

Genetic Relationships of Korean Ocenebrine Species (Gastropoda: Prosobranchia: Muricidae)

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Allele frequencies in twenty-two populations from nine Korean muricid species of five genera (Rapaninae and Ocenebrinae) were analyzed genetically using 13 loci from 11 allozyme systems. The clustering patterns of these species were basically consistent with traditional groupings to two subfamilial categories based on shell and radula morphologies. Within six ocenebrine species it was apparent that *Ceratostoma inornata* and *Pteropurpura adunca* were most closely related to each other than to any other species belonging to the genus *Ceratostoma*. These results, along with other anatomical features [morphologies of albumin gland (female), egg capsule], suggest that the generic position of *C. inornata*, previously classified to be congeneric with other western Pacific *Ceratostoma* species, should be reconsidered. Our results show the close relationship of *Nucella freycineti* with other ocenebrine species, rather than with rapanines, which supports a previous suggestion that the genus *Nucella* should be placed with the subfamily Ocenebrinae rather than the subfamily Rapaninae.

The subfamily Ocenebrinae is one of the major rocky-intertidal marine gastropod groups. The subfamily has a worldwide distribution, ranging from temperate to boreal waters. Members of this group are mainly composed of ecologically and environmentally important species: they are mostly voracious predators of marine bivalves (Hancock, 1960; Morgan, 1972; Kent, 1981; Ovens, 1982; Buyanovsky, 1992), and very useful indicators of marine pollution (Crothers, 1978; Gibbs et al., 1987; Stickle et al., 1990).

Morphologically the shell of this group bears 3-5 winged or lamellar-shaped longitudinal varices on the body whorl, thus the number and the architecture of this structure have been used as diagnostic characters to outline the boundaries of its subordinate genera. Nevertheless, irregularities in the shell morphology of some species prevent a comprehensive diagnosis for this group and are sometimes responsible for the uncertainty in the systematic classification.

Six ocenebrine species from three genera (*Pteropurpura*, *Nucella*, and *Ceratostoma*) are common in the littoral zone of the Korean coast (Choe and Park, 1997). The groupings of these species into genera are generally accepted, but systematic position of *Ceratostoma inornata* (Récluz, 1851), commonly known as the oyster driller, has remained unclear. Although this spe-

cies had been mainly regarded as being congeneric with other western Pacific forms (*C. burnetti*, *C. rorifluum*, and *C. fourrieri*) of the genus *Ceratostoma* Herrmannsen, 1846, based almost entirely on shell sculptures (Radwin and D'Attilio, 1976; Okutani and Habe, 1983; Okutani, 1986), the details of shell characters of this species show extreme habitat-specific variations depending on the local populations (Choe and Park, 1997). Moreover, the number and pattern of the longitudinal varices, which have been used for the recognition of the genus, are different from the common forms of other *Ceratostoma* species. Therefore, the systematic classification of this species using shell characters alone is difficult or even impossible.

During the last few decades, the technique of enzyme electrophoresis has been widely used in attempts to quantify the level of genetic differentiation between populations, or else to confirm the genetic relationships between congeneric or intergeneric species in a variety of organisms (Thorpe, 1982). One main focus of this study is to discuss the systematic relationships of Récluz (1851)'s *Inornata* based on genetic relationships with other ocenebrine species using allozyme electrophoresis.

In addition, the systematic position of the genus *Nucella* Röding 1798 is recently controversial. The genus *Nucella* had been regarded as a subgenus or synonym of the genus *Thais* Röding 1798, one of the major genera of the subfamily Rapaninae Gray 1853, based primarily on the shell and operculum morphologies. Recently, however, Kool (1993) proposed a

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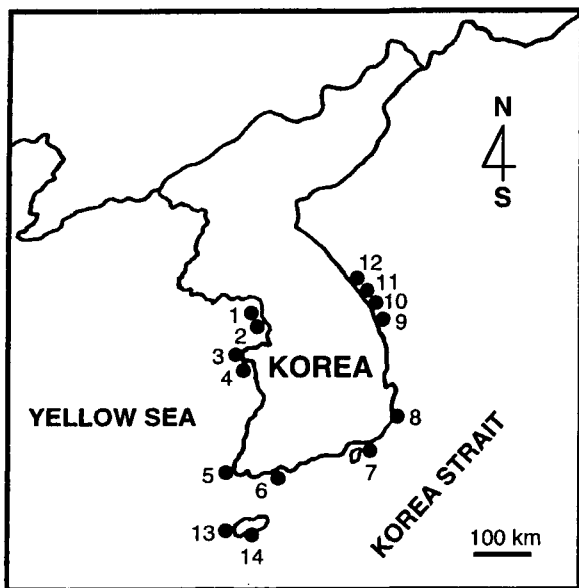


