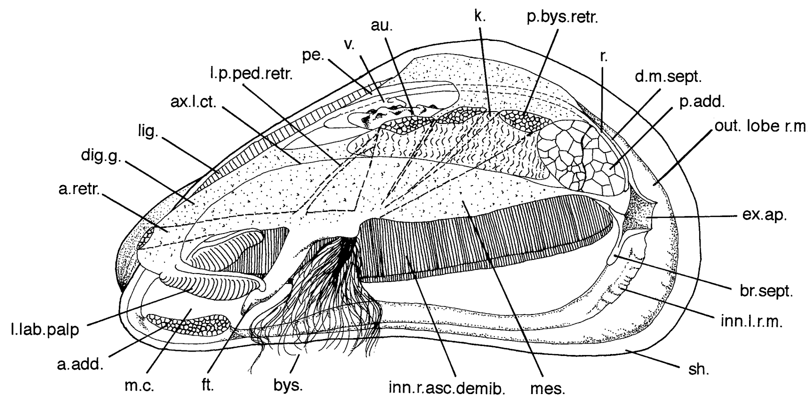

Fig. 3. Semi-diagrammatic lateral view of soft body parts of *Limnoperna fortunei kikuchii*.
The specimens were collected from Aichi Prefecture. Ctenidium and mantle of the left side are removed. The posterior end is presented as sagittal section to expose details of the structure of the inhalent and exhalent siphons. Shell length: 25.3 mm. 愛知県産コウロエンカワヒバリガイの軟体部の半模式図（殻長 25.3mm）．左側の鰓と外套膜は除いてある．後端は出入水管の構造を明らかにするために断面図で示す．
a.add.: anterior adductor muscle 前閉殻筋; a.retr.: anterior retractor muscle 前牽引筋; au.: auricle 心房; ax.l.ct.: axis of left ctenidia 左鰓軸; br.sept.: branchial septum (in section) 鰓隔壁（断面）; bys.: byssus 足糸; d.m.sept.: dorsal mantle septum 背側の外套膜隔壁; dig.g.: digestive gland 中腸腺; ex.ap.: exhalent aperture 出水孔; ft.: foot 足; inn.l.r.m.: inner mantle lobe of right side 右側外套膜内褶; inn.r.asc.demib.: inner ascending demibranch of right ctenidium 右側内鰓; k.: kidney 腎臓; l.lab.palp.: left labial palp 左側唇弁; l.p.ped.retr.: left posterior pedal retractor muscle 左側後収足筋; lig.: ligament 靱帯; m.c.: mantle cavity 外套腔; mes.: mesosoma 中体部; out.lobe r.m.: outer lobe of right mantle 右側外套膜外褶; p.add.: posterior adductor muscle 後閉殻筋; p.bys.retr.: posterior byssal retractor muscle 後足糸牽引筋; pe.: pericardium 心嚢; r.: rectum 直腸; sh.: shell 殻; v.: ventricle 心室.

fortunei fortunei collected at the three sites in Japan and Taiwan (Kruskal-Wallis test, $H = 8.7 - 17.0$, $p < 0.05$), while the difference was not significant for the ratio of SH/SL (Kruskal-Wallis test, $H = 5.2$, $p = 0.07$). The rate of correct discrimination was 64.0 %, using data of SL, SH and SW. Significant differences were detected for the ratios of SW/SL and SH/SW between specimens of *X. securis* collected at the two sites in Western Australia (Mann-Whitney's U-test, $p < 0.01$), while the difference was not significant for the ratio of SH/SL (Mann-Whitney's U-test, $p = 0.39$). The rate of correct discrimination was 84.2 %, using data for SL, SH and SW. Significant differences were detected for the ratios of SH/SL, SW/SL and SH/SW between specimens of *L. fortunei kikuchii* and *L. fortunei fortunei* (Scheffe's test, $p < 0.01$). The rate of correct discrimination between the two species using SL, SH and SW was 75.3 %. Significant differences were detected for the ratios of SH/SL, SW/SL and SH/SW between specimens of *L. fortunei kikuchii* and *X. securis* (Scheffe's test, $p < 0.01$). The rate of correct discrimination between the two species was 76.4 % using data of SL, SH and SW.

