Notes on the Classification of Actinopterygian Intestinal Patterns

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Abstract A classification of actinopterygian intestinal patterns represented by 596 species is presented. Individual and developmental variations, distribution, and interrelationships of intestinal patterns were studied. The low conspecific variation, non-random pattern variation in groups with complex patterns, and resemblance of intestinal patterns among members of monophyletic groups suggest that intestinal pattern provides valuable information regarding phylogenetic interrelationships.

Suyehiro's (1942) study of a variety of teleostean digestive systems is the only systematic survey of the digestive system within this group. His objective was to understand fish feeding habits by studying the digestive organs. He discovered various types of intestinal patterns (within the peritoneal cavity the positions of the various gastrointestinal segments form the fish intestinal pattern; the elements of the pattern are the relative positions of the segments). In contrast to this ecological-anatomical study, Harder (1960) used superficial gut morphology (the stomach and pneumatic duct) as a basis for interpreting the phylogeny of the clupeoids. Greenwood (1968) described the gut and other viscera in *Denticeps clupeoides* in an attempt to resolve its systematic position among clupeiforms. Nelson (1972) found evidence for monophyly of osteoglossomorphs (including hiodontids) from the intestinal pattern. A similar systematic survey of the digestive system, swimbladder, and related tissues (e.g., the gas-gland) of tetraodontiforms was conducted by Mok (1975). Results of that study suggested that the intestinal pattern might be applicable to the reconstruction of phylogenetic relationships among other fishes. Accordingly, the major objectives of the present study are 1) to classify the types of intestinal patterns that generally appear in actinopterygians, 2) to survey the distribution of these types, and 3) to understand individual and developmental variations of intestinal patterns. This study will provide baseline information about actinopterygian intestinal

patterns which can be significant to phylogenetic studies. After the generalized actinopterygian patterns were recognized, patterns that differ from these generalized types may be treated as apomorphic or derived characters at various taxonomic levels (Hennig, 1966).

Materials and methods

Specimens of 596 actinopterygian species examined were on loan from the American Museum of Natural History, Academy of Natural Sciences of Philadelphia, Australian Museum in Sidney, Bernice P. Bishop Museum, California Academy of Sciences, South Australian Museum, Scripps Institution of Oceanography, Institute of Animal Resource Ecology, University of British Columbia, Western Australian Museum, Zoology Museum, National Taiwan University, and Zoology Museum, University of Michigan. Data from examined specimens are not listed herein, but are available in Mok (1978).

Dissections were made on one or more individuals of each species studied. The fish were cut on the right side of the body cavity. Intestinal pattern was recorded by tracing the coiling pathway with a continuous line.

Results

Loop f and loop a

In most actinopterygians, the anterior part of the intestine proceeds anteriorly and then displaces to the right of the stomach, which is, in most cases, either U-, V-, or T-shaped
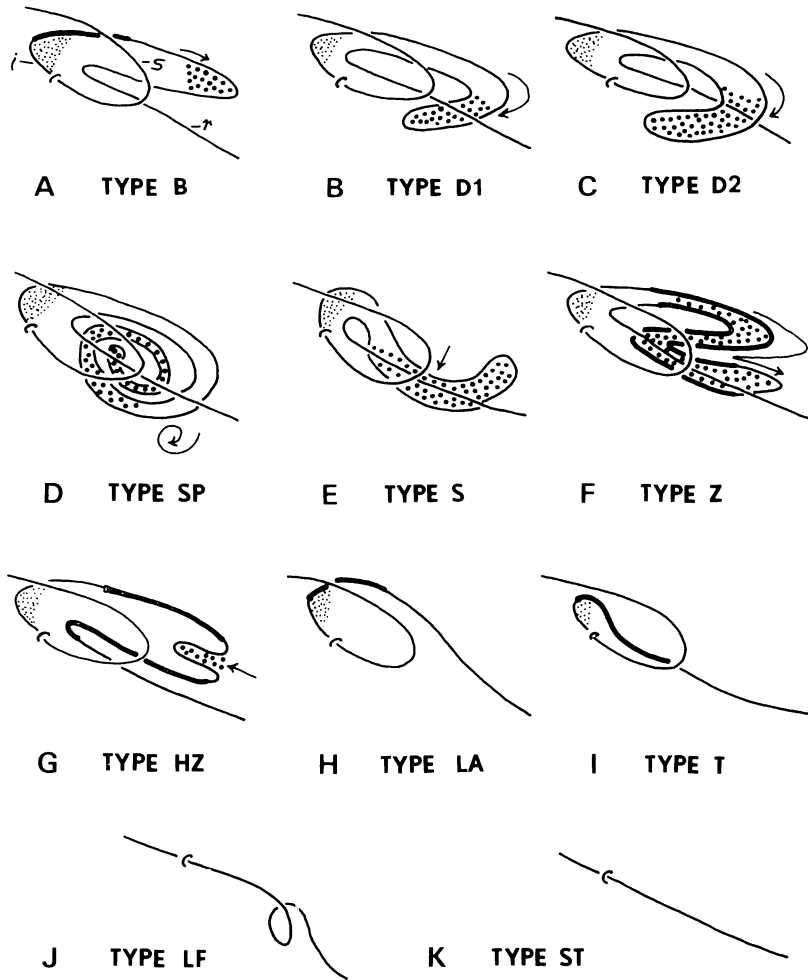
Fig. 1. Left side-view of eleven basic types of actinopterygian intestinal patterns. A: Type B. B: Type D1. C: Type D2. D: Type SP. E: Type S. F: Type Z. G: Type HZ. H: Type LA. I: Type T. J: Type LF. K: Type ST. i, intestine; r, rectum; s, stomach. Arrows, coiling (or folding) directions of loop a; fine stippled areas, loop f; heavy stippled areas, loop a; heavy lines, specific sections of the patterns (see text for explanation); ─(─, junction of stomach and intestine.

