Japanese Journal of Ichthyology
Vol. 26, No. 3 1979

魚類学雑誌
26巻3号 1979年

Differentiation and Zoogeography of Two Species of the Cyprinid Genus *Puntioplites*

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(Received June 22, 1979)

Abstract Pronounced geographic variation in meristic characters is found in two Southeast Asian cyprinid species, *Puntioplites proctozysron* and *Puntioplites waandersi*. When local populations of each species are combined with other conspecific populations, these two forms overlap in all meristic and morphological characters examined. The only phenotypically detectable difference between the two is the nature of the principal simple anal ray; the ray is serrated in *P. proctozysron* and entire in *P. waandersi*. This difference is shown not to represent individual or sexual dimorphism within a species. *P. proctozysron* and *P. waandersi* are considered to be distinct species directly differentiated from a common ancestor belonging to the same genus, *Puntioplites*, which is distinct from the genus *Puntius*.

Zoogeographical examination suggests the occurrence of *Puntioplites waandersi* throughout the continental and insular sections of Southeast Asia in the lower Tertiary or earlier, when these two sections constituted a continuous landmass, and subsequent isolation of continental populations in the middle Mekong basin. The present geographic range of *Puntioplites proctozysron*, being restricted to the continental section, seems to indicate the derivation of this species in continental Southeast Asia from *P. waandersi* or a *waandersi*-like ancestral form. Some aspects of the geohistory of the Indochinese Peninsula are discussed from a zoogeographical viewpoint.

Bleeker (1865), Weber and de Beaufort (1916) and Smith (1929) noticed the uniqueness of *Puntius proctozysron* (Bleeker) among Southeast Asian species of the Cyprinidae in possessing a strongly ossified and serrated principal (=last) simple ray of the anal fin. The last-named author erected the genus *Puntioplites* for this species recognizing this feature of the anal fin as the major diagnostic character of the genus. The only other cyprinids having such a serrated simple anal ray are the temperate Eurasian *Cyprinus* Linnaeus, *Carassius* Linnaeus, and their allies. Currently these temperate Eurasian species are classified in the subfamily Cyprininae and separated from the Barbinae to which the tropical Asian genus *Puntius* is referred.

Among the numerous Southeast Asian members of the Cyprinidae there are six species in which the principal simple anal ray is strongly ossified, though not serrated, as in *Puntioplites*. Two of these six species are given the unique generic status *Scaphognathops* Smith, and the other four have been referred to *Puntius* Hamilton or *Barbus* Cuvier.

The two species of *Scaphognathops*, i.e., *S. stejnegeri* (Smith) and *S. bandanensis* Boonyaratpalin et Srirungroj (syn. *S. mekongensis* Taki, 1974a), are confined in the Mekong basin. Taki (1974b) suggested their rather distant relationship with *Puntius*.

The four species of *Puntius* with an ossified and entire principal simple anal ray occur in continental and/or insular Southeast Asia. They are *Puntius bulu* (Bleeker), *P. lawak* (Bleeker), *P. waandersi* (Bleeker) and *P. nini* Weber and de Beaufort. All of them closely resemble *Puntioplites proctozysron* in external features, particularly in having a high body, no barbels, a dorsal fin with an elongated, greatly ossified, serrated principal simple ray. Among others, *Puntius waandersi* is closely similar to *Puntioplites proctozysron* in appearance, and hence some workers recognized no specific separation between these two forms. Thus Volz (1904, cited from Weber and de Beaufort, 1916) identified his specimen with an entire principal simple anal ray as *Barbus proctozysron* (=*Puntius proctozysron*), and Taki (1974b) suggested the possibility that the

Laotian *Puntius waandersi* might be an individual or sexual variant of *Puntioplites proctozysron*.

If *Puntioplites proctozysron* and *Puntius waandersi* are very closely related or even identical specifically and therefore to be united in the same genus or species, the question then arises of whether they are phyletically distinct from *Puntius* or are aberrant forms within the limits of the genus *Puntius*.

The purpose of this study is to examine relationships between *Puntioplites proctozysron* and *Puntius waandersi* from morphological and zoogeographical viewpoints. For the sake of convenience, our arguments will start with the initial hypothesis (and also our final conclusion) that *Puntioplites proctozysron* and *Puntius waandersi* are distinct species but represent the same genus, *Puntioplites*. *Puntius bulu* and other hard-anal-rayed species of *Puntius* are also referred to *Puntioplites*. The term Southeast Asia used in this paper refers to the area comprising the Indochinese Peninsula, the Malay Peninsula, and the Greater Sunda Islands. According to physiographical conditions, the Thai-Lao Mekong drainage upward from the Khong Falls at the Lao-Cambodian border is called the middle Mekong, and the Cambodian-Vietnamese Mekong drainage below the Khong Falls the lower Mekong.

Material examined

Specimens dealt with in this study are all from the fish collection in the Institute for Breeding Research, Tokyo University of Agriculture (IBRP). The length of specimens given in the list below is the standard length.