In short, although intraspecific variations in the above ratios of *L. fortunei kikuchii*, *L. fortunei fortunei* and *X. securis* were recognized, statistically significant differences were detected in shell shape between *L. fortunei kikuchii* and *X. securis*, and between both *L. fortunei kikuchii* and *L. fortunei fortunei*.

3. Anatomy of *Limnoperna fortunei kikuchii*

No remarkable differences were detectable among specimens of *L. fortunei kikuchii* collected at

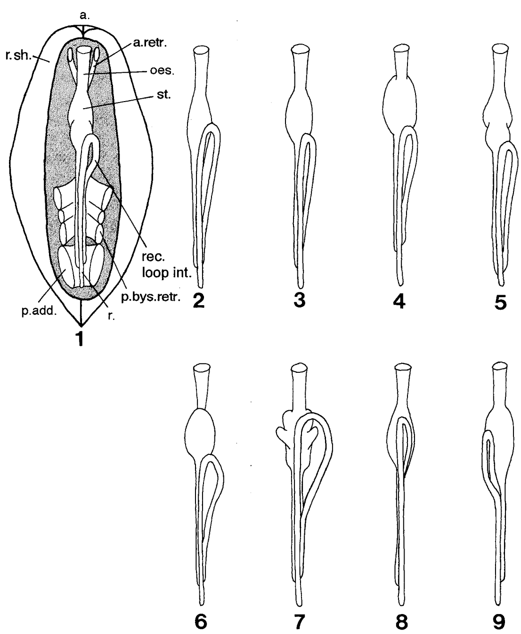

Fig. 4. Dorsal views of musculature and alimentary tract of *Limnoperna fortunei kikuchii*, *L. fortunei fortunei* and *Xenostrobus* species. コウロエンカワヒバリガイ，カワヒバリガイとクログチガイ属各種の背側から見た筋肉系と消化器系.

a.: anterior 前; a.retr.: anterior retractor muscle 前牽引筋; oes.: oesophagus 食道; p.add.: posterior adductor muscle 後閉殻筋; p.bys.retr.: posterior byssal retractor muscle 後足糸牽引筋; r.: rectum 直腸; r.sh.: right shell 右殻; rec.loop int.: recurrent loop of the intestine 腸の旋回部; st.: stomach 胃.

1: *L. fortunei kikuchii* from Hamana Lake; 2: *X. securis* from Swan River, WA; 3: *Xenostrobus* sp. from Fiji Is.; 4: *X. inconstans* from Oyster Harbor, WA; 5: *X. pulex* from Woodman point, WA; 6: *X. atratus* from Koajiro Bay; 7: *X. balani* from Ao Nam Bor, Phuket; 8: *X. mangle* from Jeram, W. coast of Malaysia; 9: *L. fortunei fortunei* from Nagara River.

the five sites from Japan, for the following anatomical characteristics: the recurrent loop of the mid-intestine lies on the right side of the stomach; extensible incurrent and excurrent siphons are present (Fig. 3, 4); coloration of the soft parts is generally pale yellow to dirty orange; two portions of the posterior adductor are markedly unequal in size (Fig. 3); the posterior byssus retractor splits into two main bundles (Fig. 5); the anterior one with growth becoming incompletely subdivided into 2-3 portions attaching to a narrow, oblong scar of the shell, each pair of the posterior pedal retractors consists of a single bundle connecting with the shell side of the anterior retractor; the gonad prevails within the pallium and the mesosoma; the exhalent siphon is well-developed with muscular walls; the inner mantle lobe is sheet-like and ruffled but does not bear guard papillae (Fig. 6).

4. Isozymatic analysis specimens of *Limnoperna fortunei kikuchii* and *Xenostrobus securis*

Ten loci were presumed for eight enzymes examined in this study. Chi-square tests of allelic frequencies were applied to each locus to detect the deviation from the Hardy-Weinberg equilibrium. There were no significant differences between the expected and observed frequencies (χ^2 = 0.005 - 1.556, $0.20 < P < 0.95$). Allele frequencies at the loci are shown in Table 4. A brief description of the eight enzymes is given as follows:

A single locus was coded for AAT, G3PDH, GPI, PEPB, PGDH and SOD. Two loci were

Table 4. Allele frequency at 10 loci for *Limnoperna fortunei kikuchii* and *Xenostrobus securis*.
コウロエンカワヒバリガイと *Xenostrobus securis* の遺伝子頻度.