(Suyehiro, 1942; Greenwood, 1968; Nelson, 1972). The loop formed by the anterior section of the intestine at the front of the peritoneal cavity I designate **loop f** (first loop; Fig. 1, fine stippling). By definition, this loop can be found in species in which the stomach is not straight or I-shaped. The intestine in the rear of the peritoneal cavity commonly forms another loop, which I designate **loop a** (Fig. 1, heavy stippling). Loop a may be recognized in most cases, because the length of the intestine between its beginning and the tip of the loop, and the length from the tip of the loop to the anus, are about the same. With this mid-intestinal position as a basic criterion, mistakes in recognizing this loop will be few. Sometimes, however, the intestine is long and the pattern too complex to recognize loop a. In such cases, comparisons may be limited to the overall winding tendencies of the intestine, not the exact numbers and shapes of loops.
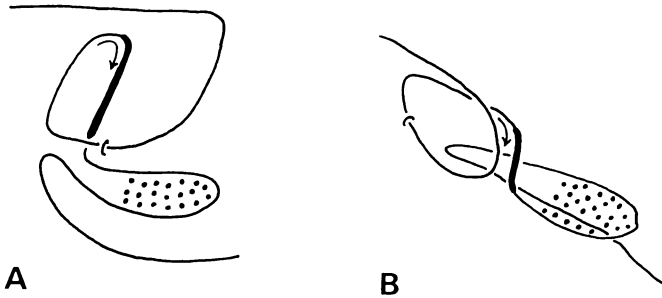
Fig. 2. Left side-view of the intestinal pattern of *Mene annocarolina* (A) and *Lumpenus lumpretaeformis* (B). Arrows, the downward bending of the anterior section of the intestine (heavy line); stippling, loop a; —(—, junction of stomach and intestine.
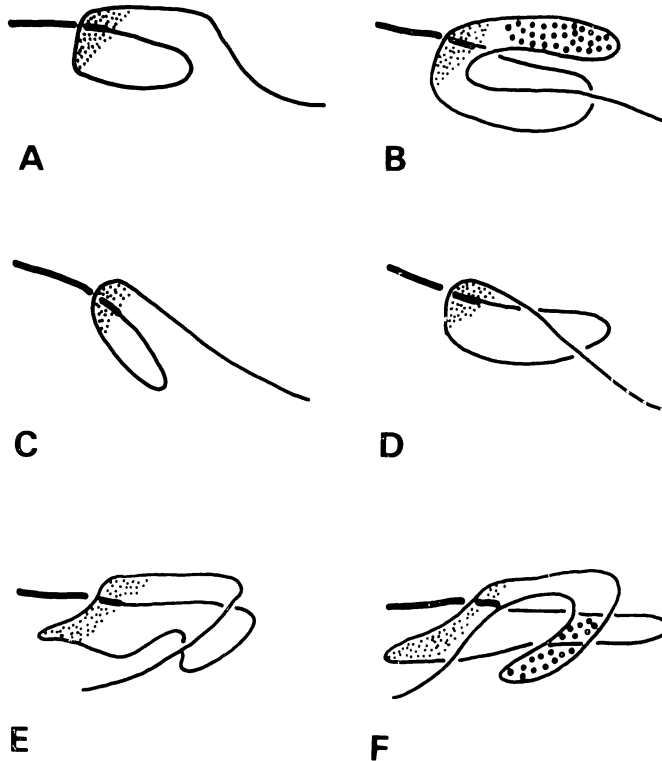

Fig. 3. Left side-view of the intestinal patterns of six atherinoids. A: *Allanetta harringtonensis*. B: *Atherinops affinis*. C: *Membras vagrans*. D: *Menidia menidia*. E: *Chilatherina* sp. F: *Melanotaenia nigrans*. Fine stippling, loop f; heavy stippling, loop a; heavy line, esophagus.

