Cephalic Lateral-line Systems and Geographical Distribution in the Genus Tribolodon (Cyprinidae)

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Abstract Cephalic lateral-line systems are effective diagnostic characters for each species in the genus *Tribolodon*. When canal pore numbers are considered in relation to the presence or absence of the connection between the preoperculomandibular canal (POM) and the postocular commisure (POC), these are grouped into three patterns, i.e., 1) lower number of pores and absence of the connection between POM and POC, 2) higher number of pores and absence of the connection between POM and POC, and 3) higher number of pores and presence of the connection between POM and POC. Three patterns are also observed concerning differences in the geographical distribution and habitats of the species within its geographical range in Japan, i.e., 1) the entire range of distribution and habitats of *Tribolodon*, 2) restricted to the northern half of the range, and 3) restricted to a limited area, as in Ukekuchi-ugui.

Relationships of each species of *Tribolodon* and these patterns described above seem to indicate that the species-specificity of each species can be categorized by a certain pattern of coordination to the environmental factors, which themselves are, more or less, shared in common by all species of the genus.

Characteristics of the lateral-line system have been used frequently in evaluating the systematic relationship of many fishes. As shown in *Hybopsis* (Reno, 1969), however, a certain aspect of sensory canal systems is plastic and responsive to environmental influences in some groups of the genus *Hybopsis*, although these characters are relatively stable and provide a useful indication of phylogenetic relationships in other groups of *Hybopsis*. Reno (1969) suggested that these ambiguous aspects of lateral-line systems in *Hybopsis* are attributed partly to the doubt about the validity of lumping together all of barbeled minnows examined as materials in his study.

The cephalic lateral-line system is also an effective tool used to identify each species in *Tribolodon* (Nakamura, 1963, 1969; Onodera and Honma, 1976), but this character in *Tribolodon* seems to show the ambiguous aspect as seen in *Hybopsis*. To clarify the ambiguous aspect of the character, cephalic lateral-line systems of four species of *Tribolodon* were analized as the patterns based on combinations of two factors, i.e., lower or higher number of canal pores and the presence or absence of the connection between the preoperculomandibular canal (POM) and the postocular commisure

(POC). As results, three patterns were recognized, and then, these patterns were compared with the patterns observed on combinations of differences in the geographical distribution and those of habitats of species in the genus *Tribolodon*. Finally, a discussion on what is the species-specificity of each species represented by characteristics of lateral-line systems was attempted.

Methods

The lateral-line system was observed as follows. Materials preserved in 10% formalin were washed by water. Then, water was squeezed out from sensory canals by applying soft pressure in all directions over dry cloth which was wrapped around the head of the specimen. The dye was applied on pores along canals by tapping over pores a piece of absorbent cotten soaked in dye, until the dye entered and spread in canals by capillary action. Excess dye was carefully removed from the skin. Suminol cyanine 5R used in this study gave good results with this procedure. Caution was taken not to scratch or damage the thin mucous layer of the skin because this could result in artificially stained areas on the skin. As the skin of Tribolodon is usually lightly

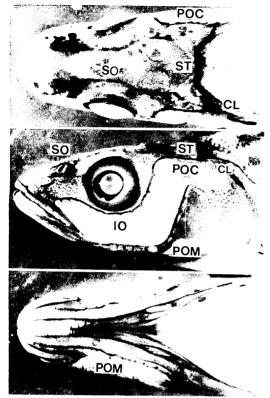


Fig. 1. Lateral-line system of young Ukekuchiugui, *Tribolodon* sp., dyed with Suminol cyanine 5R, 91.6 mm TL, from the River Shinano-gawa, Niigata Prefecture. SO, supraorbital canal; IO, infraorbital canal; POC, postocular commisure; POM, preoperculomandibular canal; ST, supratemporal canal; CL, cephalic lateralis.

pigmented, bleaching is unnecessary.

In young, smaller than 50 to 60 mm in total length (TL), the lateral-line system is still incomplete, forming grooves on the skin as noted by Lekander (1949). Canals are usually completed in the young of 100 mm in TL. In larger specimens beyond 300 mm in TL, canals are not conspicuous, but can be confirmed by the removal of the skin when injection of the dye to canals is successful.