Fig. 1. Locations of 14 sampling sites for 22 populations of 9 muricid species. 1, Yongjongdo Isl.; 2, Chakyakdo Isl.; 3, Taeon; 4, Anmyondo Isl.; 5, Chindo Isl.; 6, Kokeumdo Isl.; 7, Isudo Isl.; 8, Tangsa; 9, Tonghae; 10, Taepo Harbour; 11, Youngkeumjong; 12, Chonjin; 13, Chagwido Isl.; 14, Munsom Isl.

completely different systematic conclusion in that it should be placed in the subfamily Ocenebrinae Cossmann 1903, based on cladistic analyses using comparative anatomical characters as well as external shell and radula morphologies of several selected muricid species. In this study, we also included three rapanine species as reference taxa to appraise on genetic grounds whether or not Kool's opinion is reasonable.

Materials and Methods

A total of 358 specimens were collected from 14 locations, along the coast of Korea (Fig. 1, Table 1),

Table 1. The sample size of 22 populations of 9 Korean muricid species and voucher specimen information (Mollusk Division Catalog Number, University of Michigan Museum of Zoology)

Species	Locality	Sample size	UMMZ Catalog No.
<i>Rapana venosa</i> (Valenciennes, 1846)	Yongjongdo Isl.	23	266237
	Anmyondo Isl.	25	
<i>Thais clavigera</i> (Küster, 1858)	Chakyakdo Isl.	18	266238
	Isudo Isl.	15	
<i>T. bronni</i> (Dunker, 1860)	Munsom Isl.	19	266239
	Anmyondo Isl.	14	
	Kokeumdo Isl.	3	
	Tonghae	14	
<i>Nucella freycineti</i> (Deshayes, 1839)	Youngkeumjong	23	266240
	Chindo Isl.	19	
<i>Cerastostoma inornata</i> (Récluz, 1851)	Taeon	15	266241
	Chonjin	13	
<i>Pteropurpura adunca</i> (Sowerby, 1834)	Tangsa	24	266242
	Taepo Harbour	26	
<i>C. rorifluum</i> (Adams & Reeve, 1848)	Anmyondo Isl.	18	266243
	Taeon	16	
<i>C. burnetti</i> (Adams & Reeve, 1848)	Chonjin	3	266244
	Tangsa	13	
	Taepo Harbour	14	
	Tonghae	18	
<i>C. fourieri</i> (Crosse, 1861)	Munsom Isl.	8	266245
	Chagwido Isl.	17	

and transported and kept alive in running sea water tanks in the laboratory. Foot muscles of the snails were dissected and stored at -70°C until they were processed for electrophoresis. Muscle tissues were homogenized with an equal volume of distilled water, and soluble proteins were obtained by centrifugation at $39,000\text{ g}$ for 60-70 min at 4°C . Horizontal electrophoresis was performed using 13% starch gels (Sigma starch) as described by Yang et al. (1991). The staining procedures followed were those of Selander et al. (1971), Buth (1986) and Pasteur et al. (1988). Thirteen loci from 11 enzymes (Table 1) for which the resolutions were commonly shown for all species of this study were selected for data analysis: malate dehydrogenase (MDH, EC 1.1.1.37), glycerol-3-phosphate hydrogenase (αGPD , EC 1.1.1.8), sorbitol dehydrogenase (SDH, EC 1.1.1.14), aconitate hydratase (ACO, EC 4.2.1.3), leucine aminopeptidase (LAP, EC 3.4.11.-), glutamate oxaloacetate transaminase (GOT, EC 2.6.1.1), acid phosphatase (ACP, EC 3.1.3.2), phosphoglucomutase (PGM, EC 2.7.5.1), mannose phosphate isomerase (MPI, EC 5.3.1.8), 6-phosphogluconate dehydrogenase (6PGD, EC 1.1.1.43), peptidase (Leu-Ala) (PEPT, EC 3.4.-). BIOSYS-1 (Swofford & Selander, 1989) was used to calculate allele frequencies and Nei's genetic identity, I and genetic distance, D (Nei, 1972) between all pairs of populations.

