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Comparative Morphology and Interspecific Relationships of the Cyprinid Genus *Puntius*

Yasuhiko Taki, Akari Katsuyama and Tousei Urushido

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Abstract Interspecific relationships were investigated in 23 species of the cyprinid genus *Puntius* on the basis of the features of infraorbital bones, pharyngeal bones and their teeth, lateral folds and barbels on the snout, and color pattern. Six phyletic groups were recognized in these fishes. In general, species belonging to the same group have overlapped or about equal geographic distributions. Between Southeast Asian and Indo-Ceylonese groups a more or less distinct gap is found in the degree of development of lateral folds and barbels. The results of this study indicate that Bleeker's (1863) division of *Puntius* into the subgenera *Puntius*, *Barbodes* and *Capoeta* is not acceptable from a phylogenetic viewpoint.

Introduction

The genus *Puntius* Hamilton is the largest in number of species of all cyprinid genera in Asian tropics. Fishes of this genus occur throughout the region from Pakistan to southern China, inhabiting various types of fresh waters. The status of *Puntius* is obscure; the delimitation and nomenclatural validity of the genus have remained unsettled (Hora and Mukerji, 1934; Smith, 1945; Hoedeman, 1958; Myers, 1960), largely owing to the scantiness in the knowledge of its inter- and infrageneric relationships.

The primary aim of this study is to investigate relationships among species of *Puntius* on morphological bases, in order to provide data necessary for the assessment of evolutionary lines within the genus. To this end, internal and external characters were examined on a total of 23 species.

Materials and methods

This study was based primarily on specimens collected from Southeast Asia and deposited in the Institute for Breeding Research, Tokyo University of Agriculture (abbreviation for catalogue number, IBRP). It also dealt with specimens obtained from aquarium fish suppliers in Tokyo and those raised in the laboratory. In the following list of materials, number of specimens, their range for standard length, collecting locality and catalogue number (in the case of catalogued specimen) are given in order.

Southeast Asian species. *P. altus* (Günther): 25; 41.5～105.0 mm; Thailand, Vietnam; IBRP 3112, 3218, 3283, 6092, 6485. *P. schwanenfeldi* (Bleeker): 17; 35.0～163.0 mm; Thailand, Vietnam, Indonesia; IBRP 3187, 3197, 3282, 6705. *P. gonionotus* (Bleeker): 14; 70.0～182.5 mm; Laos, Thailand, Vietnam, Indonesia; IBRP 3180, 3195, 3234, 3289. *P. orphoides* (Valenciennes): 15; 66.0～122.0 mm; Laos, Thailand, Vietnam; IBRP 3079, 3182, 3285, 4376, 6223. *P. tetrazona* (Bleeker): 24; 23.5～47.0 mm; Indonesia; IBRP 3184, 6874. *P. partipentazona* Fowler: 24; 21.0～35.5 mm; Thailand; IBRP 3068, 3166, 3261. *P. pentazona* (Boulenger): 11; 21.5～51.0 mm; Iodonesia; IBRP 3265. *P. rhomboocellatus* Koumans: 2; 27.5, 32.0 mm; Indonesia; IBRP 3190. *P. everetti* (Boulenger): 18; 16.0～83.0 mm; 5 of 18, Indonesia; IBRP 6726, 6754; 13 of 18, aquarium-rised non-catalogued specimens. *P. lateristriga* (Valenciennes): 15; 11.0～66.0 mm; Indonesia; IBRP 6720, 6768. *P. fasciatus* (Bleeker): 18; 20.0～88.5 mm; 10 of 18, Indonesia; IBRP 3266, 6618; 8 of 18, aquarium-raised non-catalogued specimens. *P. binotatus* (Valenciennes): 12; 49.0～82.5 mm; Vietnam, Malaysia; IBRP 6231, 6736, 6875. *P. oligolepis* (Bleeker): 4; 24.0～32.0 mm; 1 of 4, Indonesia; IBRP 6827; 3 of 4, non-catalogued specimens from an

aquarium fish dealer. *P. stigmatosomus* Smith: 8; 37.5～68.0 mm; Laos, Vietnam; IBRP 3094, 6231, 6736. *P. leiacanthus* (Bleeker): 26; 35.5～83.0 mm; Laos, Thailand, Vietnam; IBRP 3038, 3211, 3235, 4772, 5209, 6353.