Nomenclature used in describing canals of the cephalic lateral-line system follows that of Reno (1969).

Cephalic lateral-line systems

The cephalic lateral-line system of four species in the genus *Tribolodon* (Nakamura, 1963,

1969) is composed of the supraorbital canal (SO), infraorbital canal (IO), postocular commisure (POC), supratemporal canal (ST), preoperculomandibular canal (POM), and cephalic lateralis (CL) (Figs. 1 and 2).

In "Maruta" or "Jusan-ugui" *T. taczanow-skii*, POM and POC are connected to each other at the temporal region (Fig. 2), but not in "Ugui" *T. hakonensis*, "Ezo-ugui" *T. ezoe*, and "Ukekuchi-ugui" *T.* sp. (see Nakamura, 1963): POM is clearly terminated at the upper end of the posterior margin of the preopercle (Figs. 1 and 2).

Although variable in each species, pore numbers of total IO and POC, SO, and POM are lower in *T. hakonensis* and *T. ezoe*, but higher in *T. taczanowskii* and *T.* sp. (Ukekuchi-ugui) as shown in Tables 1 and 2. In *T. ezoe* and *T. taczanowskii*, the number of pores seems to vary within the range of geographical distribution, higher in the north and lower in the south, but such a geographical cline in pore numbers is not conspicuous in *T. hakonensis*.

Geographical distribution

Numerous records were added in Fig. 3, which included also those reported by Nakamura (1963), Tanaka and Miyazaki (1976), and Onodera and Honma (1976) who identified the species by the cephalic lateral-line system.

In Pacific slope of Japan, 25 specimens of *T. ezoe* were collected from the River Ukedogawa in Fukushima Prefecture by the author in 1966 (Fig. 4). This record extends the range of *T. ezoe* southward to Fukushima Prefecture from the River Kitakami-gawa in Iwate Prefecture (Nakamura, 1963).

A young specimen identified as *T. taczanowskii* from Lake Hojozu-gata in Toyama Prefecture in the 1929 collection of Dr. C. L. Hubbs is reported here for the first time. This record seems to support existence of the established stock of *T. taczanowskii* around the area reported by Tanaka and Miyazaki (1976). Also a young specimen of Ukekuchi-ugui (Fig. 5) was collected from the River Shin-Shinanogawa, the overflow of the River Shinano-gawa, in Niigata Prefecture in 1976, together with *T. hakonensis* and mature adults of the anadromous *Gasterosteus aculeatus* in spawning run,

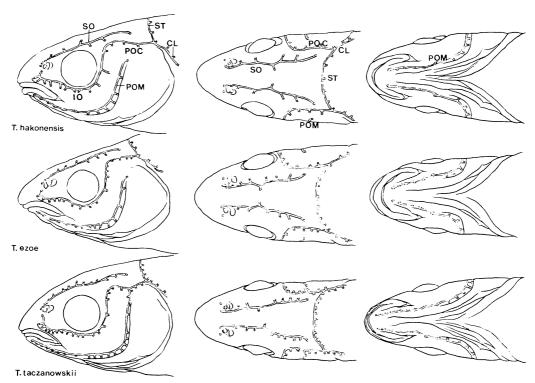


Fig. 2. Diagrammatic drawing of the lateral-line system on the head in *T. hakonensis*, *T. ezoe*, and *T. taczanowskii*. As for abbreviations, see the legend of Fig. 1.

by hook and line with the bait of fly maggot. This information seems to indicate that the food habit of young Ukekuchi-ugui is similar to that of *T. hakonensis* (Nakamura and Mochizuki, 1953).

It is clearly seen that *T. hakonensis* occurs throughout the range of geographical distribution and habitats of *Tribolodon* but *T. ezoe* and *T. taczanowskii* are restricted to the northern half of the range, in spite of the difference of habitat between the two species: the former is restricted to freshwater and the latter to brackishwater (Nakamura, 1963, 1969). Ukekuchi-ugui seems to be restricted to the small area around the River Agano-gawa but is distributed widely throughout the River Agano-gawa (Onodera and Honma, 1976).