Puntioplites proctozysron. Middle Mekong system: 9 specimens, 56.5～166.5 mm, Mekong River (R.) at Vientiane, 24 Nov. 1969, IBRP 3196; 5, 32.5～50.0 mm, Mekong R. at Sai Fong, 11 June 1970, IBRP 4067; 2, 30.0 and 47.5 mm, Mekong R. at Sithan Tay, 6 Aug. 1970, IBRP 4558-1; 4, 57.0～80.5 mm, Mekong R. near Tha Bo, 14 Sep. 1970, IBRP 4696-1; 2, 61.0 and 115.0 mm, Mekong R. near Tha Bo, 6 Nov. 1970, IBRP 4959-1; 3, 71.5～76.5 mm, Nam Kem Stream at Tha Ngon, 12 Sep. 1970, IBRP 4652; 1, 86.5 mm, Nam Ngum R. at Nam Ngum dam site, 14 Oct. 1970, IBRP 5624; 2, 51.0 and 56.5 mm, Mekong R. at Hatsalao, 25 May 1970, IBRP 4007; 1, 73.0 mm, Mekong R. at Hatsalao, 3 Apr. 1971, IBRP 5599; 3, 118.0～123.5 mm, Mekong R. at Bang Lieng, 26 May 1970, IBRP 4027. Lower Mekong system: 1, 82.0 mm, Bassac R. at Chau Doc, 19 Mar. 1974, IBRP 6183; 1, 53.5 mm, canal near Chau Doc, 14 Oct. 1974, IBRP 6524; 2, 58.0 and 59.0 mm, Bassac R. at Chau Doc, 14 Oct. 1974, IBRP 6461; 1, 78.0 mm, Bassac R. below Chau Doc, 19 Mar. 1974, IBRP 6200; 1, 91.5 mm, Bassac R. at Long Xuyen, 19 Mar. 1974, IBRP 6162; 2, 46.0 and 57.0 mm, Bassac R. at Can Tho, 1 Mar. 1974, IBRP 6085; 2, 92.0 and 96.0 mm, Bassac R. at Can Tho, 7 Mar. 1974, IBRP 6132; 1, 33.0 mm, Bassac R. at Can Tho, 12 Oct. 1974, IBRP 6541. Menam Chao Phya system: 5, 82.5～100.5 mm, Kreing Klai Canal near Nakorn Sawan, 11 Dec. 1969, IBRP 3281.

Puntioplites waandersi. Middle Mekong system: 1, 56.0 mm, Nam Ngum R. at Tha Ngon, 3 Oct. 1966, IBRP 3078; 3, 110.0～119.0 mm, Nam Khon R. at Tha Ngon, 17 July 1970, IBRP 4377; 24, 36.5～58.5 mm, Mekong R. at Sithan Tay, 6 Aug. 1970, IBRP 4558-2; 1, 56.5 mm, Mekong R. near Tha Bo, 14 Sep. 1970, IBRP 4696-2; 3, 55.5～120.5 mm, Mekong R. near Tha Bo, 6 Nov. 1970, IBRP 4959-2. Borneo: 1, Kapuas R. at Sintang, 11 Apr. 1975, IBRP 6617; 1, 40.5 mm, Lubuk Kechil R. near Sanggau, 16 Apr. 1975, IBRP 6752-2; 5, 117.5～134.5 mm, fish market at Sintang, 11 June 1978, IBRP 7224.

Puntioplites bulu. Borneo: 3, 82.5～124.5 mm, Kapuas R. at Sintang, 11 Apr. 1975, IBRP 6616.

Puntioplites lawak? Borneo: 10, 19.0～24.5 mm, Kapuas R. at Sintang, 13 Apr. 1975, IBRP 6860; 3, 29.5～38.5 mm, Lubuk Kechil R. near Sanggau, 16 Apr. 1975, IBRP 6752-1.

Puntius leiacanthus. Middle Mekong system: 1, 63.5 mm, Mekong R. at Ban Kouai Deng, 20 Oct. 1966, IBRP 3211; 1, 62.0 mm, Nam Ngum R. at Tha Ngon, 7 Jan. 1971, IBRP 5029. Lower Mekong system: 6, 35.5～65.0 mm, Cai Bang Canal at Long Dinh, near Sadec, 15 Sep. 1974, IBRP 6353.

Puntius schwanefeldi. Middle Mekong system: 4, 35.5～92.0 mm, Mekong R. at Vientiane, 24 Nov. 1969, IBRP 3187. Borneo: 1,

107.0 mm, Kapuas R. at Sanggau, 15 Apr. 1975, IBRP 6705.

Methods

Lateral line scale counts indicate the total number of perforated scales including those on the basal part of the caudal fin. Scale counts for body-circumference series express the total number above the lateral line for a series containing the posteriormost, free-margined, predorsal scale (upper circumferential scales) and below the lateral line for a series including the posteriormost, free-margined, preanal scale (lower circumferential scale), and circumpeduncular scales. Numbers of predorsal bones and vertebrae were determined from both transparent specimens and radiographs. Terminology for the pharyngeal bones and their teeth follows Taki et al. (1978).

Measurements were made on large undamaged specimens, using dial calipers, read to the nearest 0.5 mm. Caudal fin length is defined as the straight distance from the base of the middle caudal ray to the tip of the upper lobe.

Specific status

Morphological variation in *Puntioplites proctozysron*. *Puntioplites proctozysron* (Fig. 1) is confined to continential Southeast Asia. It has been recorded from the Chao Phya basin (Bleeker, 1865; von Martens, 1876, cited from Weber and de Beaufort, 1916; Sauvage, 1881; Hora, 1923; Smith, 1927, 1929, 1945; Fowler, 1934a, b, 1935, 1937), the Mekong basin (Sauvage, 1881; Chevey, 1932a, b; Smith, 1929; Fowler, 1934a, 1937; Chevey and le Poulain, 1940; Taki, 1968, 1974b, 1975; Chen and Hwang, 1977), and the Malay Peninsula (Fowler, 1939; Smith, 1945; Tweedie, 1952; Menon, 1954).