Indian and Ceylonese species. All of the following materials are non-catalogued specimens obtained from aquarium fish dealers. *P. chola* (Hamilton): 2; 50.0, 55.0 mm. *P. arulius* (Jerdon): 3; 53.0～64.5 mm. *P. filamentosus* (Valenciennes): 2; 34.5, 85.0 mm. *P. titteya* Deraniyagala: 3; 16.0～27.0 mm. *P. conchonius* (Hamilton): 9; 41.0～62.5 mm. *P. cumingi* (Günther): 2; 37.5, 44.0 mm. *P. ticto* (Hamilton): 8; 30.5～49.0 mm. *P. nigrofasciatus* (Günther): 12; 25.0～43.0 mm.

Infraorbital bones were observed on alizarin-stained transparent specimens. Identification of the bones was based on Nelson (1969). Pharyngeal bones were removed from the pharynx, stained with alizarin red, and then cleaned. For cyprinid pharyngeal bones and their teeth, Chu's (1935) terminology has been employed by many authors. He used the terms 'anterior' and 'posterior' (e.g., anterior edentulous process, posterior angle) to indicate the positions of regions of the bones. The pharyngeal bones of cyprinids, however, are in reality more upright than recumbent, and there are some cases where this indication does not apply (e.g., the anterior angle is sometimes posterior to the posterior angle in actual position). We therefore consider it proper to use 'dorsal' in place of posterior and 'ventral' instead of anterior. Terms pertaining to pharyngeal bones and their teeth used in this study are shown in Fig. 2.

Comparative observations

Infraorbital bones. In all species under study the infraorbital series consists of a lacrimal, three infraorbitals, and a dermosphenotic (Fig. 1). The antorbital is missing. The third and fourth infraorbitals are fused together into a large bone bordering the bottom of the orbit. This fused element is termed infraorbital 3+4. In *P. conchonius*, *P. cumingi*, *P. ticto* and *P. nigrofasciatus*, the infraorbital 3+4 is much broader than other infraorbital elements, with the outer margin greatly elevated (Fig. 1A). Whereas in the remaining species the bone is only as broad as the other infraorbitals (Fig. 1B).

Pharyngeal bones and their teeth. All of the 23 species examined have three rows of pharyngeal teeth. In general, the first (outer) row has two slender teeth, the second (middle) row three teeth slightly thicker than the first-row teeth, and the main (third or inner) row four or five teeth, of which the third and fourth teeth are large and broad. The tooth formula for each species is shown in Table 1.

The number of teeth in the main row is stable in the 2, 3, 5-5, 3, 2 species. While in two of the 2, 3, 4-4, 3, 2 species, *P. tetrazona* and *P. lateristriga*, a fifth tooth is added to the main row in some individuals. Of the total of 23 specimens of *P. tetrazona*, two had 2, 3, 5-4, 3, 2 teeth, one 2, 3, 4-5, 3, 2, and one 2, 3, 5-5, 3, 2; of the 15 specimens of *P.*

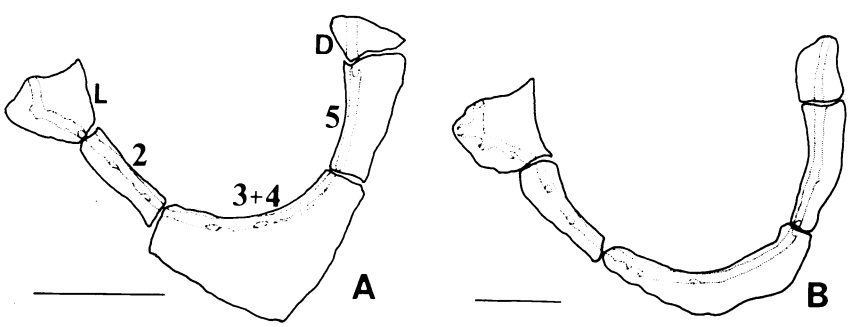

Fig. 1. Two different types of infraorbital bones in *Puntius*. A, *P. comingi*, 37.5 mm SL; B, *P. orphoides*, 66.0 mm SL. Scales indicate 1 mm. Abbreviations: D, dermosphenotic; L, lacrimal; 2～5, infraorbitals 2～5.