Discussion

As shown in Table 3, patterns observed on the canal system in the genus *Tribolodon* seem to be arranged as combinations of two factors, i.e., the lower or higher number of canal

pores and the presence or absence of the connection between POM and POC. However, one of probable four combinations, the combination with the lower number of pores and the presence of the connection between POM and POC, is missing in *Tribolodon*. The two species, *T. hakonensis* and *T. ezoe*, belong to the pattern composed of the lower number of pores and the absence of the connection between POM and POC.

Three patterns were observed on differences in geographical distribution of the species (Fig. 3): 1) the entire range of distribution in *Tribolodon*, as in the case of *T. hakonensis*, 2) restricted to the northern half of the range, as in the case of *T. ezoe* and *T. taczanowskii*, and 3) restricted to a limited area, as in the case of *T.* sp. (Ukekuchi-ugui). Sorted in the manner described above, the pattern restricted to the southern half of the range is missing in *Tribolodon* from Japan. The two species, *T. ezoe* and *T. taczanowskii*, belong to the same pattern. Moreover, three patterns are

Table 1. Geographical variation of pore numbers of the infraorbital canal (IO), postocular commisure (POC), and supraorbital canal (SO) in four species of *Tribolodon*. Six localities in the River Aganogawa in *T. hakonensis* range from coastal water (1) to the upper part of drainage (6): (1) Niigata City; (2) Tsugawa Town; (3) Nishiaizu Town; (4) Aizubanke Town; (5) Mishima Town; (6) Tadami Town.

		Total of IO and POC									SO																		
•	15	16	17	18	19	20	21	22	23	24	25	26	27	7 2	8 2	29	8	9	10	11	1	12	13	14	15	16	17	18	19
Tribolodon hakonensis																													
R. Iwaki-gawa		1	1	1														2	: 1										
R. Mogami-gawa		1	4		1														8										
R. Agano-gawa (1)			7			1													10										
(2)	10			7	2	2													20			1							
(3)		3		1													1		4										
(4)			10		4												1		15										
(5)			29		3														36			2	2						
(6)	1	2	4	1														2											
R. Ukedo-gawa	1		2																3										
R. Natsui-gawa		1	1	•														1											
R. Edo-gawa	1		4	3													,	1											
L. Ashino-ko	4	13	6	3		1											6	12	2 9	2	2								
Tribolodon ezoe																													
R. Ishikari-gawa					2	5	1												4	. 5	5								
R. Kawauchi-gawa						1	1	4	1	1									1		5	2							
R. Kitakami-gawa							1	1														2							
R. Agano-gawa				1	1	2	1		1											1	l	3	1						
R. Ukedo-gawa			1	1	1														3	,									
Tribolodon taczanowsi	kii																												
R. Iwaki-gawa											1	2			1									1		1	2		
R. Kitakami-gawa											1	1			1									1	1		_		
R. Abukuma-gawa											1	1													1			1	
R. Natsui-gawa												1	1	ı											1		1		
R. Edo-gawa							1	1	5	3	3	•	,	•		1							6	3			2		
-																													
Tribolodon sp. (Ukekuchi-ugui)																													
R. Agano-gawa											1	1			1											1	1		1
R. Shinano-gawa									1																1				

also recognized by differences of habitats of the species as follows, 1) all range of habitats in *Tribolodon*, from coastal water to upper part of river, in the case of *T. hakonensis*, 2) restricted to river in the case of *T. ezoe* and *T.* sp. (Ukekuchi-ugui), and 3) restricted to brackishwater in the case of *T. taczanowskii*. The pattern restricted to coastal water is missing here, and the two species, *T. ezoe* and *T.* sp. (Ukekuchi-ugui), belong to the same pattern.