Types of intestinal patterns

Actinopterygian patterns can be classified into eleven basic types with reference to the variations of loop f and loop a. They are types B, D1, D2, SP, S, Z, HZ, LA, T, LF, and ST (Fig. 1 A~K).

Type B: Loop f is to the right of the esophagus, and loop a extends horizontally to the posterior part of the peritoneal cavity (Fig. 1A). This is the basic and most widely distributed pattern in acanthopterygians, although it occurs also in some pre-acanthopterygian
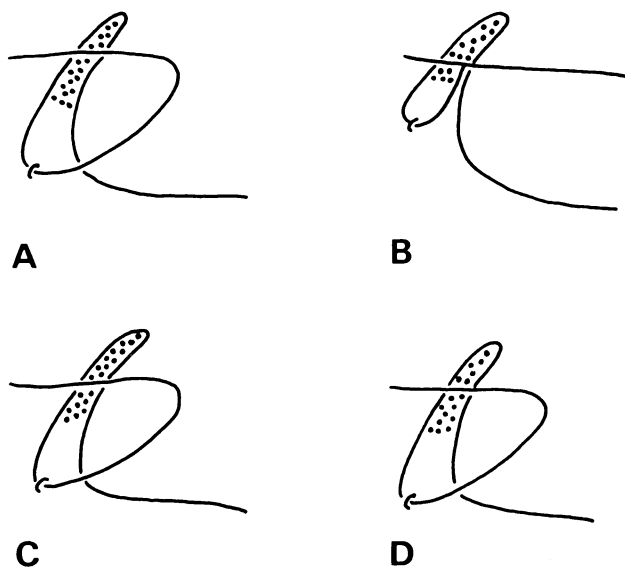
Fig. 4. Left side-view of the intestinal pattern of A: *Bostockia porosa*. B: *Astrapogon stellatus*. C: *Cheilodipterus macrodon*. D: *Glossamia aprion*. Stippling, loop a; —(—, junction of stomach and intestine.

teleosts. Nelson (1972) reported the same pattern in primitive actinopterygians, *Acipenser oxyrhynchus* (Acipenseridae) and *Lepisosteus platyrhincus*. Among the perciforms I have studied, the vast majority (more than 80%) have this pattern (Mok, 1978). It is, therefore, a generalized or primitive character state for acanthopterygians as a whole.

There are some perciforms with patterns that seem to be variants of Type B. In *Mene annocarolina* (Menidae) and *Lumpenus lumpretaeformis* (Stichaeidae) (Fig. 2A and B, respectively) the patterns are similar in that the anterior section of the intestine bends downward (arrows in these illustrations show the bending direction of that section of the intestine).

In osteoglossiforms and some atherinoids loop f occurs left of the esophagus and stomach (Suyehiro, 1942; Nelson, 1972). Nelson considered the left position of loop f as an apomorphic character of osteoglossomorphs (including hiodontids). Interestingly, loop f of atherinoids, *Allanetta harringtonensis*, *Atherinops affinis*, *Membras vagrans*, and *Menidia menida* (Atherinidae), *Chilatherina* sp., and *Melanotaenia nigrans* (Melanotaeniidae) (Fig. 3) all occur left of the esophagus and sto-

mach. I have not yet examined the patterns of Isonidae, Neostethidae, and Phallostethidae. A survey of these groups would be helpful in understanding the generalized (or primitive) pattern of this suborder.

Loop a of Type B generally does not bend. Exceptions occur in loop a of *Bostockia porosa* (Serranidae), *Glossamia aprion*, *Cheilodipterus macrodon*, *Astrapogon stellatus* (Apogonidae), and *Doratonotus megalepis* (Labridae) which distinctively tilt upward at a very steep angle (Fig. 4).