Geographic variation was seen in all scale counts examined in this study except for lateral line scales, with a general trend toward increase from the middle Mekong to the lower Mekong and then to the Chao Phya (Table 1). This trend is most clear in circumpeduncular scale counts. In scale counts for transverse series below the lateral line to the pelvic insertion, there is a distinct gap between the middle Mekong on the one hand and the lower Mekong and Chao Phya on the other hand. Thus the lower Mekong specimens

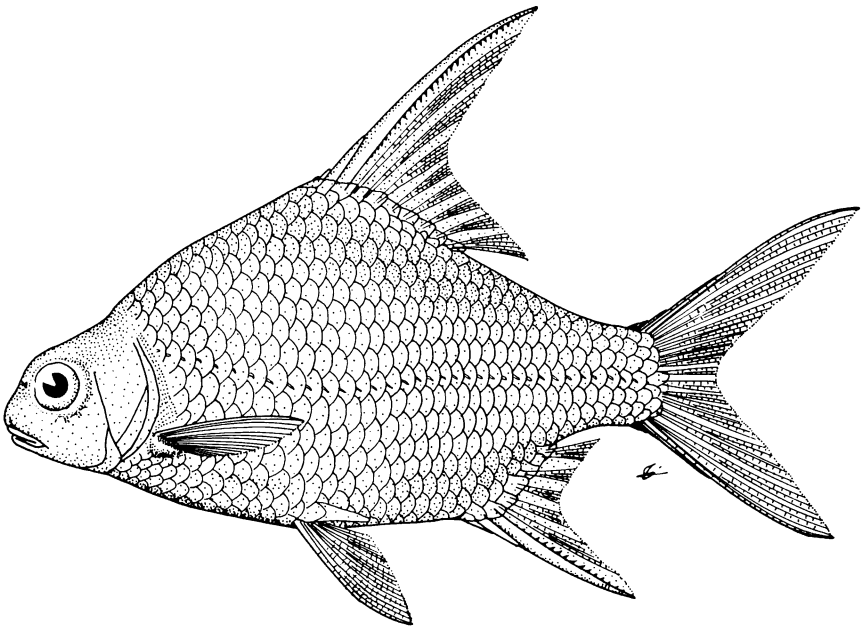

Fig. 1. *Puntioplites proctozysron* from the middle Mekong, 118.0 mm SL, IBRP 4027.

Table 1. Frequency distribution by locality of selected counts of *Puntioplites proctozysron* and *P. waandersi*.

Species/locality	Total lateral line scales								Upper circumferential scales				
	33	34	35	36	37	38	x̄	N	15	17	19	x̄	N
P. proctozysron													
Middle Mekong	1	3	12	8			35.1	24	9	19		16.4	28
Lower Mekong		2	6	1			34.9	9		6	1	17.3	7
Chao Phya			3	1			35.3	4		1	3	18.5	4
P. waandersi													
Middle Mekong		2	7	11	1		35.5	21		26	1	17.1	27
Borneo					5	2	37.3	7		7		17.0	7

	Lower circumferential scales					Circumpeduncular scales				
	13	15	17	x̄	N	16	18	20	x̄	N
P. proctozysron										
Middle Mekong	16	14		13.9	30	28			16.0	28
Lower Mekong		8	2	15.4	10		8		18.0	8
Chao Phya		2	3	16.2	5		1	3	19.5	4
P. waandersi										
Middle Mekong		18	11	15.8	29		4	25	19.7	29
Borneo		1	6	16.7				7	20.0	7

	Scales below lateral line to pelvic insertion						Predorsal scales					
	5	5.5	6	6.5	x̄	N	12	13	14	15	x̄	N
P. proctozysron												
Middle Mekong		22			5.5	22	2	18	10	1	13.3	31
Lower Mekong				9	6.5	9		3	6	1	13.8	10
Chao Phya				5	6.5	5			3	2	14.4	5
P. waandersi												
Middle Mekong	1	22		3	5.6	26	2	10	14	2	13.6	28
Borneo		3		4	6.1	7	5	1	1		12.4	7

	Total pectoral rays					Predorsal bones			
	16	17	18	19	x̄	N	4	5	x̄	N
P. proctozysron										
Middle Mekong	4	8	15	5	17.7	32	29	1	4.0	30
Lower Mekong	2	8	1		16.9	11	11		4.0	11
Chao Pyha		3	2		17.4	5	5		4.0	5
P. waandersi										
Middle Mekong	2	11	14	5	17.7	32		31	5.0	31
Borneo	2	2	3		17.1	7	7		4.0	7

	Total gill rakers													
	25	26	27	28	29	30	31	32	33	34	37	38	x̄	N
P. proctozysron														
Middle Mekong		3	3	4	1								27.3	11
Lower Mekong			2	2	2		1						28.4	7
Chao Phya				1									28.0	1
P. waandersi														
Middle Mekong	3	4	2	1									26.1	10
Borneo					1		1		1	1	1	1	33.7	6

are, on the whole, closer to the Chao Phya specimens than to the middle Mekong samples. Counts for lateral line scales, pectoral rays and gill-rakers also show considerable variations, but none are associated with localities (Table 1). Other counts are completely or nearly invariable (N=48): dorsal rays, iv, 8; anal rays, iii, 5; total pelvic rays, 10; principal caudal rays, 19; vertebrae, 34, rarely 33 (N=3) or 35 (N=1); predorsal bones 4, rarely 5 (N=1).

Specimens from different localities show almost complete overlap in all proportional measurements except for the length of the caudal fin (Table 2).

The snout is devoid of barbels and shows a well-developed lateral fold on each side (see Taki, 1974a, for the structure of the cyprinid lateral fold). The principal simple anal ray is stout, strongly ossified, and serrated (Fig. 3A). The dorsal limb of the pharyngeal bones is elongated, greatly recurved downward and forward at its apical portion (Fig. 4A). Pharyngeal teeth (from 5 specimens) are triserial, 2,3,4-4,3,2.