Results

Four loci (*Mdh-2*, *Aco-1*, *Got-1* and *Pgm-1*) lacking consistencies of resolution or activities through various taxa of this study were not included in the genotypic determinations. Allele frequencies at 13 loci for the 22 populations from nine species are presented in Table 2. Genetic frequencies were similar between populations within a species, but differed markedly among species belonging to different genera.

Table 2. Allele frequency in 22 populations of 9 Korean muricid species

Locus	Population										
	VENO	CLAV1	CLAV2	CLAV3	BRON1	BRON2	BRON3	BRON4	FREY	INOR1	INOR2
MDH-1											
(N)	23	25	18	15	19	14	3	14	23	19	15
A	1.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	1.000
C	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.000	.000	.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.870	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.130	.000	.000
MDH-3											
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.000	.395	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	1.000	.000	.000	.000	.000	.000	.000	.000	.000	.237	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	1.000	.368	1.000
αGPD											
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	1.000
SDH											
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
E	.087	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	1.000	1.000	1.000
G	.543	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
H	.130	.000	.000	.000	.053	.179	.000	.143	.000	.000	.000
I	.239	1.000	1.000	1.000	.947	.821	1.000	.857	.000	.000	.000
ACO-2											
A	.000	1.000	1.000	1.000	.000	.000	.000	.000	.000	.000	.000
B	1.000	.000	.000	.000	1.000	1.000	1.000	1.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	1.000	1.000	1.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
LAP-1											
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.974	1.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.026	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	1.000	.000	.000
D	.000	.000	.000	.000	.895	.571	1.000	.000	.000	.000	.000
E	1.000	.000	.111	.000	.105	.357	.000	1.000	.000	.000	.000
F	.000	1.000	.889	1.000	.000	.071	.000	.000	.000	.000	.000
LAP-2											
A	.000	.040	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.920	1.000	.733	1.000	.929	1.000	1.000	.000	.000	.000
C	.000	.040	.000	.267	.000	.071	.000	.000	1.000	.000	.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.289	.100
E	1.000	.000	.000	.000	.000	.000	.000	.000	.000	.711	.900
GOT-2											
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	1.000
B	1.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.000	.000
ACP											
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.026	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.974	1.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.891	.360	.417	.167	.000	.000	.000	.000	.826	.000	.000
E	.109	.480	.444	.767	.079	.071	.000	.357	.174	.000	.000
F	.000	.160	.139	.067	.684	.286	.167	.357	.000	.000	.000
G	.000	.000	.000	.000	.237	.643	.833	.286	.000	.000	.000
PGM-2											
A	.000	.180	.028	.267	.000	.000	.000	.036	.239	.000	.000
B	.000	.020	.111	.133	.053	.036	.000	.000	.609	1.000	1.000
C	.000	.600	.361	.333	.895	.964	1.000	.929	.152	.000	.000
D	.913	.140	.472	.233	.053	.000	.000	.036	.000	.000	.000
E	.065	.060	.028	.000	.000	.000	.000	.000	.000	.000	.000
F	.022	.000	.000	.033	.000	.000	.000	.000	.000	.000	.000