When spaces occupied by each species are

schematized in altitude and latitude, with reference to patterns recognized by differences in the geographical distribution and habitats in *Tribolodon* (Fig. 6), the spaces occupied by three species, *T. ezoe*, *T. taczanowskii*, and *T.* sp. (Ukekuchi-ugui), are included within that of *T. hakonensis*. Any pattern observed in these three species may be categorized by a certain pattern of environmental factors shared almost always by *T. hakonensis*. In contrast, *T. hakonensis* has no pattern space of its own comparable with those in other

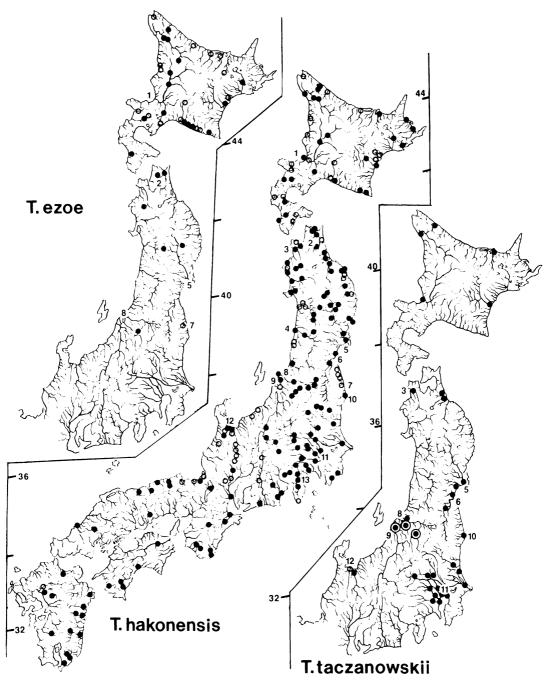


Fig. 3. Geographical distribution of four species of the genus *Tribolodon* in Japan. ○, records added in this paper; ●, records by Nakamura (1963), Onodera and Honma (1976), and Tanaka and Miyazaki (1976); ●, localities of Ukekuchi-ugui, *T.* sp. (see Nakamura, 1963). 1, River Ishi-kari-gawa; 2, R. Kawauchi-gawa; 3, R. Iwaki-gawa; 4, R. Mogami-gawa; 5, R. Kitakami-gawa; 6, R. Abukuma-gawa; 7, R. Ukedo-gawa; 8, R. Agano-gawa; 9, R. Shinano-gawa; 10, R. Natsui-gawa; 11, R. Edo-gawa; 12, Lake Hojozu-gata; 13, L. Ashino-ko.

Table. 2. Geographical variation of pore numbers of the preoperculomandibular canal (POM) and supratemporal canal (ST) in *Tribolodon* from Japan. As for six localities in the River Aganogawa in *T. hakonensis*, see Table 1.

	POM											ST																
	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	3	4	5	6	7	8	9	10	11	12	13
Tribolodon hakonensis																												
R. Iwaki-gawa			1	2																3								
R. Mogami-gawa			5	2	1														1	5	1	1						
R. Agano-gawa(1)		5	13	6	1	3	1													18	3	5						
(2)		6	25		3													1		35	2	9			1			
(3)		3	7	2																8	4							
(4)		9	20																	28	2	6						
(5)	4	15	40	15	2														1	50	12	9		1	1		1	
(6)		1	4	3																4	3							
R. Ukedo-gawa			2	1																2	1							
R. Natsui-gawa		1		1																2								
R. Edo-gawa	2		8																1	8	1							
L. Ashino-ko		7	11	8	1	1	1													24	2		1					
Tribolodon ezoe																												
R. Ishikari-gawa			5	3	1															1		:	8					
R. Kawauchi-gawa			1	2	2	3	1																4 3	2				
R. Kitakami-gawa				1	1																		1	. 1				
R. Agano-gawa				4	2															1		:	2	2			1	
R. Ukedo-gawa		1	1	1																1	2							
Tribolodon taczanowskii																												
R. Iwaki-gawa										1	1		1			1							1		1	. 2	,	
R. Kitakami-gawa										•	•		1			•							•		•]		
R. Abukuma-gawa																	1]		
R. Natsui-gawa										1		1					•							1		1		
R. Edo-gawa									3		5	4	1										1 2					
									Ī	-	-	·	_											_		_		
Tribolodon sp. (Ukekuchi-ugui)																												
R. Agano-gawa										1	1			1											1	. 2	2	
R. Shinano-gawa											1																	1

species, and seems to coordinate itself to any pattern in other species by differentiating itself into local stocks, a sea-run form, and a freshwater form (Nakamura, 1963, 1969; Tanaka and Miyazaki, 1976; Onodera and Honma, 1976).