Morphological variation in *Puntioplites waandersi*. *Puntioplites waandersi* (Fig. 2) has discontinuous geographic ranges, occurring on Sumatra and Borneo on the one hand (Bleeker, 1858-1859, 1863; Günther, 1868; Volz, 1904 cited from Weber and de Beaufort, 1916; Weber and de Beaufort, 1916; Hardenberg, 1936) and in the middle Mekong on the other hand (Taki, 1968, 1974b).

Between middle Mekong and Bornean populations a decided gap is found in counts for predorsal bones and gill-rakers (Table 1). Also, a more or less pronounced difference lies in counts for lateral line scales and transverse scales below the lateral line to the pelvic insertion (Table 1). Other scale counts and pectoral fin-ray counts are also subject to variation, but are not associated with the geographic distribution of the fish. Stable

Table 2. Proportional measurements of *Puntioplites proctozysron* and *P. waandersi*.

Character	*Puntioplites proctozysron*						*Puntioplites waandersi*			
	Middle Mekong N=22 *N=14		Lower Mekong N=10		Chao Phya N=5		Middle Mekong N=7		Borneo N=6	
	Range	x	Range	x̄	Range	x̄	Range	x̄	Range	x̄
Standard length (mm)	56.5~166.5		46.0~96.0		82.5~100.5		55.5~120.5		102.~134.5	
In % of standard length										
Head length	27.1~31.9	29.1	27.0~32.7	30.1	27.5~29.6	28.5	26.8~29.3	28.3	29.0~31.2	30.5
Head depth at occiput	22.8~25.7	24.7	23.4~27.1	25.2	23.4~25.4	24.4	23.8~25.4	24.4	24.5~25.5	24.9
Body depth	41.6~53.2	48.5	42.9~51.2	46.9	46.8~51.7	49.4	41.4~52.2	48.5	47.2~51.3	49.2
Body width	14.2~17.7	15.7	15.5~19.5	17.1	15.8~17.1	16.6	13.5~17.2	15.8	15.6~16.9	16.0
Caudal peduncle length	16.7~18.6	17.9	17.3~19.5	18.2	18.1~20.0	19.0	18.0~19.1	18.4	17.0~19.9	18.3
Caudal peduncle depth	14.2~16.0	15.1	14.0~16.0	15.0	14.7~15.7	15.2	13.5~16.1	15.3	14.5~16.1	15.1
Predorsal length	56.2~62.7	59.2	56.7~61.0	58.6	56.7~60.0	58.9	56.7~63.8	60.2	56.9~60.4	58.6
Preanal length	71.7~76.9	74.2	71.9~77.5	74.5	71.7~75.7	73.0	72.0~78.5	74.5	72.3~74.1	73.5
Prepelvic length	49.6~54.7	51.6	49.4~54.2	50.7	48.2~50.9	49.3	50.4~53.5	51.4	50.2~51.7	51.1
Caudal fin length	41.2~47.2	44.3*	37.1~41.5	39.5	38.8~41.3	39.8	44.5~46.5	45.3	42.4~47.8	44.7
In % of head length										
Snout length	27.5~33.7	30.5	25.7~29.1	27.7	27.0~28.8	27.9	25.0~28.3	26.8	28.5~30.4	29.4
Orbit diameter	33.7~41.1	36.9	34.2~40.0	36.9	35.1~37.5	36.4	37.3~43.2	40.3	35.4~39.6	36.3
Postorbital length	39.5~44.7	42.2	40.0~45.7	42.6	41.6~44.4	42.7	37.5~44.7	41.7	42.2~45.4	43.6
Interorbital width	32.4~43.2	36.8	34.2~40.3	37.4	38.7~41.6	40.1	30.3~38.8	35.1	34.9~38.7	37.0

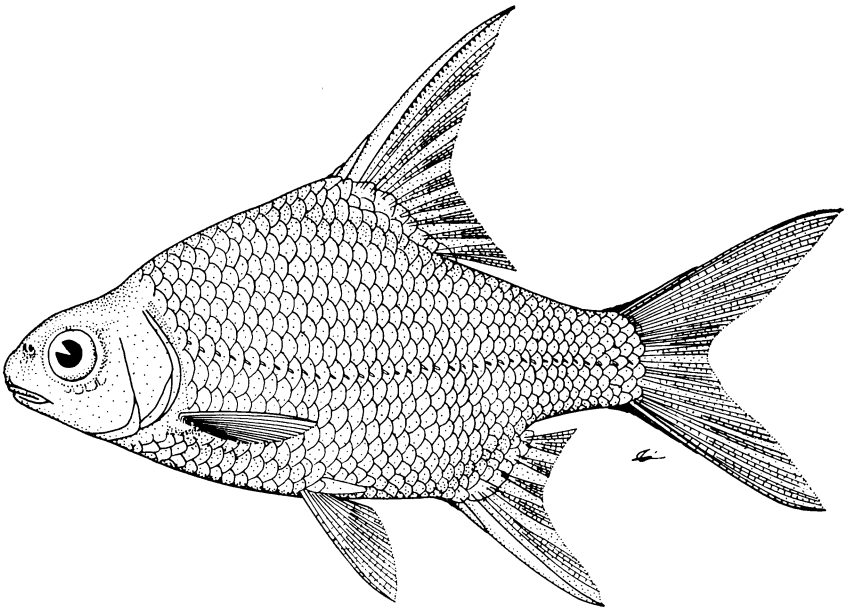

Fig. 2. *Puntioplites waandersi* from the middle Mekong, 120.5 mm SL, IBRP 4959-2.