Table 1. Comparison and grouping of 23 species of *Puntius*. Types of pharyngeals and their teeth and of color pattern are indicated by the symbols as designated in the text. nrw, narrow; brd, broad; −, absent; ±, vestigial; +, well developed; C, continental Southeast Asia; I, insular Southeast Asia (Greater Sunda Islands). * including *P. mahecola* as a synonym.

Group	Species	Infra-orbital 3+4	Pharyngeal tooth formula	Type of pharyn-geals and teeth	Lateral fold	No. of barbels (pair)	Type of color pattern	Geographic distribution
altus-group	*P. altus*	nrw	2, 3, 5—5, 3, 2	A	−	2	A	S. E. Asia (C, I)
	P. schwanenfeldi	nrw	2, 3, 5—5, 3, 2	A	−	2	A	S. E. Asia (C, I)
	P. gonionotus	nrw	2, 3, 5—5, 3, 2	A	−	2	A	S. E. Asia (C, I)
	P. orphoides	nrw	2, 3, 5—5, 3, 2	A	−	2	A	S. E. Asia (C, I)
tetrazona-group	*P. tetrazona*	nrw	2, 3, 4 (or 5)—4 (or 5), 3, 2	B	−	1	B	S. E. Asia (I)
	P. partipentazona	nrw	2, 3, 4—4, 3, 2	B	−	1	B	S. E. Asia (C)
pentazona-group	*P. pentazona*	nrw	2, 3, 4—4, 3, 2	B	−	2	C	S. E. Asia (I)
	P. rhomboocellatus	nrw	2, 3, 4—4, 3, 2	B	−	2	C	S. E. Asia (I)
	P. everetti	nrw	2, 3, 5—5, 3, 2	B	−	2	C	S. E. Asia (I)
	P. lateristriga	nrw	2, 3, 4 (or 5)—4 (or 5), 3, 2	B	−	2	C	S. E. Asia (C, I)
	P. fasciatus	nrw	2, 3, 5—5, 3, 2	C	−	2	C	S. E. Asia (I)
binotatus-group	*P. binotatus*	nrw	2, 3, 5—5, 3, 2	D	±	2	D	S. E. Asia (C, I)
	P. oligolepis	nrw	2, 3, 5—5, 3, 2	D	±	2	D	S. E. Asia (I)
	P. stigmatosomus	nrw	2, 3, 5—5, 3, 2	D	±	1	D	S. E. Asia (C)
	P. leiacanthus	nrw	2, 3, 5—5, 3, 2	D	±	1	E	S. E. Asia (C, I)
	P. chola	nrw	2, 3, 5—5, 3, 2	D	±	1	E	Burma to Ceylon
arulius-group	*P. arulius*	nrw	2, 3, 5—5, 3, 2	E	±	1	F	S. India
	*P. filamentosus**	nrw	2, 3, 5—5, 3, 2	E	±	1 or 0	F	S. India, Ceylon
	P. titteya	nrw	2, 3, 5—5, 3, 2	E	±	1	F	Ceylon
conchonius-group	*P. conchonius*	brd	2, 3, 5—5, 3, 2	E′	+	0	G	N. E. India
	P. cumingi	brd	2, 3, 4—4, 3, 2	E′	+	0	G	Ceylon
	P. ticto	brd	2, 3, 5—5, 3, 2	E′	+	0	G	Whole India, Ceylon
	P. nigrofasciatus	brd	2, 3, 4—4, 3, 2	E′	+	0	G	Ceylon

lateristriga, one was 2, 3, 4-5, 3, 2, and another one 2, 3, 5-4, 3, 2. Variations in the number of teeth in the minor rows appear arbitrary and are observed in both the 2, 3, 4-4, 3, 2 and 2, 3, 5-5, 3, 2 species but more frequently in the former. The deviant formulae observed are: 1, 3, 4,-4, 3, 2 (*P. tetrazona*, 1 specimen; *P. fasciatus*, 1), 2, 3, 4-4, 3, 1 (*P. lateristriga*, 1), 2, 4, 4-4, 3, 2 (*P. tetrazona*, 1; *P. lateristriga*, 1), 1, 3, 5-5, 3, 1 (*P. altus*, 1), 2, 5, 6-7, 3, 2 (*P. everetti*, 1), and 3, 3, 4-4, 3, 2 (*P. partipentazona*, 1).