The sea-run form of *T. hakonensis* is similar to *T. taczanowskii* but differs from the freshwater form of *T. hakonensis* in its annual growth pattern (Tanaka and Miyazaki, 1976), and the salinity tolerance of freshwater form of *T. hakonensis* is lower than that of *T. taczanowskii* (see Nakamura and Mochizuki, 1953). This evidence seems to support the

heterogeneous constitution of T. hakonensis by its local stocks, and some of T. hakonensis may represent or may have represented such missing pattern as restricted to the southern half of the range or to coastal water.

It seems to be possible that the presumed species-specificity of each species for existence can be categorized by the coordination to a certain pattern of environmental factors in actual time and space throughout its life cycle as seen in Fig. 6, and almost all of these factors themselves may be, more or less, shared in common by the species and local stocks of all. Unless what is species-specificity of

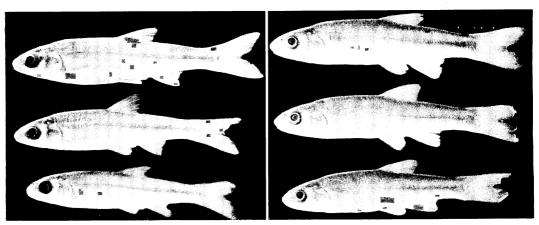


Fig. 4. Young of *T. hakonensis* (left), 74.7, 67.7, and 64.1 mm in TL, and *T. ezoe* (right), 76.6, 74.3, and 68.4 mm in TL. Specimens of both species were collected in the River Ukedo-gawa, Fukushima Prefecture.

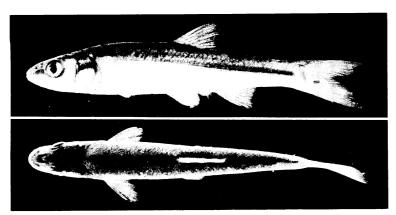


Fig. 5. Young of Ukekuchi-ugui, *Tribolodon* sp. (see Nakamura, 1963), 91.6 mm in TL from the River Shinano-gawa, Niigata Prefecture.

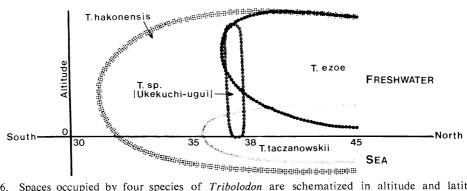


Fig. 6. Spaces occupied by four species of *Tribolodon* are schematized in altitude and latitude, based on the geographical distribution of the species in Fig. 3.

Table 3. Cephalic lateral-line systems of four species of *Tribolodon* are sorted by two factors: the lower or higher number of pores and the presence or absence of the connection between POM and POC. Four species in the genus are included in three combinations of two factors, but no species belongs to the combination of the lower number of pores and the presence of the connection between POM and POC.

	Lower number of pores	Higher number of pores
Presence of the connection	no species	T. taczanowskii
Absence of the connection	T. hakonensis T. ezoe	T. sp. (Ukekuchi-ugui)

each species for its existence is known, the comparison among species for their relationships and their processes of speciation by differences of environmental factors which may be shared in common by species will not be possible.

On the other hand, to clarify the problem on wide-spread species widely overlapping each other (as in Tribolodon), it is important to compare morphological characteristics of Japanese specimens with those of specimens from the Asian Continent (Nakamura, 1969; Onodera and Honma, 1976). Presumably, similarities or differences in morphological characteristics between the species of Japan and the Asian Continent may give information about how the species here and there should be diagnosed. However, the results could not give any useful explanation about the mechanism of isolation of species in Tribolodon, because the really important but still unknown aspect of species-specificity in nature, i.e., a certain mode of life maintained by the mechanism of isolation in each species, may be the reflect of relative relationships of species and detectable in the environmental characters shared in common by all species in the genus.