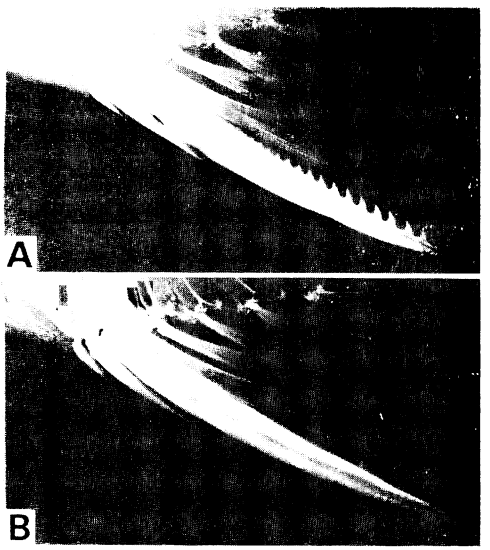

Fig. 3. Principal simple anal ray of *Puntioplites*. A: *P. proctozysron*. B: *P. waandersi*.

counts (N=39) are: dorsal rays, iv, 8; anal rays, iii, 5; total pelvic rays, 10; principal caudal rays, 19; verterbrae, 34, rarely 33 (N=2).

In proportional dimensions, Bornean and middle Mekong specimens overlap in all respects save for the relative length of the snout (Table 2).

The structure of the snout region is similar to that in *Puntioplites proctozysron*. The principal simple anal ray is stout, strongly ossified; its hind edge is entire (Fig. 3B). The shape of the pharyngeal bones and their teeth are the same as in the foregoing species (Fig. 4B). The arrangement of teeth is represented by the formula 2,3,4-4,3,2, with the exception of the presence of a rudimentary lowermost tooth in the left main row of a single specimen.

The difference between middle Mekong and Bornean specimens in predorsal bone and gill-raker counts may indicate a period of isolation. However, middle Mekong and Bornean populations are treated as conspecific in this study because of the overwhelming similarity in all other meristics and in all body proportions other than the length of the snout.

Specific status of *Puntioplites proctozysron* and *Puntioplites waandersi*. The two species under study hold a close resemblance in the contour of the body and in the plain silvery body without markings (Figs. 1, 2). They are further similar in the number of vertebrae and vertical and pelvic fin-rays, as well as in the structure of the snout region and pharyngeal bones (Fig. 4A, B).

Comparison of the morphometric characters

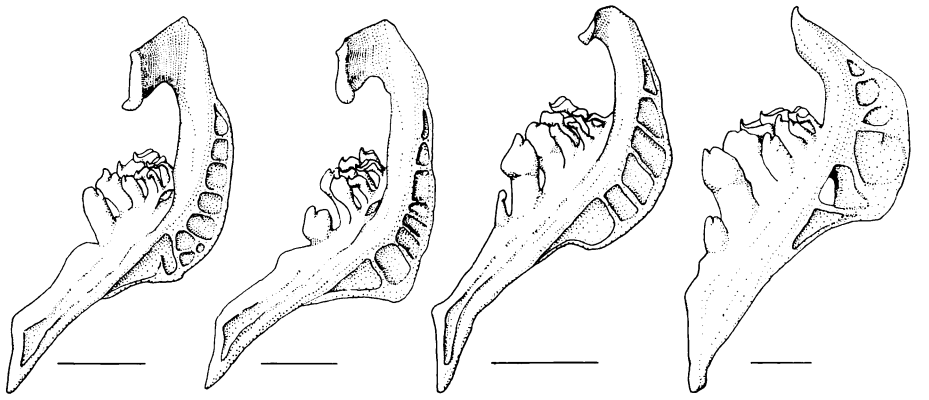

Fig. 4. Left pharyngeal bone and its teeth. A: *Puntioplites proctozysron*. B: *Puntioplites waandersi*. C: *Puntius leiacanthus*. D: *Puntius schwanenfeldi*. Scales indicate 5 mm.

of these two species also shows overlaps between local populations in all respects except for the relative length of the caudal fin (Table 2). Yet agreement in the caudal fin length is seen between *Puntioplites proctozysron* from middle Mekong and *Puntioplites waandersi* from both the middle Mekong and Borneo. Thus there is no morphometric separation between the two species when local populations are combined in each species (Table 2).

In scale counts these two species exhibit mosaic patterns of similarity between local populations. For example, in the number of scales between the lateral line and pelvic insertion the middle Mekong *Puntioplites waandersi* is closer to the middle Mekong *Puntioplites proctozysron* than to *P. proctozysron* from the other two localities, while in circumpeduncular scale counts the middle Mekong *P. waandersi* agrees with the lower Mekong and Bornean, rather than the middle Mekong, *P. proctozysron* (Table 1).

In the number of predorsal bones, which is subject to pronounced geographic variation in *Puntioplites waandersi*, *Puntioplites proctozysron* from all localities (all in the continental section of Southeast Asia) agrees with *P. waandersi* from the insular section (Borneo) and differs from *P. waandersi* from the continental section (middle Mekong) (Table 1). Whereas the continental *P. proctozysron* from all localities is close to the continental, rather than insular, *P. waandersi* in gill-raker counts, another meristic character showing geographic variation in *P. waandersi*.

Thus, as in morphometric characters, *Puntioplites proctozysron* and *Puntioplites waandersi* show no significant meristic difference when local populations are united in each species.