Genetic Relationships of Korean *Ocenebrine* Species

Table 2. Continued

Locus	Population										
	VENO	CLAV1	CLAV2	CLAV3	BRON1	BRON2	BRON3	BRON4	FREY	INOR1	INOR2
MPI											
(N)	23	25	18	15	19	14	3	14	23	19	15
A	.000	.000	.000	.000	.000	.000	.000	.000	.109	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.891	.000	.033
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.156	.033
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.188	.200
E	.000	.000	.000	.000	.000	.000	.000	.036	.000	.031	.000
F	.000	.800	.667	.800	1.000	1.000	1.000	.964	.000	.625	.733
G	1.000	.200	.333	.200	.000	.000	.000	.000	.000	.000	.000
6PGD											
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.816	.833
B	.000	.000	.000	.000	1.000	.929	1.000	1.000	.957	.184	.133
C	1.000	.000	.000	.067	.000	.071	.000	.000	.043	.000	.000
D	.000	1.000	1.000	.933	.000	.000	.000	.000	.000	.000	.033
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
PEPT-1											
A	.022	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.978	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.000	.460	.611	.267	.000	.000	.000	.036	.000	1.000	1.000
E	.000	.020	.000	.133	.263	.000	.000	.071	.065	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.480	.167	.467	.737	1.000	1.000	.786	.739	.000	.000
H	.000	.020	.167	.133	.000	.000	.000	.107	.196	.000	.000
I	.000	.020	.056	.000	.000	.000	.000	.000	.000	.000	.000
Locus	Population										
	INOR3	INOR4	ADUN	RORI1	RORI2	BURN1	BURN2	BURN3	BURN4	FOUR1	FOUR2
MDH-1											
(N)	13	24	26	18	18	3	13	14	18	8	17
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	1.000	.938	1.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.000	.063	.000	.000	.000	.000	.000	.000	.000	1.000	1.000
D	.000	.000	.000	.000	.000	1.000	1.000	1.000	1.000	.000	.000
E	.000	.000	.000	1.000	1.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
MDH-3											
A	.000	.000	.000	1.000	1.000	.000	.000	.000	.000	.000	.000
B	.077	.000	.000	.000	.000	1.000	.231	.714	.111	.000	.000
C	.000	.000	.000	.000	.000	.000	.038	.000	.000	.000	.000
D	.000	.000	.000	.000	.000	.000	.731	.286	.889	.000	.000
E	.923	1.000	1.000	.000	.000	.000	.000	.000	.000	1.000	1.000
αGPD											
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
C	1.000	1.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
SDH											
A	.000	.000	.000	.222	.125	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.778	.875	.000	.000	.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.063	.088
D	.000	.063	.000	.000	.000	.000	.000	.357	.000	.938	.912
E	1.000	.938	1.000	.000	.000	1.000	1.000	.643	1.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
I	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
SDH											
A	.000	.000	.000	.222	.125	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.778	.875	.000	.000	.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.063	.088
D	.000	.063	.000	.000	.000	.000	.000	.357	.000	.938	.912
E	1.000	.938	1.000	.000	.000	1.000	1.000	.643	1.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
I	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000

Table 2. Continued

Locus	Population										
	INOR3	INOR4	ADUN	ROR1	ROR2	BURN1	BURN2	BURN3	BURN4	FOUR1	FOUR2
ACO-2											
(N)	13	24	26	18	18	3	13	14	18	8	17
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	1.000	1.000	1.000	1.000	1.000	1.000	.000	.000
C	1.000	1.000	1.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	1.000
LAP-1											
A	1.000	1.000	1.000	1.000	1.000	1.000	.923	.929	.889	.000	.000
B	.000	.000	.000	.000	.000	.000	.077	.071	.111	1.000	1.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
LAP-2											
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	.382
D	.038	.000	.000	1.000	1.000	1.000	1.000	1.000	1.000	.000	.618
E	.962	1.000	1.000	.000	.000	.000	.000	.000	.000	.000	.000
GOT-2											
A	1.000	1.000	1.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.813	.912
C	.000	.000	.000	1.000	1.000	1.000	1.000	.000	1.000	.188	.088
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
ACP											
A	.423	.063	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.577	.938	1.000	.056	.000	.000	.077	.143	.139	1.000	1.000
C	.000	.000	.000	.944	1.000	1.000	.923	.857	.861	.000	.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
PGM-2											
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	1.000	.979	1.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.000	.021	.000	.028	.000	.000	.000	.000	.000	1.000	1.000
D	.000	.000	.000	.972	1.000	1.000	1.000	1.000	1.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
MPI											
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.021	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.000	.021	.038	.000	.000	.000	.000	.000	.000	.000	.000
D	.423	.417	.481	.056	.031	.867	.231	.321	.111	.125	.147
E	.000	.000	.000	.944	.969	.000	.000	.000	.000	.875	.853
F	.577	.542	.481	.000	.000	.333	.769	.679	.889	.000	.000
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
6PGD											
A	.962	.917	.038	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.042	.462	.000	.000	.000	.000	.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.038	.042	.500	.000	.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PEPT-1											
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.000	.000	.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
D	1.000	1.000	1.000	.000	.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
I	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000