Locus		*L. f. kikuchii*	*X. securis* (Upper site)	*X. securis* (Lower site)
*AAT**	**35*	0.000	0.010	0.000
	**90*	0.060	0.000	0.000
	**100*	0.940	0.990	0.980
	**125*	0.000	0.000	0.020
*G3PDH**	**70*	0.010	0.000	0.000
	**100*	0.990	1.000	1.000
*GPI**	**70*	0.000	0.000	0.010
	**75*	0.060	0.000	0.000
	**85*	0.000	0.100	0.060
	**100*	0.910	0.880	0.920
	**120*	0.000	0.020	0.010
	**125*	0.030	0.000	0.000
*IDHP-1**	**80*	0.000	0.000	0.030
	**100*	1.000	1.000	0.970
*IDHP-2**	**100*	1.000	0.980	0.980
	**135*	0.000	0.020	0.020
*MDH-1**	**90*	0.000	0.010	0.000
	**100*	1.000	0.990	1.000
*MDH-2**	**100*	1.000	1.000	1.000
*PEPB**	**100*	1.000	1.000	1.000
*PGDH**	**-35*	0.120	0.220	0.300
	**100*	0.750	0.750	0.680
	**155*	0.020	0.020	0.010
	**185*	0.040	0.010	0.010
	**210*	0.070	0.000	0.000
*SOD**	**100*	1.000	0.990	1.000
	**135*	0.000	0.010	0.000

coded for IDHP and MDH. Three-banded in heterozygotes were coded for AAT, G3PDH, GPI, IDHP, MDH, PGDH and SOD, which were dimeric enzymes. One-banded were coded for PEPB. There were genetic variations for 10 loci without allelic substitution among the three samples. Nei's (1972) genetic distance (D) among the three samples was 0.003 – 0.008. Genetic polymorphism ($p < 0.95$) was confined to *AAT**, *GPI** and *PGDH**. The observed average heterozygosities (Ho) in specimens were 0.0140 – 0.0148, differences among the three samples were not statistically significant (Friedman test, $p = 0.6873$).

Discussion

Limnoperna fortunei kikuchii has been reported as a subspecies of *L. fortunei fortunei*, based on

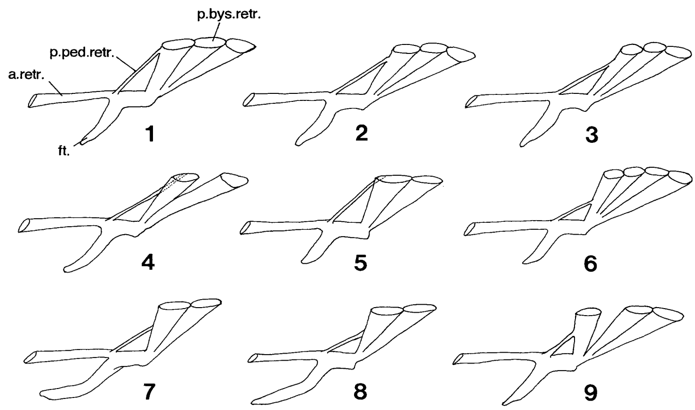

Fig. 5. Muscles supporting foot and byssus of *Limnoperna fortunei kikuchii*, *L. fortunei fortunei* and *Xenostrobus* species. コウロエンカワヒバリガイ，カワヒバリガイとクログチガイ属の足と足糸を支持する筋肉.
a.retr.: anterior retractor muscle 前牽引筋; ft.: foot 足; p.bys.retr.: posterior byssal retractor muscle 後足糸牽引筋; p.ped.retr.: posterior pedal retractor muscle 後収足筋.
1: *L. fortunei kikuchii* from Hamana Lake; 2: *X. securis* from Swan River, WA; 3: *Xenostrobus* sp. from Fiji Is.; 4: *X. inconstans* from Oyster Harbor, WA; 5: *X. pulex* from Woodman point, WA; 6: *X. atratus* from Koajiro Bay; 7: *X. balani* from Ao Nam Bor, Phuket; 8: *X. mangle* from Jeram, W. coast of Malaysia; 9: *L. fortunei fortunei* from Nagara River.

its shell morphology (Habe, 1981). In Japan, though *L. fortunei fortunei* mainly inhabits freshwater areas and *L. fortunei kikuchii* mainly inhabits brackish water areas, these two mytilids were found to occur together in a tidal part of the Nagara River (Kimura and Tabe, 1997). Furthermore, Kimura and Tabe (1997) made clear that 13 of the 14 loci were fixed at different alleles between *L. fortunei fortunei* and *L. fortunei kikuchii*, and that no hybrid was observed between the two mytilids. In addition to the other physiological and chromosomal characteristics (Kimura *et al.*, 1995; Ieyama, 1996), these data suggest that *L. fortunei kikuchii* belongs to a species distinct from *L. fortunei fortunei*.