Despite such morphological similarities, *Puntioplites proctozysron* and *Puntioplites waandersi* cannot be considered to be intercrossing populations sharing a common gene pool and representing sexual or individual dimorphism within a species on account of the following facts: 1) In the middle Mekong drainage where these two forms occur syntopically, they show distinct morphological separation in the combination of the nature of the principal simple anal ray and the number of predorsal bones, i.e., a serrated principal ray and usually four predorsal bones in *P. proctozysron* and an entire principal ray and five predorsal bones in *P. waandersi*. 2) Though we failed in determining sex in most of the specimens at hand due to unfavorable preserving conditions, we were able to recognize ripe ovaries in a middle Mekong specimen of *P. proctozysron* (IBRP 3169) and testes in a Chao Phya specimen of the same species (IBRP 3281).

All of the findings obtained in this study indicate that *Puntioplites proctozysron* and *Puntioplites waandersi* are distinct species directly differentiated from a common ancestor. Taxonomically, we see no reason to place them in separate genera. The serration of the principal simple anal ray should not be of overriding phyletic significance in these fishes, though it is a character most clearly

distinguishing these two species phenetically.

Other species of *Puntioplites*. *Puntioplites bulu* has been reported as *Puntius bulu* from the Greater Sunda Islands (Bleeker, 1851, 1863; Weber and de Beaufort, 1916; Hardenberg, 1936; Inger and Chin, 1962), Malay Peninsula (Hora, 1924; Koumans, 1937; Herre and Myers, 1937; Tweedie, 1940; Smith, 1945; Shiraishi et al., 1972), and southern part of the Indochinese Peninsula (Chevey, 1932b; Chevey and le Poulain, 1940). The absence of this species in the senior author's rather extensive collection of fish from the Indochinese Peninsula suggests that this species is rare at best on this peninsula.

We examined three specimens referrable to *Puntioplites bulu* from Borneo, and confirmed the similarity of *P. bulu* to *Puntioplites proctozysron* and *Puntioplites waandersi* in the features of the snout region and pharyngeal bones and their teeth as well as in having a strongly osseous principal simple anal ray. On the other hand, *P. bulu* is readily distinguishable from both *P. proctozysron* and *P. waandersi* in squamation and in possessing a lower body which is brownish in color and has many narrow, irregular, oblique, dark brown cross bars on the sides. *P. bulu* is congeneric with but specifically distinct from *P. proctozysron* and *P. waandersi*.

Puntioplites lawak and *Puntioplites nini* are also hard-anal-rayed species described under the generic name of *Puntius* from the Greater Sunda Islands and adjacent region (*P. lawak*: Bleeker, 1855, 1863; Weber and de Beaufort, 1916; *P. nini*: Weber and de Beaufort, 1916). Because of the paucity of morphological information on these two forms, their status still remains obscure. We have examined 13 juvenile Bornean specimens referrable to either of these two forms, in which both six and seven branched anal rays were observed. It is possible that *P. nini* is synonymous with *P. lawak*.

Generic status

Comparison of *Puntioplites* and *Puntius*. *Puntioplites proctozysron*, *Puntioplites waandersi* and *Puntioplites bulu* are in complete agreement with one another, and distinct from *Puntius*, in the combination of the following structural characters (characters of *Puntius* are based on Taki et al., 1978): 1) the principal simple dorsal ray is prolonged, strongly ossified and serrated behind; 2) the principal simple anal ray is strongly ossified; 3) the snout has a well-developed lateral fold on each side and has no barbels; 4) the pharyngeal bones are narrow, with an elongate dorsal limb that is greatly recurved down- and forward at its apical portion.

Of these characters, the prolongation of the principal simple dorsal ray (1) and the complete ossification of the principal simple anal ray (2) are not seen in species of *Puntius*. A snout of the same structure as in (3) is known only in the South Asian (Indian and/or Ceylonese) *Puntius conchonius* (Hamilton), *Puntius cumingi* (Günther), *Puntius ticto* (Hamilton), and *Puntius nigrofasciatus* (Günther). A recurved dorsal limb of the pharyngeal bone is seen in the Southeast Asian *Puntius binotatus* (Valenciennes), *Puntius oligolepis* (Bleeker), *Puntius stigmatosomus* Smith, and *Puntius leiacanthus* (Bleeker) and in the South Asian (Burma to Ceylon) *Puntus chola* (Hamilton). But the curvature of the limb in these species is not so great as in *Puntioplites* (Fig. 4). Furthermore, it was suggested by W. Rainboth (personal communication) that *Puntioplites* is further distinguished from *Puntius* in a few meristic characters, which are carried in the generic diagnosis below.

The morphological distinctiveness of *Puntioplites* as shown above seems sufficient to recognize *Puntioplites* as a genus distinct from *Puntius*.

Genus *Puntioplites*. The affiliation of *Puntioplites waandersi* and *Puntioplites bulu* (and *Puntioplites lawak* and *Puntioplites nini*, if they are not nominal) in the genus *Puntioplites* necessitates a modification of the diagnosis of this genus. The genus *Puntioplites* is defined as follows:

Puntioplites Smith

Puntioplites Smith, 1929: 11 (type species: *Putius* (*Puntius*) *proctozysron* Bleeker)

Adamacypris Fowler, 1934a: 125

Diagnosis: A genus of the Cyprinidae characterized by: a compressed, high body with a greatly elevated back; a prolonged,

strongly ossified, serrated principal simple ray in the dorsal fin; a stout, strongly ossified, serrated or entire principal simple ray in the anal fin; nine branched pelvic rays; three free-margined scales between the anus and anal fin; a well-developed lateral fold on each side of the snout; no barbels; pharyngeal bones with an elongated dorsal limb recurved down- and forward at its appical portion and with well-congregated, usually 2,3,4-4,3,2 pharyngeal teeth.

Species contained: The following five species are known in this genus: *Puntioplites proctozysron* (Bleeker), *P. waandersi* (Bleeker), *P. bulu* (Bleeker), *P. lawak* (Bleeker), and *P. nini* (Weber and de Beaufort). The last-named two species are in need of reexamination as to their specific validity.