The presumed aspect of species-specificity in *Tribolodon* seems to compare to the conventional aspect of species-specificity on which the concept of group-selection by Wynne-

Edwards (1965) seems to stand. It seems to the author that individuals compete for conventional prizes which assure the survival of their group as a whole and such competition results self-regulating systems in natural populations, which function voluntarily by the intrinsic quality of species shared in common by individuals of all in the species in nature, not enforced passively by interactions with other species.

The validity of the conventional aspect of species-specificity seems to be supported by Lorenz (1965), i.e., he emphasized the primary importance of unknown skill, "the art", of excellent keepers who maintain the experimental animals to be natural and speciesspecific in his behavioral experiment, "the deprivation experiment", in the laboratory. It seems to the author that the skill described above concerns a certain procedure of maintenance of the factors, which are, more or less, already known for the survival of experimental animals, and that the skill is conventional but essential to keep the experimental animals to be natural and speciesspecific under captivity.

The conventional aspect of species-specificity, importance of which is emphasized in ecology (Wynne-Edwards, 1965) and ethology (Lorenz, 1965), as described above, seems to explain the ambiguous aspects of characteristics in the cephalic lateral-line system in Tribolodon. Because the species-specificity of each species represented by these characters is presumed to be conventional, not directly related to the environmental factors assuring the survival of individuals in nature: the genuine state of nature is presumed to meet the needs to assure the simple survival of individuals of the species in Tribolodon. The ambiguous aspects of characteristics, e.g., the cephalic lateral-line system, seem to be imperative when the species-specificity of species has a conventional aspect discussed above.

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Literature cited

- Lekander, B. 1949. The sensory line system and canal bones in the head of some Ostariophysi. Acta Zool., 30 (1): 1~131, 67 figs.
- Lorenz, K. 1965. Evolution and modification of behavior. The University of Chicago Press, Chicago, 121 pp.
- Nakamura, M. 1963. Keys to the freshwater fishes of Japan fully illustrated in colors. Hokuryukan, Tokyo, 260 pp., 175 figs. In Japanese.
- Nakamura, M. 1969. Cyprinid fishes of Japan. Special Publications of the Research Institute for Natural Resources, No. 4, Tokyo, 455 pp., 149 pls. In Japanese.
- Nakamura, M. and Y. Mochizuki. 1953. On the differentiation of freshwater and brackishwater forms of Japanese cyprinid fish referred to genus *Tribolodon*. Misc. Rep. Res. Inst. nat. Resources, Tokyo, (32): 11~22, figs. 1~5, pls. 2~3. In Japanese.
- Onodera, T. and Y. Honma. 1976. Racial differentiation of the Japanese dace (genus *Leuciscus*) in the north-eastern Japan. Proc. Jap. Soc.

- Syst. Zool., 12: 65~77, figs. 1~2. In Japanese. Reno, H. W. 1969. Cephalic lateral-line systems of the cyprinid genus *Hybopsis*. Copeia, 1969 (4): 736~773, figs. 1~32.
- Tanaka, S. and S. Miyazaki. 1976. On the annual growth of Ugui, *Tribolodon hakonensis* and Maruta, *T. taczanowskii* in Zinzu river, Toyama Prefecture, central Japan. Physiol. Ecol. Japan, 17 (1/2): 401~406, figs. 1~3. In Japanese.
- Wynne-Edwards, V. C. 1965. Self-regulating systems in populations of animals. Science, 147: 1543~1548.
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ウケイ属の頭部側線感覚管と地理的分布について 倉若 欣司

ウグイ属4種の頭部側線感覚管は、種の同定に有効な特徴を示すばかりでなく、頭部感覚管孔数の多寡および前鳃蓋下顎管(preoperculomandibular canal: POM)と眼下管眼後部 (postocular commisure: POC)の接続の有無との組合わせによって 3 つのパターンに類別される。地理的分布・棲息域についても salinity と altitude との組合わせから 3 つのパターンに類別される。これらは頭部側線感覚管のパターンと極めて類似していることから、ウグイ属の種の独自性は、ウグイ属のすべてがほぼ共有し得る環境条件によって構成されるパターンの独自性、と理解すべきことが考察された。

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