Rapana venosa; VENO (Yongjongo Isl.). *Thais clavigera*; CLAV1 (Anmyondo Isl.), CLAV2 (Chakyakdo Isl.), CLAV3 (Isudo Isl.). *Thais bronni*; BRON1 (Munsom Isl.), BRON2 (Anmyondo Isl.), BRON3 (Kokeumdo Isl.), BRON4 (Tonghae). *Nucella freycineti*; FREY (Youngkeumjong). *Cerastostoma inornata*; INOR1 (Chindo Isl.), INOR2 (Taeon), INOR3 (Chonjin), INOR4 (Tangsa). *Pteropurpura adunca*; ADUN (Taepo Harbour). *Cerastostoma rorifluum*; ROR1 (Anmyondo Isl.), ROR2 (Taeon). *Cerastostoma burnetti*; BURN1 (Chonjin), BURN2 (Tangsa), BURN3 (Taepo Harbour), BURN4 (Tonghae). *Cerastostoma fourieri*; FOUR1 (Munsom Isl.), FOUR2 (Chagwido Isl.).

Table 3. Genetic variation in 22 populations of 9 Korean muricid species

Species (population)	Mean sample size per locus (\pm SD)	Mean no. of alleles per locus (\pm SD)	Percentage of polymorphic loci	Mean heterozygosity (\pm SD)	
				Observed	Expected
<i>Rapana venosa</i> (Yongjongdo Isl.)	23.0 (.0)	1.5 (.3)	23.1	.020 (.009)	.080 (.050)
<i>Thais clavigera</i> (Anmyondo Isl.)	25.0 (.0)	2.0 (.4)	38.5	.126 (.059)	.175 (.072)
(Chakyakdo Isl.)	18.0 (.0)	1.8 (.4)	38.5	.094 (.045)	.194 (.077)
(Isudo Isl.)	15.0 (.0)	1.9 (.4)	46.2	.087 (.055)	.210 (.078)
<i>T. bronni</i> (Munsom Isl.)	19.0 (.0)	1.5 (.2)	38.5	.024 (.013)	.106 (.046)
(Anmyondo Isl.)	14.0 (.0)	1.6 (.2)	38.5	.044 (.029)	.133 (.056)
(Kokeumdo Isl.)	3.0 (.0)	1.1 (.1)	7.7	.026 (.026)	.026 (.026)
(Tonghae)	14.0 (.0)	1.7 (.3)	30.8	.077 (.032)	.118 (.058)
<i>Nucella freycineti</i> (Youngkeumjong)	22.3 (.7)	1.6 (.2)	38.5	.050 (.033)	.138 (.053)
<i>Pteropurpura adunca</i> (Taepo Harbour)	26.0 (.0)	1.3 (.2)	15.4	.053 (.038)	.084 (.057)
<i>Ceratostoma inornata</i> (Chindo Isl.)	18.8 (.2)	1.7 (.3)	30.8	.117 (.052)	.159 (.068)
(Taeon)	15.0 (.0)	1.5 (.3)	23.1	.036 (.021)	.071 (.040)
(Chonjin)	13.0 (.0)	1.4 (.1)	23.1	.083 (.048)	.101 (.052)
(Tangsa)	24.0 (.0)	1.7 (.3)	38.5	.074 (.041)	.085 (.042)
<i>C. rorifluum</i> (Anmyondo Isl.)	18.0 (.0)	1.3 (.1)	23.1	.021 (.017)	.048 (.028)
(Taeon)	16.0 (.0)	1.2 (.1)	7.7	.014 (.010)	.022 (.018)
<i>C. burnetti</i> (Chonjin)	3.0 (.0)	1.1 (.1)	7.7	.051 (.051)	.041 (.041)
(Tangsa)	13.0 (.0)	1.4 (.2)	30.8	.041 (.036)	.084 (.042)
(Taepo Harbour)	14.0 (.0)	1.4 (.1)	38.5	.038 (.038)	.134 (.054)
(Tonghae)	18.0 (.0)	1.3 (.1)	30.8	.013 (.009)	.066 (.029)
<i>C. fournieri</i> (Munsom Isl.)	8.0 (.0)	1.2 (.1)	23.1	.038 (.022)	.053 (.030)
(Chagwido Isl.)	17.0 (.0)	1.3 (.1)	30.8	.054 (.027)	.083 (.042)

*A locus is considered polymorphic if the frequency of the most common allele does not exceed .95

**Unbiased estimate (Nei, 1978)

The amount of common alleles shared between the taxa varies depending on the enzyme systems and the taxa to which certain taxa were compared. Compared to three *Ceratostoma* species (*C. rorifluum*, *C. burnetti* and *C. fournieri*), *C. inornata* and *Pteropurpura adunca* shared five diagnostic loci (*aGpd*, *Aco-2*, *Got-2*, *6Pgd* and *Pept-1*), where the allele frequency distributions do not overlap, out of 13 loci analysed in this study. In particular, *aGpd* and *Aco-2* were monomorphic for all taxa examined, with a fixed homozygote allele depending on the species.