According to the present study, *L. fortunei fortunei* has several morphological and anatomical characteristics different from those of *L. fortunei kikuchii*: the umbones of adult shell are with the anterior end in position, the shell color is olive brown in adults, and the juvenile shell color is clearly dark purple in the dorsal posterior part and yellow in the ventral anterior part. The posterior byssal retractor scar is divided into two parts (P1. 1, figs. 12, 15; Fig. 2). The recurrent loop of the mid-intestine of *L. fortunei kikuchii* lies on the right side of the stomach, while that of *L. fortunei fortunei* lies on the left side of the stomach (Fig. 4).

The recurrent loop of the mid-intestine of *L. fortunei kikuchii* lies on the right side of the stomach, this being with extensible in- and excurrent siphons (Fig. 4). These characteristics are shared only with the *Xenostrobus* species of Mytilidae. The genus *Xenostrobus* includes the following seven living species (Ockelmann, 1983): *X. inconstans*, *X. pulex*, *X. securis*, *X. hepaticus**, *X. atratus*, *X. mangle* and *X. balani*. Of these species, four species (*X. inconstans*, *X. pulex*, *X. securis* and *X. hepaticus*) are reported from Australian and Fiji waters, while the other three species are from

**Modiolus hepaticus* from Fiji Island was moved to the genus *Xenostrobus* by Ockelmann (1983). However, shell morphology of the type specimen of *M. hepaticus*, deposited in the Smithsonian Institution, clearly indicates that the above type specimen would not belong to the genus *Xenostrobus* (Pl. 1, fig. 6; Fig. 6). *Xenostrobus* specimens (Figs. 4, 5, 6) collected around Fiji Island by Mr. Eiji Tsuchida (Ocean Research Institute, University of Tokyo) were very similar anatomically and morphologically to *X. securis*.

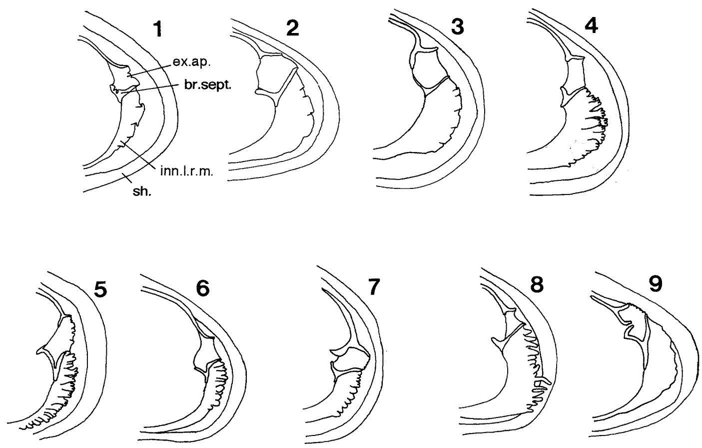

Fig. 6. Exhalent siphon and papillae surrounding the posterior region of inhalent siphon of *Limnoperna fortunei kikuchii*, *L. fortunei fortunei* and *Xenostrobus* species. コウロエンカワヒバリガイ，カワヒバリガイとクログチガイ属の出水管と入水管周辺の突起.

br.sept.: branchial septum (in section) 鰓隔壁（断面）; ex.ap.: exhalent aperture 出水孔; inn.l.r.m.: inner mantle lobe of right side 右側外套膜内褶; sh.: shell 殻.

1: *L. fortunei kikuchii* from Hamana Lake; 2: *X. securis* from Swan River, WA; 3: *Xenostrobus* sp. from Fiji Is.; 4: *X. inconstans* from Oyster Harbor, WA; 5: *X. pulex* from Woodman point, WA; 6: *X. atratus* from Koajiro Bay; 7: *X. balani* from Ao Nam Bor, Phuket; 8: *X. mangle* from Jeram, W. coast of Malaysia; 9: *L. fortunei fortunei* from Nagara River.