Type D1: Loop a winds dextrally to the right of the rectum (Fig. 1B). Type D1 has a broad distribution among perciforms. Some examples are *Scomberoides toloo*, *Vomer declivifrons* (Carangidae), *Cirrhitichthys falco* (Cirrhitidae), *Kuhlia taeniura*, *K. malo* (but not in *K. marginata* and *Nantherina balstoni*, Kuhliidae), *Gnathodentex aurolineatus*, *Monotaxis grandoculis* (Lethrinidae), *Monodactylus falciformis* (Monodactylidae), *Oplegnathus* sp. (Oplegnathidae), *Pseudopriacanthus atlus* (Priacanthidae), *Dampieria cyclophthalma*, *Gramma* sp. (Pseudochromidae), *Stellifer rastrifer* (Sciaenidae), *Amniataba percoides* (Teraponidae), and *Trichodon trichodon* (Trichodontidae). This type does not characterize a
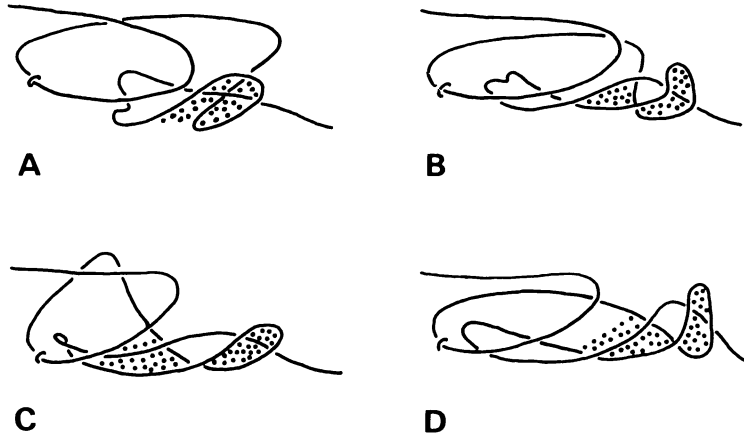
Fig. 5. Left side-view of the intestinal pattern of A: *Archosargus probatocephalus*. B: *Bryostemma nigator*. C: *Holocentrus rufus*. D: *Hexagrammos decagramma*. Stippling, loop a; —(—, junction of stomach and intestine.

genus or family as a whole, but might be applied to the interpretation of species inter-relationships.

Type D1 is uncommon in non-perciform actinopterygians. Among those examined, I have seen this type in *Myoxocephalus quadricornis* (Cottidae), *Limanda* sp. (Pleuronectidae), and *Achirus lineatus* (Soleidae) (Mok, 1978). Ochiai (1966) found Type D1 in some Japanese soles *Liachirus melanospilus* and *Pardachirus pavoninus*.

Type D2: Loop a winds dextrally to the left of the rectum and may extend anteriorly to the left of the stomach (Fig. 1C). Type D2 is limited to *Chironemus marmoratus* (Chironemidae), *Dentex japonicus* (Sparidae), and *Nomeus gronovii* (Nomeidae) among the perciforms examined.

In two Perciforms, *Archosargus probatocephalus* (Sparidae) and *Bryostemma nigator* (Stichaeidae), and also in some non-perciform teleosts such as *Holocentrus rufus* (Holocentridae) and hexagrammines (*Hexagrammos* spp. and *Agrammus agrammus*) loop a runs underneath the rectum and folds upward to the left of the rectum (Fig. 5). These character states of the position of the tip of loop a are apomorphic.

Type SP: The long loop a winds dextrally to the right of the rectum, forming a spiral intestinal mass (Fig. 1D). Type SP has a limited distribution within the Perciformes.

Examples include most acanthurids (Mok, 1977), anabantoids (e.g., *Colisa lalia*, *Macropodus opercularis*, *M. viridiauratus*, *Trichogaster trichopterus*, *Helostoma temmincki*, *Osphronemus goramy*), siganids (e.g., *Lo vulpinus*, *Siganus rostratus*), scatophagids (*Scatophagus argus*), chaetodontids, and stromateids (e.g., *Pampus argenteus*). Among non-perciform actinopterygians, it has only been found in a few ostariophysans (e.g., *Hypostomus* sp. and *Loricaria cataphracta*) and cyprinodontoids (e.g., *Goodea* sp.).

The exact patterns of the aforementioned group differ to various degrees. The intestinal patterns of anabantoids, siganids, and scatophagids reveal a greater similarity between themselves than to the other groups with the Type SP. Loop a of these three groups is the only major loop and is coiled strictly in a spiral. The patterns of acanthurids (Mok, 1977), chaetodontids, and stromateids diverge from this basic pattern (Mok, 1978).

Type S: The middle part of loop a is slightly depressed, and loop a is to the right of the rectum (Fig. 1E). This type occurs only in adult *Dipterygonotus gruveli* (Emmelichthyidae), *Premnas biaculeatus* (Pomacentridae), *Psenopsis anomala* (Centrolophidae) and juvenile *Amphiprion ocellaris* (Pomacentridae).