In contrast to the inconstancy in tooth formula, the structure of the pharyngeal bones and their teeth are uninform within a species. In the combination of the structural features of the pharyngeal bones and teeth, six different types are recognized in the 23 species examined in this study (Fig. 2). Characters of each type are briefly described as follows. Type A: pharyngeal bones very broad and stout; dorsal limb broad, its tip truncate; ventral limb short; upper angle hardly recognizable; teeth congregated, thick, swollen at apex. Type B: pharyngeal bones narrow; tip of dorsal limb pointed, sometimes slightly recurved in- and upward; upper angle conspicuous; teeth coarsely set, slender. Type C: pharyngeal bones stout, broad; tip of dorsal limb truncate; upper

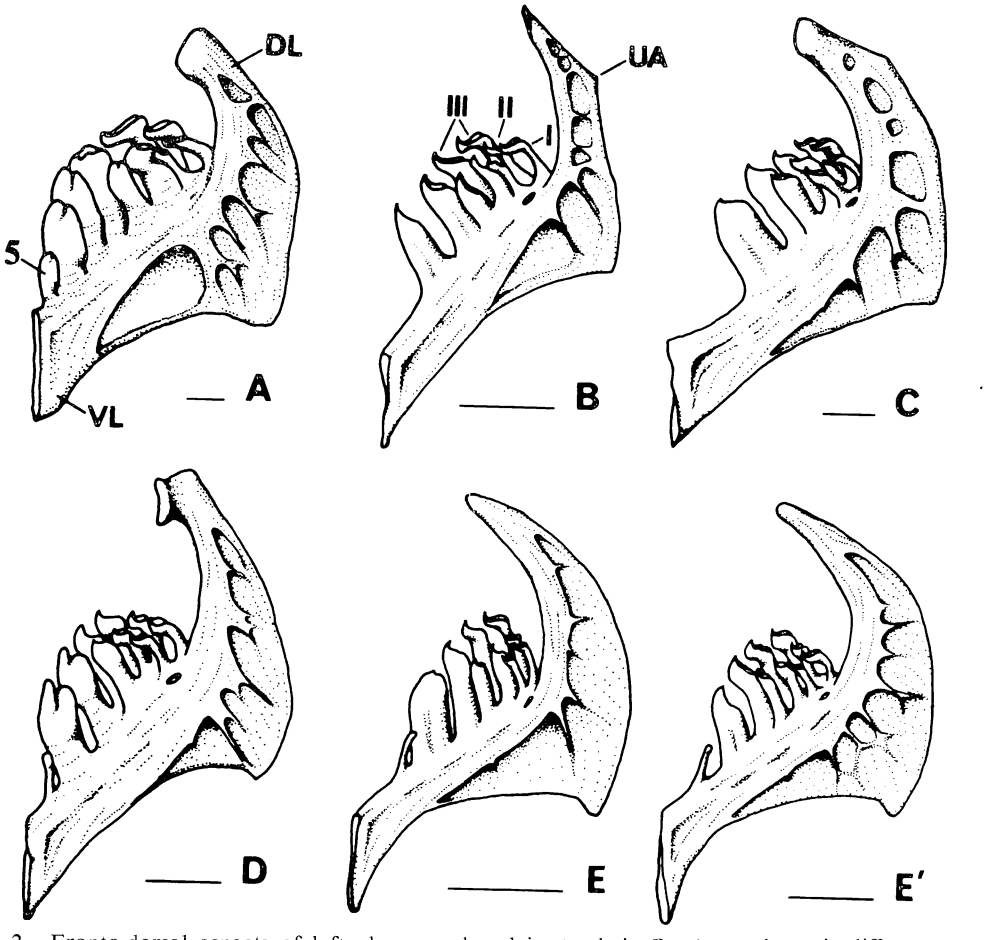

Fig. 2. Fronto-dorsal aspects of left pharyngeal and its teeth in *Puntius* to show six different types of their structure. A, *P. gonionotus*, 115.0 mm SL; B. *P. tetrazona*, 36.5 mm SL; C. *P. fasciatus*, 88.5 mm SL; D, *P. binotatus*, 56.0 mm SL; E, *P. filamentosus*, 34.5 mm SL; E′, *P. conchonius*, 50.5 mm SL. Scales indicate 2 mm. Abbreviations: DL, dorsal limb; UA, upper angle; VL, ventral limb; I~III, first, second and main rows of teeth; 5, fifth tooth in the main row.