Southeast Asia, the south coast of mainland China, and Japan. *L. fortunei kikuchii* shares several characteristics (umbones position, shell color, sheet like mantle lobe and position of the posterior pedal retractors) with *X. securis* (Pl. 1, figs. 3, 14, and Figs. 4, 5, 6) a species that is distinguished from the other *Xenostrobus* species based on these characteristics (Pl. 1 and Figs. 5, 6; Wilson, 1967; Ockelmann, 1983; Kimura, 1966). Deducing from Wilson (1968), Kimura (1994c) and Kimura *et al.* (1995), environmental characteristics of the habitats of *L. fortunei kikuchii* inhabiting the brackish waters of Hamana Lake are similar to those of *X. securis* found in the tidal area of the Swan River: the range of water temperature and salinity are similar in both habitats where salinities fluctuate drastically from < 3 to > 30 in a few days.

In the present study, genetic variations for 10 loci were observed without allelic substitution between specimens of *L. fortunei kikuchii* in Japan and *X. securis* in Western Australia, and therefore these two populations should belong to the same species. On the other hand, these two species were significantly different in shell allometry, remarkable intraspecific variations that have been known to be influenced by various factors (age and density of mussels, tidal level and habitat type) (see Seed, 1968). In short, in spite of Habe (1981) describing *L. fortunei kikuchii* as a subspecies of *L. fortunei fortunei*, it is concluded that *L. fortunei kikuchii* is a junior synonym of *X. securis*. A synonymic list of *X. securis* is shown in Table 5.

Xenostrobus securis (excluding *L. fortunei kikuchii*) is distributed in the areas from the Swan estuary in Western Australia to Rockhampton in Queensland of eastern Australia and in New Zealand. *X. securis* was introduced to the Adrian Sea in the 1990's (Sabelli and Speranza, 1993; Lazzari and Rinaldi, 1994). According to the present study, *X. securis* (= *L. fortunei kikuchii*) in Japanese waters must have been introduced from Australia or New Zealand, 5000 km from Japan, in the 1970's. Kimura and Sekiguchi (1996) made clear in the laboratory that most planktonic larvae of *X. securis* settled on the bottom 15 days after fertilization at 25 and 30 °C. Based on the above experimental evidence and on the fact that commercial vessels usually take nearly 15 days

Table 5. A synonymic list of *Xenostrobus securis*.
コウロエンカワヒバリガイのシノニムリスト.

***Xenostrobus securis* (Lamarck, 1819)** (Wilson, 1967, p. 289 - 292, pl. 37, fig. 5 - 10.)
Modiola securis Lamarck, 1819, p. 113.
Modiola vexillum Reeve, 1857, pl. 8, fig. 40.
Perna confuse Angus, 1871, p. 21, pl. 1, fig. 33.
Modiola securis Hutton, 1873, p. 78.
Modiola fluviatilis Hutton, 1878, p. 53.
Modiolus pulex Thiele, 1930, p. 589.
Limnoperna fortunei kikuchii Habe, 1981, p. 47, pl. 2, fig. 2.; Matsukuma, 1986, p. 286, 287. Higo and Goto, 1993; Kimura and Sekiguchi, 1994; Kimura, 1994a; Kimura, 1994c; Kimura, Kakuta and Kurokura, 1995; Kimura and Sekiguchi, 1996; Ieyama, 1996; Kimura and Tabe, 1997.
Limnoperna fortunei (Dunker): Asakura, 1992, p. 3.
Limnoperna kikuchii Habe, 1977: Fukuda, 1994, p. 11, fig. 9; Fukuda and Fukuda, 1995.

from Japan to Australia (Carlton, 1985), the larvae of the species could cross the distance from Japan to Australia or New Zealand.

Carlton (1985) reviewed the introduction of many marine organisms over long distance through the ballast waters. Examples of the introduction of marine organisms from Japan or its neighboring areas to Australia and/or New Zealand include (Middleton, 1982; Slack-Smith and Brearly, 1987; Ward and Andrew, 1995): *Musculista senhousia*, *Theora lubrica* (bivalves); *Acanthogobius flavimanus* (Pisces); *Asterias amurensis* (echinoderms). On the other hand, *Ficopomatus enigmaticus*, *Hydroides elegans* (polychaete) and *X. securis* were introduced from Australia and/or New Zealand to Japan (Carlton, 1987; present study). Introduction of *X. securis* to Japan may be related intimately with drastic increases in trade between Japan and Australia and/or New Zealand since the 1970's (Kojima, 1981; Okada, 1988).