Type Z: The winding of both sides (or the anterior and posterior sections; heavy
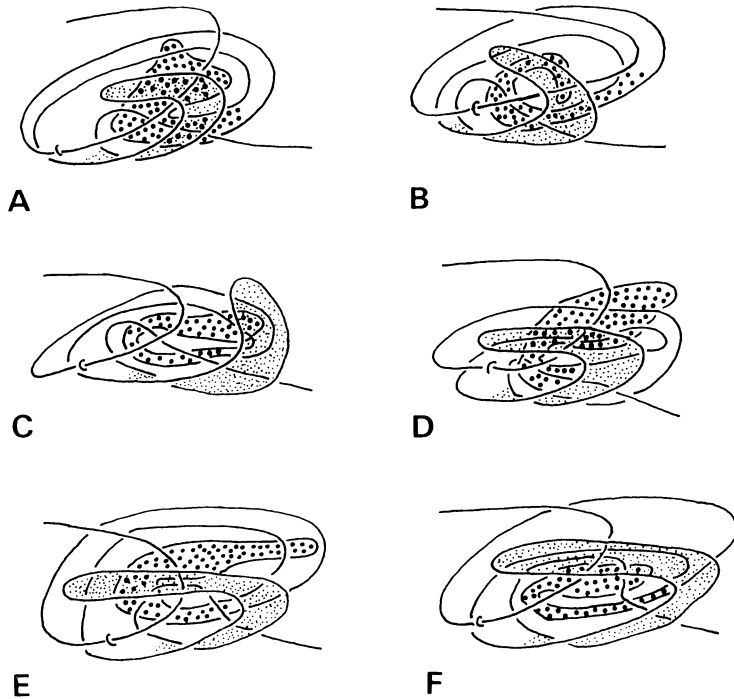
Fig. 6. Developmental change of the intestinal pattern of *Acanthurus bahianus*. A: 30 mm. B: 32 mm. C: 50 mm. D: 59 mm. E: 75 mm. F: 100 mm. Fine stippling, loop b; heavy stippling, loop a; —(—, junction of stomach and intestine.

lines in Fig. 1F) of loop a follows a Z-shaped pathway (Fig. 1F; arrow indicates the winding route) to the right of the rectum. It occurs widely in perciforms such as *Crinodus lophodon* (Aplodactylidae), kyphosids, most pomacentrids (also see Aoyagi, 1941), *Agonostomus monticola* (Mugilidae), and *Psenes cyanophrys* (Nomenidae). Loop a of *Cichlasoma heterospilum*, *C. spilurum*, *Haplochromis eucinostomus*, and *Melanochromis johannii* (Cichlidae) also winds in a Z-shaped pathway. However, the homolog of loop f cannot be recognized in the examined cichlids (Mok, 1978).

Type HZ: Loop a turns at the rear of the peritoneal cavity and extends anteriorly such that the tip is located between the anterior and posterior section of loop a (Fig. 1G; heavy lines represent these sections). This type can be distinguished from Type Z in that the posterior section of loop a does not wind in a Z-shaped manner.

There are only a few examples of Type HZ found in perciforms: *Leiognathus rivulatus*

(Leiognathidae), *Abudefduf saxatilis*, and young *A. taurus* (Pomacentridae). Other actinopterygians with this pattern are monacanthids (Mok, 1975).

Type LA: Loop f occurs, and loop a is absent (Fig. 1H). This type occurs in actinopterygians with a short intestine having only one loop. It is not limited to specific groups, but occurs in various actinopterygian families.

Type T: The portion of the intestine corresponding to the convex section of loop f in Type B and Type LA (Fig. 1A, H; heavy lines) is concave (Fig 1I; heavy line) and loop a is absent. *Brachyistius frenatus* (Embiotocidae) is the only examined perciform with this pattern. However, Type T consistently characterizes the patterns of some cyprinodontoids, such as *Profundulus punctatus* (Cyprinodontidae), *Oryzias latifer* (Oryziatidae), *Belonesox belizanus*, *Gambusia* sp. (Poecilidae). This pattern has not been found in other actinopterygians.