The genetic variability of all populations of the nine species is summarized in Table 3. The level of polymorphism of most populations in this study were moderately high, except for 2 local populations (*T.*

bronni of Kokeumdo and *C. burnetti* of Chonjin) represented respectively by three individuals. A total of 12 loci did not show heterozygotes for these two populations, which was due to the small sampling size.

Nei's genetic distance, *D*, and identity, *I* (Nei, 1972) between all pairs of populations are given in Appendix 1. Fig. 2 shows the UPGMA dendrogram based on genetic distance (*D*).

Discussion

The grouping patterns of nine Korean muricid species were basically consistent with two subfamilial categories based on shell and radula morphologies: subfamilies Rapaninae and Ocenebrinae. Although all pairs

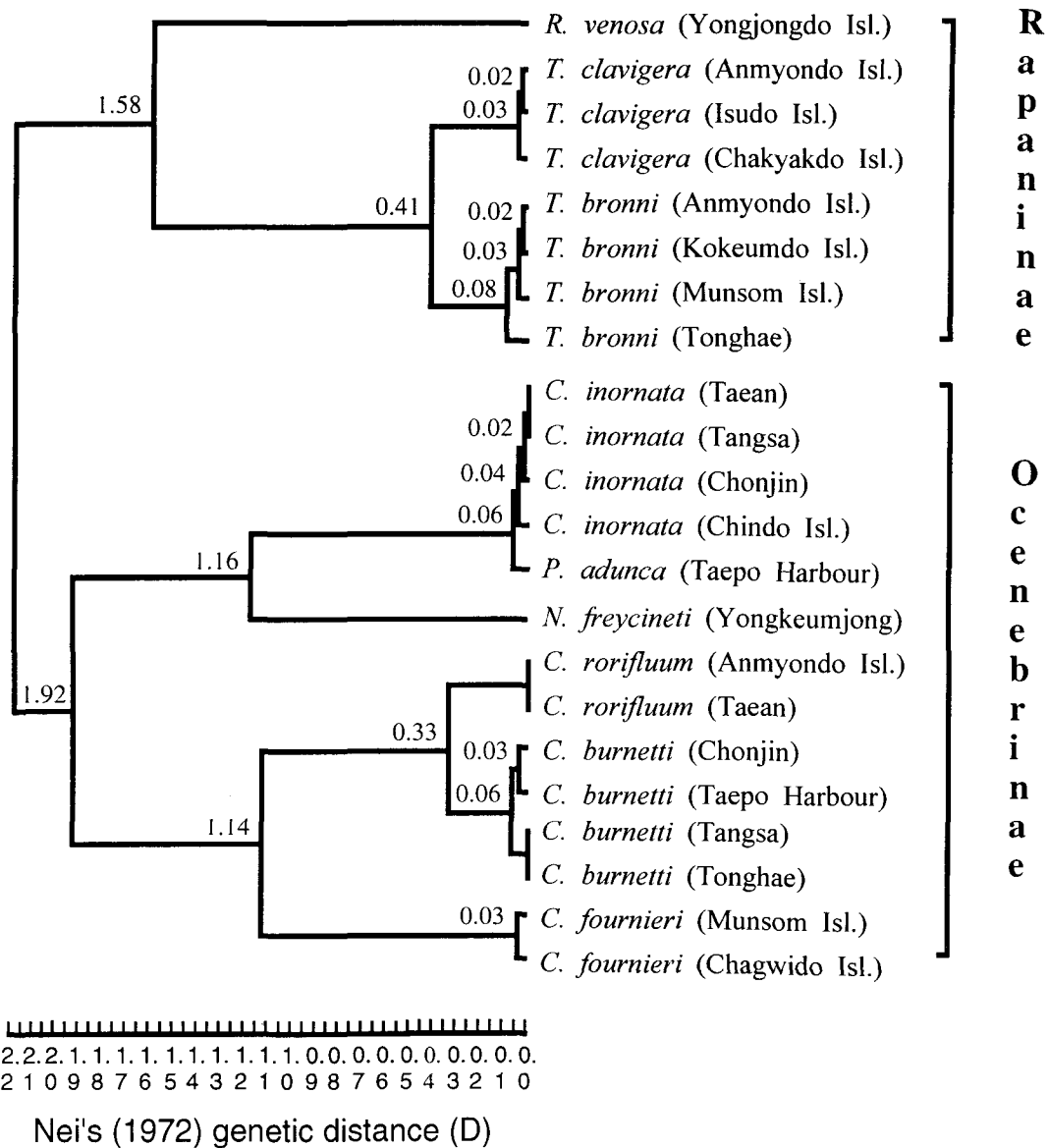


Fig. 2. UPGMA dendrogram for 22 populations of 9 muricid species based on Nei's genetic distance (Nei, 1972).

of conspecific populations grouped closely together, with low genetic distance values less than at D of 0.06 (Fig. 2), high levels of genetic divergence at supra-specific levels were so distinct as to readily distinguish congeneric or intergeneric relationships among taxa. Within ocenebrine species, we could easily recognize two genetically distinct groups: one is composed of *Ceratostoma inornata* + *Pteropurpura adunca* + *Nucella freycineti*; the other of three species of the genus *Ceratostoma* (*C. rorifluum*, *C. burnetti*, *C. fournieri*). It is apparent that *C. inornata* and *Pteropurpura adunca* are more closely related to each other than to any of the other taxa examined in this study. All populations of *C. inornata* clustered together at distance values <0.039, and these in turn grouped with *P. adunca* at D

of 0.064. Out of 13 loci examined, in particular, more than 90% of the alleles of *C. inornata* were coincident with those of *P. adunca*, and the percent diagnostic loci between these two species was 38% (five of 13 loci; *aGpd*, *Aco-2*, *Got-2*, *6Pgd* and *Pept-1*) (Table 2). The close relationship between these species on genetic grounds is incompatible with most previous systematic assignments of *C. inornata* to the genus *Ceratostoma* based mostly on shell morphologies (Radwin and D'Attilio, 1976; Okutani and Habe, 1983; Okutani, 1986). In fact, a great deal of variation in the number of longitudinal varices (usually more than three, in some case up to 12), as well as their structure obscured an accurate recognition for taxonomic placement of this species. As Radwin and D'Attilio mentioned (1976), the