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オーストラリア・ニュージーランドに生息する *Xenostrobus securis* （コウロエンカワヒバリガイ *Limnoperna fortunei kikuchii*） （二枚貝綱，イガイ科）の日本への移入

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要　約

イガイ科カワヒバリガイ属は日本ではカワヒバリガイ *Limnoperna fortunei fortunei* とコウロエンカワヒバリガイ *L. fortunei kikuchii* の2種類が知られている。カワヒバリガイは1990年代に日本の淡水域に移入した。一方，コウロエンカワヒバリガイは波部（1981）により記載された内湾汽水域に分布する亜種である。これらは形態やアイソザイムなどが明らかに異なり，両者を亜種として扱うのには問題があるとされてきた。

今回，コウロエンカワヒバリガイの殻や内部形態の比較を行い，本種がクログチガイ属 *Xenostrobus* 属の特徴である腸の右旋を持つことが明らかとなった。クログチガイ属は現在7種が知られている。現在日本に生息するクログチガイ属としてはクログチガイ *X. atratus* 1種が知られている。これらの外部内部形態を比較した結果，コウロエンカワヒバリガイはオーストラリアとニュージーランドに生息する *X. securis* に特徴が一致した。

さらにコウロエンカワヒバリガイと *X. securis* 間で相対成長とアイソザイム分析の比較を行った。その結果，相対成長はコウロエンカワヒバリガイと *X. securis* 間で異なっていたが，それぞれの種内の地点間においても統計的に有意な差異が認められた。アイソザイム分析は，10遺伝子座が確認され，対立遺伝子の置換は認められなかった。形態およびアイソザイムにおいて高い類似性を示すことから，コウロエンカワヒバリガイに対して用いられてきた学名 *L. fortunei kikuchii* は *X. securis* の新参シノニムであり，オーストラリアかニュージーランドから日本に移入したと考えられる。

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Plate 1. Shells of *Limnoperna fortunei kikuchii*, *L. fortunei fortunei* and *Xenostrobus* species. (See Table 1 for abbreviations of institutions) コウロエンカワヒバリガイ，カワヒバリガイとクログチガイ属各種.

1. *L. fortunei kikuchii* (TMNH-MO001982) from Ona, Hamana Lake, Shizuoka Pref., Japan. SL = 26.5 mm
2. *L. fortunei kikuchii* (Holotype: NSMT Mo. 58959) from Koroen, Hyogo Pref., Japan. SL = 20.7 mm
3. *X. securis* (TMNH-MO002217) from Swan River, WA, Australia. SL = 28.9 mm
4. *X. securis* (Paralectotypes: NMHN) from Australia. SL = 41.8 mm and 40.3 mm
5. *Xenostrobus* sp. (TMNH-MO002496) from Suva Point, Fiji Is. SL = 17.7 mm
6. *X. hepaticus* (Holotype: USNM 18000) from Fiji Is. SL = 33.6 mm
7. *X. inconstans* (WAM846) from Oyster Harbor, Lower King River, WA, Australia. SL = 22.0 mm
8. *X. pulex* (WAM2589) from Woodman point, WA, Australia. SL = 22.5 mm
9. *X. atratus* (TMNH-MO002498) from Koajiro Bay, Kanagawa Pref., Japan. SL = 12.1 mm
10. *X. mangle* (Holotype: ZMC) from Jeram, W. coast of Malaysia. SL = 6.7 mm
11. *X. balani* (Holotype: ZMC) from Ao Nam Bor, Phuket, Thailand. SL = 8.4 mm
12. *L. fortunei fortunei* (TMNH-MO002502) from Nagara River, Gifu Pref., Japan. SL = 26.2 mm
13. *L. fortunei kikuchii* (Juveniles: TMNH-MO001983, 001984) from Hamana Lake, Shizuoka Pref., Japan. SL = 8.0 mm and 6.5 mm
14. *X. securis* (Juveniles: TMNH-MO002218, 002219) from Swan River, WA, Australia. SL = 8.7 mm and 6.8 mm
15. *L. fortunei fortunei* (Juveniles: TMNH-MO002503, 002504) from Nagara River, Gifu Pref., Japan. SL = 7.8 mm and 5.9 mm


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