Distribution: The Indochinese Peninsula including the Mekong and the Menam Chao Phya drainages, the Malay Peninsula, Riouw (probably=Riau), the Greater Sunda Islands including Sumatra, Borneo and Java.

Remarks on subfamily placement. Bănărescu (1972) and Chen and Hwang (1977) placed *Puntioplites* in the subfamily Cyprininae to which the temperate Eurasian *Cyprinus*, *Carassius* and other related forms belong, rather than in the Barbinae together with the South and Southeast Asian *Puntius*. However, the taxonomic affiliation by these authors is based solely on the ossification of the principal simple anal ray. In reality *Puntioplites* is much closer to *Puntius* than to *Cyprinus* and *Carassius* in morphological characters other than the nature of the principal simple dorsal anal ray, such as the features of the snout region and pharyngeal bones and their teeth, and the number of the dorsal fin-rays. We regard *Puntioplites* as belonging to the Barbinae, so far as our concept of cyprinid classification recognizes these two subfamilies as distinct.

Zoogeography

According to de Beaufort (1951: 82~83), the distribution of freshwater fishes on Borneo offers a clue to distinguish old and new elements in the fish fauna of the Sunda region. The fish fauna of the Kapuas River of western Borneo is closely similar to that of the rivers of eastern Sumatra. This similarity is usually accounted for by the connection of Sumatra and Borneo during the Pleistocene glacial periods. On the contrary the fish fauna of the Mahakam River of eastern Borneo includes a considerable number of endemic forms and shows much less affinity with the fauna of Sumatra than that of the Kapuas does. De Beaufort (1951) explains this endemism and dissimilarity of the Mahakam fauna by the geographic isolation of the Mahakam basin. Based on these observations, he concludes that the fishes common to Sumatra and the Kapuas but not found in the Mahakam are new or Pleistocene migrants and those also occur in the Mahakam are of older distribution. He appears to reinforce this theory by the presence in the Mahakam of all of the existing genera (except *Barbus*) found in the Eocene fossil freshwater fish fauna reported from Sipang, Sumatra, by Sanders (1934).

Based on Weber and de Beaufort (1916) and Silas (1951), the Mahakam fish fauna contains 47 primary freshwater genera including one endemic to the river. After the catalogues of Mekong fishes by Taki (1974b, 1975), all of the 46 non-endemic Mahakam genera are represented in the middle and lower Mekong, 38 in the middle section and 36 in the lower section.

The 11 existing genera in the Sipang fossil fauna are the osteoglossiform *Scleropages* and *Notopterus*, the cypriniform *Rasbora*, *Barbus*, *Osteochilus*, *Puntius*, and *Thynnichthys*, the siluriform *Pangasius* and *Mystus*, the anabantoid *Osphronemus*, and the percoid *Toxotes*. All these genera except for *Barbus* are widely distributed in Southeast Asia and are found in the Mekong, eight in the middle section and nine in the lower section.

The affinities of the Mekong fish fauna with the present Mahakam fauna and with the fossil Sipang fauna show that the dispersal history of the fish fauna of the Mekong and of continental Southeast Asia should be traced back to the early Tertiary or earlier when the present-day continental and insular sections of Southeast Asia constituted a continuous dry landmass known as the Sundaland or Indosinian-Cathaysian land.

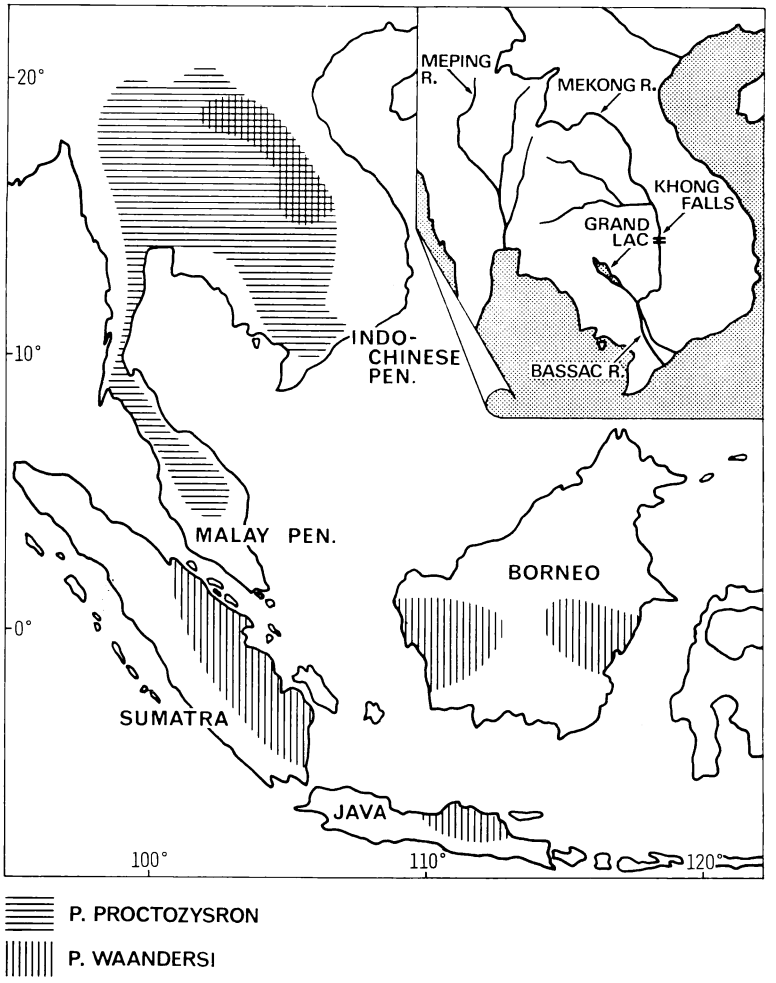

Fig. 5. Approximate known ranges (hatched areas) of *Puntioplites proctozysron* and *Puntioplites waandersi*, and localities mentioned in the text. The river system including the Meping is the Menam Chao Phya system. The course of the Mekong River covered in this study is divided into middle and lower sections with the Khong Falls as the boundary.