angle more or less conspicuous; teeth aggregated, broad. Type D: pharyngeal bones rather broad; tip of dorsal limb blunt, greatly recurved in- and forward; no upper angle; teeth aggregated, moderate in size. Type E: pharyngeal bones broad; tip of dorsal limb pointed; upper angle unrecognizable; teeth congregated, moderate in size. Type E′: pharyngeal bones and their teeth resemble those of the type E in shape and structure, but teeth more coarsely set (this type was represented by E′ because of its similarity to the type E). Characters of the pharyngeal bones and their teeth of each species are indicated in Table 1 by type.

Lateral folds and barbels on snout. In some cyprinid species a lateral fold is developed on each side of the snout. An example of its shape and position is illustrated in Taki (1975). In the species of *Puntius* dealt with in this study, the lateral folds show various degrees of development. They are well developed in *P. conchonius*, *P. cumingi*, *P. ticto* and *P. nigrofasciatus*; vestigial in *P. binotatus*, *P. oligolepis*, *P. stigmatosomus*, *P. leiacanthus*, *P. chola*, *P. arulius*, *P. filamentosus* and *P. titteya*; totally absent in the remaining species.

The number of barbels is also subject to interspecific variation. Barbels are missing in *P. conchonius*, *P. cumingi*, *P. ticto* and *P. nigrofasciatus*; one pair is present near the tip of the rostrum in *P. tetrazona*, *P. partipentazona*, *P. stigmatosomus*, *P. leiacanthus*, *P. chola*, *P. arulius* and *P. filamentosus*; one pair near the tip of the rostrum and another one pair near the mouth angle are present in all other species.

Color pattern. Many species of *Puntius* possess black body markings, which are quite various in size and shape. However, homologies in the markings can be assessed by the location of pigmentations in relation to body parts (Kortmulder, 1972). In this study the black body markings are categorized according to their position into orbital, nuchal, pectoral, subdorsal, supra-anal, anal-basal, postanal, and caudal markings. Locations of these markings are shown in Fig. 3.

In the combination of the body markings, seven different types of color pattern are recognized in the 23 species. It is noted that these markings are often subject to age variations, and some markings appear only during certain stages of growth. The seven types of color pattern are characterized as follows. Type A: body plain or with a caudal blotch which tends to fade with growth. Type B: with cross bars in orbital, supra-anal and caudal positions. Type C: with cross bars or roundish blotches in pectoral, subdorsal, supra-anal and caudal positions; an orbital marking may be present. Type D: with pectoral, subdorsal, supra-anal, anal-basal, postanal and caudal spots or blotches; some of them may be indistinct or absent, or connected to each other. Type E: with a caudal spot similar in shape and position to that in type D. Type F: with cross bars or roundish blotches in nuchal, subdorsal, supra-anal and caudal positions; a spot may be present on back at posterior end of dorsal fin base and another one on each side below it in *P. filamentosus*. Type G: with pectoral, postanal and caudal cross bars or roundish spots; orbital and subdorsal bars present in adult *P. nigrofasciatus* and juvenile *P. cumingi*. Species included in each type are shown in Table 1.

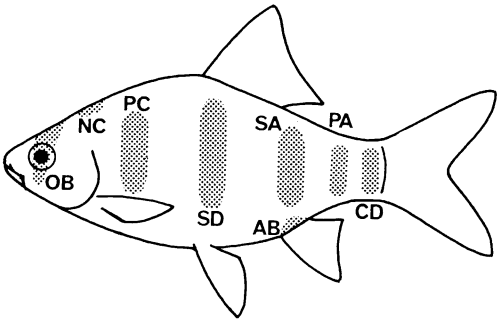

Fig. 3. Semidiagrammatic illustration to show the location and naming of black body markings in *Puntius*. Abbreviations: AB, anal-basal marking; CD, caudal marking; NC, nuchal marking; OB, orbital marking; PA, postanal marking; PC, pectoral marking; SA, supraanal marking; SD, subdorsal marking.