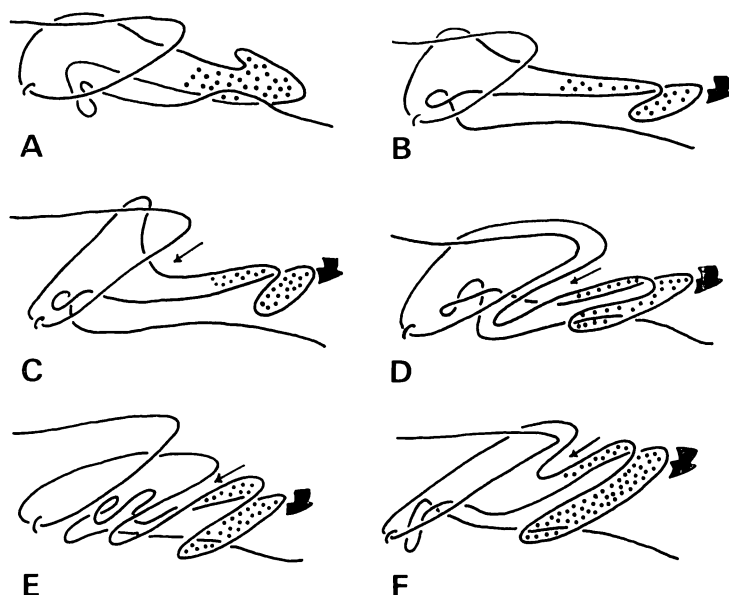**Type LF:** Loop f is absent (Fig. 1J).

Fig. 7. Developmental change of the intestinal pattern of *Nomeus gronovii*. A:
19 mm. B: 42 mm. C: 54 mm. D: 60 mm. E: 62 mm. F: 70 mm. Large
arrows, dextral winding tendency of loop a; small arrows, leftward folding of
the anterior intestinal section; stippled areas, loop a.

Stomach of the species with this type is
straight. The anterior section of the intestine
proceeds to the rear of the peritoneal cavity
where it turns and runs forward. Type LF
occurs at least in some species of the follow-
ing perciform families: Carangidae, Cichlidae,
Ephippidae, Serranidae, Gobioididae, Clin-
idae, Chaenopsidae, Gobiidae, Pholididae,
and Ammodytidae (Mok, 1978). In non-
perciform actinopterygians, Type LF occurs
in some species of the families Cyprinidae,
Gasterosteidae, Macrorhamphosidae, and Tri-
glidae. Loop f is absent also from all tetra-
odontids, diodontids, molids (Mok, 1975) and
triodontids (Breder and Clark, 1947). Type
LF is most widely distributed among gobioids
and blennioids of the families Chanopsidae,
Clinidae, and Eleotridae.

Type ST: The simplest pattern is the
straight gut (Fig. 1K). In actinopterygians,
it occurs in some species of the families
Gobiesocidae, Belonidae, Exocoetidae, Aulo-
stomidae, Syngnathidae, Symbranchidae, Ech-
eneidae, Odacidae, Kraemeridae, Microdesm-
idae, and Triacanthodidae (Mok, 1975, 1978).

Developmental variation

To determine possible ontogenetic change
in intestinal patterns specimens of various
sizes were studied in *Acanthurus bahianus* (10
specimens, 30~100 mm SL), *Lepomis gibbosus*
(36 specimens, 24~70 mm SL), *Nomeus gronovii*
(6 specimens, 19~70 mm SL). The patterns
of *A. bahianus* and *N. gronovii* are shown in
Figs. 6 and 7, respectively. The patterns of
the individuals of *L. gibbosus* are similar.

Little ontogenetic change was seen in the
acanthurids examined. All specimens of *A.
bahianus* examined are similar in having two
loops—loop a and loop b; the latter is unique
to acanthurids and is located left of the
stomach (Mok, 1977). The pattern develops
early (prior to 30 mm SL), and no further
change takes place beyond this stage.

Unlike *A. bahianus*, *N. gronovii* manifests
developmental change in specimens between
19~70 mm. Loop a can be recognized in all
specimens; a dextral winding tendency of
loop a is found in these developmental stages
(Fig. 7A~F; heavy stippling indicates loop a;
large arrows show the dextral developing
tendency of loop a). A leftward folding

appears at a standard length of 54 mm (Fig. 7C; small leftward pointing arrow). This folding tends to increase in depth during development (Fig. 7D~F). The pattern typical of this species is formed in specimens of

60 mm or longer in standard length.