The genus *Puntioplites* is known from both continental Southeast Asia and the Greater Sunda Islands including the Mahakam basin of Borneo. This genus can therefore be considered to be of old distributional origin in Southeast Asia.

The present-day geographic ranges of *Puntioplites waandersi* are discontinuous, one over the Greater Sunda Islands including the Mahakam and the other in the middle Mekong, deep in continental Southeast Asia (Fig. 5). As suggested earlier in this paper, the differentiation of the Bornean and middle Mekong populations of *P. waandersi* may or may not have reached a specific level. However, it is unlikely that, in whichever case, these two local populations have evolved in parallel in these two far isolated areas. It is more tenable to suggest that the range of *P. waandersi*, or its direct ancestral form, was once more extensive and continuous in the Sundaland and that the middle Mekong *P. waandersi* is now an isolated relict population in the continental section.

The geographic range of *Puntioplites proctozysron* is restricted to continental Southeast

Asia (Fig. 5). It is difficult to attribute the total absence of this species from the Greater Sunda Islands to complete extinction in this region which had been continually connected with the continental section up to the last glacial epoch. This species is probably not an old-time occupant of the Sundaland. On the assumption that *P. proctozysron* and *P. waandersi* are of common direct origin, it is plausible that *P. proctozysron* has evolved in continental Southeast Asia from *P. waandersi* or an ancester close to *P. waandersi*. The gap in the range of *P. waandersi* in a large part of continental Southeast Asia may be related to the occurrence of *P. proctozysron* in that very area (Fig. 5).

In some meristic characters the lower Mekong population of *Puntioplites proctozysron* is close to the Chao Phya population and both are separated from the middle Mekong population. The lower Mekong-Chao Phya and the middle Mekong populations can be regarded as two distinct geographical variants or races. The fish described as *Puntioplites falcifer* By Smith (1929) represents the middle Mekong variant (Rainboth, personal communication). The existence of two variants seems to reflect past connection between the Chao Phya and the lower Mekong and geographic segregation, at present and/or in the past, of the middle and lower courses of the Mekong.

Takaya (1974) shows a horst-graven techtonism which has occurred since the Pleiocene-Pleistocene and is probably still going on along the line connecting the Bassac, one of the two main stems of the Mekong in its lowermost course, and Grand Lac (see Fig. 5). This techtonism can be traced as far north as the Me Ping River of the Chao Phya system in northern Thailand (Takaya, personal communication). The meristic closeness of the Chao Phya and lower Mekong *P. proctozysron* may reflect the former existence of a river system along the graven.

The Khong Falls, which divides the Mekong into middle and lower sections, and a series of rapids below the falls may be serving as barrier preventing the movement of certain fish species. However, the meristic gap between the middle and lower Mekong populations is so pronounced that it cannot be considered to result merely from the present-day existence of the Khong Falls. The senior author's unpublished data on the distribution of Mekong fishes indicate sharp distributional and faunistic gaps between the middle and lower Mekong and suggest the possibility that the middle and lower courses were once distinct drainages.

Acknowledgments

We are grateful to Walter Rainboth, University of Michigan, for the critical reading of the manuscript and many valuable pieces of information and suggestions on *Puntioplites* and *Puntius*, to Dr. Yoshikazu Takaya, Kyoto University, for information on the geohistory of Southeast Asia, and to Dr. Hitoshi Ida, Kitasato University, for assistance in examining gonads of *Puntioplites proctozysron* and *Puntioplites waandersi*. Miss Tran-thi-Thu-Houng, Cantho University, Vietnam, is thanked for assistance in collecting Vietnamese specimens. We also thank Akira Imaki, Arata Kawamoto and Atsushi Suzuki of the Institute for Breeding Research, Tokyo University of Agriculture, for help in laboratory work, and Miss Chizuko Ohya for assistance in data processing and manuscript preparation.

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コイ科 *Puntioplites* 属2種の分化と動物地理

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Puntioplites proctozysron と *Puntioplites waandersi* は東南アジアに分布するコイ科魚類である．それぞれの種の計数形質には明らかな地理的変異が認められ，また調査したすべての計数・計測値について両者間で範囲の重複が見られる．この2種を分ける顕著な形態的差異は臀鰭主不分枝軟条の性質，すなわち *P. proctozysron* では後縁に鋸歯があり *P. waandersi* では鋸歯がないという点のみである．この差異は同一種内の二型に由来するものではなく，両種はごく近縁の，従って同一属に属する別種であると判断される．また，*P. waandersi* はこれまで *Puntius* 属の種として記載されることが多かったが，*Puntioplites* を独立の属と認め，両種をこの属に属せしめることが妥当と考えられる．

動物地理学的検討に基づけば，*P. waandersi* は，現在の島しょ部を含む東南アジア一帯がひとつの陸塊を形成していた古第三紀あるいはそれ以前には，この地域に広く分布していたもので，現在メコン河中流域に限られている大陸部での出現は遺存的分布を表わしているものと推定される．他方 *P. proctozysron* は *P. waandersi* あるいはそれに近い祖先型から大陸部で出現したものと思われる．このほか，インドシナ半島の地史について若干の動物地理学的検討をおこなった．

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