Type C requires special mention. Of the five species contained in this type, *P. pentazona*, *P. rhomboocellatus* and *P. everetti* are characterized by having cross bars or roundish or elliptical blotches in both juvenile and

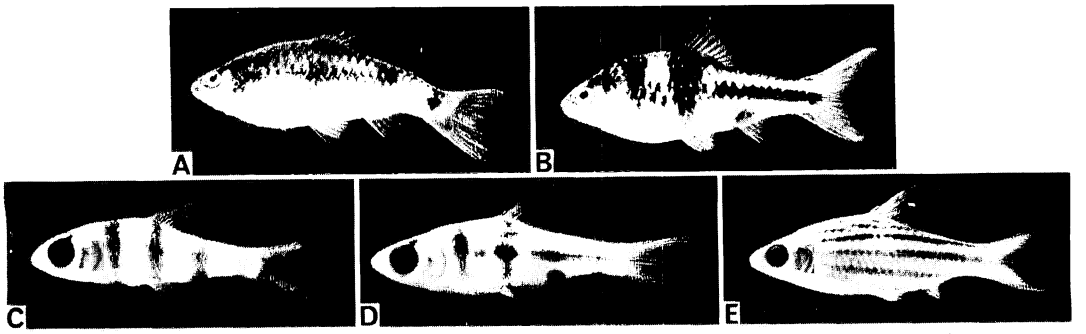

Fig. 4. Black body markings in three species of *Puntius*. A, *P. everetti*, subadult, 59.5 mm SL; B, *P. lateristriga*, subadult, 52.0 mm SL; C～E, *P. fasciatus*, C, juvenile, 20.0 mm SL, D, juvenile, 25.5 mm SL, E, adult, 63.4 mm SL. Note the resemblance of D to A and B.

adult. In *P. everetti* a narrow indistict longitudinal streak is seen in some formalin-preserved specimens (Fig. 4A). In contrast, adult *P. lateristriga* has a broad longitudinal stripe in addition to two cross bands (Fig. 4B), and adult *P. fasciatus* has a body marked with several longitudinal stripes with no trace of cross bars (Fig. 4E). In the juvenile stage, however, these two species possess only corss bars or small spots which correspond in position to the bars and spots in other members of the same group. Rearing experiments with these two species revealed that the juvenile markings are destined to be connected with each other to form a longitudinal stripe in the posteior half of the body in adult *P. lateristriga* and several rows of longitudinal stripes along the entire length of the body in adult *P. fasciatus*. In the course of change in color pattern, *P. fasciatus* even passes through stages of *everetti*- and *lateristriga*-like patterns (Figs. 4C, D). These facts suggest the existence of a more or less neotenous phenomenon in coloration among the species belonging to type C.

Other characters. Caudal skeleton and pectoral and pelvic girdles were also examined in the 23 species. There was no significant difference in these characters.

Discussion

Eastman and Underhill (1973) showed in the pharyngeal teeth of some North American cyprinids that "…when addition of a major row tooth has resulted in an asymmetrical formula the left arch has always received the extra tooth." Such a tendency is not found in *Puntius*. The plasticity in the number of main-row teeth in *P. tetrazona* and *P. lateristriga* seem to indicate that there is in *Puntius* an evolutionary trend in the number of main-row teeth toward the increase from four to five or otherwise toward the decrease from five to four, and that such species as *P. tetrazona* and *P. lateristriga* are undergoing the modification from one formula to another. Difference in the number of main-row teeth can be considered to be of rather little taxonomic significance in *Puntius* when the above evolutionary trend is taken into consideration.

The variations in minor-row tooth counts are more arbitrary, involving both addition to and subtraction from the basic numbers. These variations seem to be resulted chiefly from disturbance in the process of tooth replacement, as indicated in some North American cyprinids and catostomids by Evans and Deubler (1955), Weisel (1967) and Eastman and Underhill (1973). It is generally known that the pharyngeal teeth of cyprinids successively shed and are replaced by new teeth produced in the surrounding mucosa. Failure of a replacement tooth to ankylose to the pharyngeal bone will result in subtraction from the tooth formula, and that of an old tooth to shed as it is destined to be replaced will account for addition to the formula. It is noteworthy that the variability in the number of minor-row teeth was pronounced again in *P. tetrazona* and *P. lateristriga*. In these two species the plasticity in the number of

main-row teeth appears to accompany the instability in the minor-row dentition.