On the basis of these observations, it seems that patterns typical of adults develop early, and can be observed in early and late adult stages as was shown also for pomacentrids

Table 1. Distribution of the types of actinopterygian intestinal patterns. 1) also see Kafuku, 1958; 2) also see Matsubara, 1943; 3) Mok, 1975; * dominant type unknown due to the small sample size of the examined species; ** dominant type undistinguishable due to the equal occurring frequencies of the types; + presence of an intestinal pattern; ⧺ dominant type of the group concerned.

| Taxon	Intestinal type											
	B	D1	SP	S	Z	LA	HZ	T	LF	ST	D2	Others
Chondrostei*	+					+						
Ginglymodi*									+			
Halecomorphi	⧺											
Osteoglossomorpha	+											⧺
Elopomorpha	+					⧺			+			
Clupeomorpha	+					⧺						+
Ostariophysi[1]	+					+						⧺
Protacanthopterygii	+					⧺						
Paracanthopterygii**	+					+				+		
Atherinomorpha**	+		+					+	+	+		+
Acanthopterygii												
Beryciformes*	+											+
Zeiformes*	+					+						
Lampridiformes*									+			
Gasterosteiformes**									+	+		
Channiformes	⧺											
Synbranchiformes										⧺		
Scorpaeniformes[2]	⧺	+				+						
Perciformes	⧺	+	+	+	+	+	+		+	+	+	+
Percoidei	⧺	+	+	+	+	+	+			+	+	
Mugiloidei	+											⧺
Sphyraenoidei						⧺						
Polynemoidei*	+											
Labroidei	⧺					+				+		
Trachinoidei	⧺	+		+		+						
Notothenoidei	⧺											
Blennioidei**	+					+			+	+		+
Icosteoidei												⧺
Ammodytoidei						⧺						
Callionymoidei												⧺
Gobioidei	+					⧺				+		
Kurtoidei**	+					+						
Acanthuroidei			⧺									+
Scombroidei	+					⧺						
Stromateoidei	+		+	+	⧺							
Anabantoidei**	+		+									
Luciocephaloidei	⧺											
Mastacembeloidei						⧺						
Pleuronectiformes	⧺	+				⧺						+
Tetraodontiformes**,[3]	+					+			+	+		+
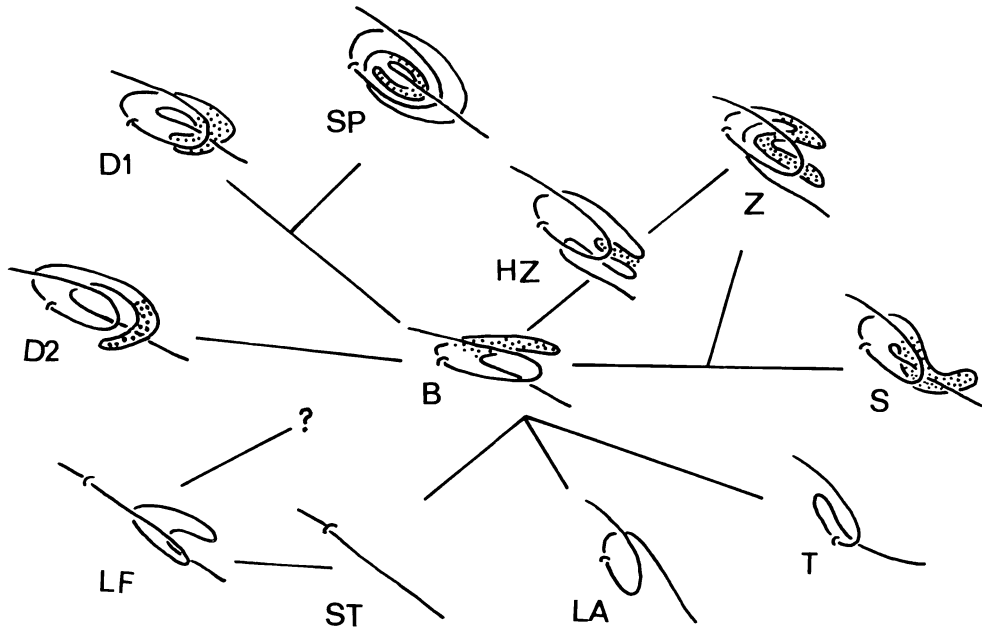
Fig. 8. A hypothetical scheme showing the possible interrelationships among the eleven types of intestinal patterns generally found in actinopterygians.

(Fukusho, 1969).

Distribution and interrelationships of the actinopterygian intestinal patterns

The distribution of the types of patterns in actinopterygians is summarized in Table 1. Type LA dominates the patterns of lower actinopterygians, such as elopomorphs, clupeomorphs, protacanthopterygians. Type B becomes the dominant one in some acanthopterygians including channiforms, scorpaeniforms, perciforms, and pleuronectiforms (also see Ochiai, 1966). Several of the patterns are unusual in perciforms: types S, Z, D2, HZ, and SP. Type HZ, which is limited to a few perciforms, becomes the dominant type in monacanthids and balistids. Its synapomorphic nature in Tetraodontiformes is unquestionable.