details of shell morphologies in this species are so variable that a simple characterization based merely on shell morphologies may not be possible for a full understanding on the systematic status of this species. Moreover, it is pertinent to note that the genetic affinity between *C. inornata* and *P. adunca* obtained from this allozyme survey is consistent with another comparative anatomical study which concluded that *C. inornata* was more closely related to *P. adunca* than to *Ceratostoma* species in the morphologies of the albumin gland (female) and egg capsule (Park, 1996). Such major differences in both electrophoretic and anatomical features between *C. inornata* and the other three *Ceratostoma* species imply that the generic position of *C. inornata* should be reconsidered. If the genus *Ocenebrellus* Jousseume 1880 is a valid taxonomic rank as a separate genus (Vokes, 1964; Kuroda et al., 1971), or else a subgenus of *Pteropurpura* Jousseum 1880 (Radwin and D'Attilio, 1976), our results here suggest that Récluz's *inornata* is better regarded as congeneric with *P. adunca*, rather than with *Ceratostoma* species. To confirm this taxonomic opinion, however, direct comparisons with other species of the genus *Ocenebra* Gray 1847, another closely related genus, are necessary.

Although the systematic significance of the clustering point at $D > 1$ may be more or less questionable due to the 'saturation' effect (Thorpe, 1982), *Nucella freycineti* can be confidently grouped with other ocenebrine species. In particular, *N. freycineti* is more closely related to the *C. inornata*-*P. adunca* group than are three *Ceratostoma* species. This finding supports Kool's conclusion (1993) that the genus *Nucella* should be placed in the subfamily Ocenebrinae, instead of the subfamily Rapaninae. To clarify the systematic position of this genus within the Ocenebrinae, however, requires a complete comparison with other major genera.