Comparison of the characters of the 23 species here examined indicates that they constitute six groups each consisting of species sharing these morphological features almost completely (Table 1). The six groups are called in this paper *altus*-group, *tetrazona*-group, *pentazona*-group, *binotatus*-group, *arulius*-group, and *conchonius*-group.

In the *pentazona*-group, *P. fasciatus* differs from other members in the structure of the pharyngeal bones. Nevertheless, its similarity to other members in all other characters seems sufficient to justify its assignment to the *pentazona*-group. In the same manner, the uniformity in major characters of the four species of the *binotatus*-group should suffice their inclusion in the same group in spite of the difference in the number of barbels. In *Puntius* the number of barbels may not be of overriding phylogenetic significance.

The morphological similarity as seen among species in each group is sufficient to suggest that members of the same group are decendants from a common direct ancestral stock. The distributional pattern of each group supports this view; except for the *binotatus*-group, species belonging to the same group have overlapped or otherwise proximate geographic ranges (Table 1).

The four species of the *altus*-group are in complete agreement in the characters examined, and similar in geographic ranges, which encompass mainland Southeast Asia and the Greater Sunda Islands. They are all large-sized fishes for *Puntius*. In contrast, the members of the *tetrazona*- and *pentazona*-groups are variable in pharyngeal tooth formula. The latter group is variable in color pattern, too. These two groups should be in the course of diversification. All species belonging to the two groups are small colorful fishes. The *binotatus*-group is peculiar, and specialized, in the structure of the pharyngeal bones (Fig. 2D). Of the three species of the *arulius*-group, *P. titteya* is a tiny species, while other two are medium-sized. The *conchonius*-group resembles the *tetrazona*- and *pentazona*-groups in color pattern, but it is peculiar, and uniform, in the shape of the infraorbital 3+4 (Fig. 1A).

A more or less pronounced gap occurs in the degree of development of barbels and lateral folds between the eastern (Southeast Asian) and western (Indian and Ceylonese) assemblages of groups (Table 1). The *binotatus*-group appears to afford a link between the two assemblages in the respects that it is intermediate between the two in these morphological characters and has a range that extends from Southeast Asia through India southward to Ceylon. However, it is difficult to consider such a group with specialized pharyngeal bones as the *binotatus*-group to be a direct transitional form linking the eastern and western groups. Between Southeast Asia and South India there are the drainages of the Salwin, Irrawaddy and Ganges Rivers, where numerous species of *Puntius* occur. Examination of species inhabiting these rivers is required to elucidate more clearly the lines of differentiation and dispersal of *Puntius*.

Bleeker (1863) divided the genus *Puntius* into three subgenera, *Puntius*, *Barbodes* and *Capoeta*, based solely on the number of barbels. Though this classification has been followed by some authors, this subdivision is not acceptable because of the limited phylogenetical significance of the number of barbels as indicated in this study.

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(YT and AK, Tokyo University of Fisheries, 4-5-7, Konan, Minato-ku, Tokyo 108; TU, The Institute for Breeding Research, Tokyo University of Agriculture, 2-4-28, Kamiyoga, Setagaya, Tokyo 158, Japan)

コイ科 *Puntius* 属魚類の比較形態と種間関係

多紀保彦・勝山明里・漆戸登宇世

熱帯アジア産のコイ科 *Puntius* 属の23種について，眼下骨，咽頭骨と咽頭歯，吻部の lateral folds と口ひげおよび斑紋の比較をおこなった．その結果，これらの魚種は6系統群に分かれることが判明した．一般に同一群に属する種は，分布域も重なり合っているかあるいは近接している．東南アジアに分布する群とインド・セイロンの群との間には，lateral folds と口ひげの発達程度に比較的明瞭な差異がある．Bleeker (1863) は *Puntius* 属を *Puntius*, *Barbodes*, *Capoeta* の3亜属に分類したが，本研究の結果からみると，この亜属分類は支持しがたい．

(多紀・勝山: 108　東京都港区港南 4-5-7　東京水産大学．漆戸: 158　東京都世田谷区上用賀 2-4-28　東京農業大学育種学研究所)