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Appendix I. Nei's genetic distance (above diagonal) and genetic identity (below diagonal) among 22 populations of 9 Korean muricid species based on 13 genetic loci

Population*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1. VENO	****	1.765	1.489	1.742	1.596	1.479	1.707	1.271	1.817	2.406	2.502	2.425	2.402	2.398	1.865	1.865	1.814	1.477	1.642	1.430	2.706	2.575
2. CLAV1	.171	****	.020	.019	.373	.363	.403	.364	1.325	2.069	2.340	2.364	2.399	2.117	4.326	4.426	2.112	2.443	2.067	2.477	1.951	1.950
3. CLAV2	.226	.980	****	.036	.427	.430	.473	.406	1.392	1.949	2.206	2.209	2.241	1.984	3.193	3.200	1.916	2.223	1.897	2.265	2.127	2.110
4. CLAV3	.175	.982	.965	****	.412	.400	.447	.392	1.243	2.109	2.399	2.426	2.471	2.184	3.871	3.896	2.029	2.333	1.983	2.365	1.956	2.048
5. BRON1	.203	.689	.652	.663	****	.031	.033	.084	1.130	2.198	2.559	2.807	2.801	2.473	2.413	2.448	1.624	1.749	1.547	1.758	1.846	1.830
6. BRON2	.228	.696	.650	.670	.970	****	.018	.047	1.067	2.208	2.574	2.817	2.813	2.510	2.446	2.485	1.632	1.761	1.555	1.770	1.760	1.765
7. BRON3	.181	.668	.623	.640	.968	.983	****	.111	1.134	2.284	2.662	2.928	2.916	2.571	2.503	2.543	1.689	1.819	1.612	1.828	1.836	1.819
8. BRON4	.280	.695	.666	.676	.920	.954	.895	****	1.104	2.223	2.601	2.855	2.845	2.502	2.391	2.426	1.630	1.765	1.558	1.776	1.807	1.790
9. FREY	.162	.266	.248	.289	.323	.344	.322	.332	****	1.260	1.131	1.180	1.170	1.051	2.603	2.621	2.475	2.450	2.865	2.460	1.701	2.022
10. INOR1	.090	.126	.142	.121	.111	.110	.102	.108	.284	****	.030	.047	.040	.083	2.151	2.208	1.368	1.322	1.378	1.309	2.105	1.968
11. INOR2	.082	.096	.110	.091	.077	.076	.070	.074	.323	.970	****	.021	.006	.048	2.351	2.418	1.605	1.490	1.595	1.466	1.799	1.750
12. INOR3	.088	.094	.110	.088	.060	.060	.054	.058	.307	.954	.980	****	.013	.073	2.400	2.452	1.545	1.530	1.623	1.534	2.048	2.011
13. INOR4	.091	.091	.106	.084	.061	.060	.054	.058	.310	.961	.994	.987	****	.051	2.424	2.498	1.630	1.585	1.669	1.578	1.739	1.719
14. ADUN	.091	.120	.138	.113	.084	.081	.076	.082	.350	.921	.953	.930	.950	****	2.419	2.496	1.596	1.571	1.666	1.569	1.774	1.752
15. RORI1	.155	.013	.041	.021	.090	.087	.082	.092	.074	.116	.095	.091	.089	.089	****	.001	.331	.326	.304	.346	1.104	.972
16. RORI2	.155	.012	.041	.020	.086	.083	.079	.088	.073	.110	.089	.086	.082	.082	.999	****	.337	.331	.311	.352	1.133	1.000
17. BURN1	.163	.121	.147	.131	.197	.196	.185	.196	.084	.255	.201	.213	.196	.203	.718	.714	****	.064	.029	.096	1.337	1.170
18. BURN2	.228	.087	.108	.097	.174	.172	.162	.171	.086	.267	.225	.217	.205	.208	.722	.718	.938	****	.031	.003	1.283	1.122
19. BURN3	.194	.127	.150	.138	.213	.211	.199	.211	.057	.252	.203	.197	.188	.189	.738	.733	.972	.970	****	.046	1.142	.997
20. BURN4	.239	.084	.104	.094	.172	.170	.161	.169	.085	.270	.231	.216	.206	.208	.708	.704	.909	.997	.955	****	1.268	1.111
21. FOUR1	.067	.142	.119	.141	.158	.172	.159	.164	.183	.122	.165	.129	.176	.170	.332	.322	.263	.277	.319	.281	****	.033
22. FOUR2	.076	.142	.121	.129	.160	.171	.162	.167	.132	.140	.174	.134	.179	.173	.378	.368	.310	.326	.369	.329	.968	****

*Abbreviations of population are same as in Table 2.