Ontogenetic change in intestinal patterns and frequency of particular intestinal pattern associated with members of monophyletic or hypothetical monophyletic groups should help elucidate intestinal pattern interrelationships. Information on ontogenetic change is limited in this study because specimens of different sizes were not usually available and no developmental change was observed in those

specimens that were examined. However, the developmental changes of the intestinal patterns of pomacentrids *Abudefduf taurus* and *Amphiprion ocellaris* suggest that Type Z can be develped from Type HZ or Type S. Smaller individuals of *A. taurus* (55 mm) and *A. ocellaris* (17 mm) have types HZ and S, respectively; whereas larger individuals of these species (135 and 42 mm, respectively) develop the Type Z pattern. A small individual of *Microcanthus strigatus* (87 mm; Kyphosidae) has Type D1, whereas a larger individual (122 mm) has Type SP (Mok, 1978). This developmental change suggests the close relationships of Types D1 and SP. The aforementioned observations provide direct indication of the close relationship between these intestinal patterns (Fig. 8).

In 48 cases of association between two types of patterns found in 31 monophyletic groups (Acipenseridae, Clupeidae, Cobitidae, Cyprinodontidae, Gasterosteiformes, Scorpaeniformes, Cottidae, Carangidae, Centrarchidae, Cirrhitidae, Echeneidae Embiotocidae, Kuhliidae, Leiognathidae, Nemipteridae, Percidae, Pomacentridae, Pseudochromidae, Sciaenidae, Sparidae, Teraponidae, Labridae, Odacidae, Pho-

lididae, Gobiidae, Kurtidae, Scombridae, Belontiidae, Pleuronectidae, and Soleidae), the frequencies of 15 kinds of association (or frequencies of co-occurrence) of the types were obtained and they are listed in decreasing order as follows: B-LA, 17; B-D1, 9; B-ST, 3; D1-LA, 3; B-S, 2; LA-ST, 2; B-D2, 1; B-HZ, 1; B-Z, 1; B-SP, 1; B-T, 1; S-Z, 1; D1-S, 1; LA-T, 1; LF-ST, 1 (Mok, 1978). Chi-square test of these data ($x^2=27.8796$, $df=10$, $P\leq0.05$) leads to the conclusion that the appearance of the types of intestinal patterns in a monophyletic group is not an independent event. This conclusion suggests that certain types tend to associate. Only 15 kinds of the 55 possible types of association between two of the eleven types appear in this sample. The extraordinarily high frequency of association between types B-LA and B-D1 suggests that Type B is closely related to types LA and D1 (Fig. 8). Grounded on the occurrence of their association within monophyletic groups and also on ontogenetic evidence, it is hypothesized that a close relationship exists between types B, HZ, S, and Z (Fig. 8). Type B is also related to types D2, T, and ST. The multiple association of Type B to the other types suggests that it is the most generalized type, at least for acanthopterygians, which changes into other intestinal patterns (Fig. 8).

The problem with other simple patterns, types T, LF, and ST, are more complicated because they may be independently evolved from various types by significant or mild reduction of intestinal length. But on the basis of the present data, Type T is related to types B and LA; Type ST is related to types B, LA, and LF (Fig. 8). No association between types B and LF was found.

Discussion

At the beginning of this study, I was bewared of the possible drawbacks of intestinal pattern as an indicator of phylogeny: (1) *high* intraspecific variation, (2) as a consequence of ecological adaptation, similarity in intestinal patterns may only indicate convergence or parallelism rather than possible monophyly, (3) the simple patterns of carnivores (due to their short intestine) carry too little information to be of any phylogenetic significance, (4) the long intestine of herbivores may associate with high variation in the pattern to such a degree that phylogenetic significance of the intestinal pattern diminishes. However, the results of this study indicate that these drawbacks have minimal "negative" effect on the phylogenetic significance of intestinal pattern (also see below).

Intraspecific variation in intestinal pattern was considered to be insignificant (Fukusho, 1969: Mok, 1977, 1978). Observations made on a limited number of individuals will, therefore, give a reliable description of the species-specific pattern.

Ecological factors such as feeding habits do not directly and significantly determine the intestinal pattern. To some extent, feeding habits may correlate with intestine length, a determinant factor of intestinal pattern. Fishes with a similar food habit may be different in their intestine length, but unique characteristic patterns may still be retained. Similarly, related species with different feeding habits were also found to share a unique intestinal pattern (Mok, 1977).

The short intestine of carnivores and piscivores shows a simple pattern and generally contains less information but does not necessarily reduce the phylogenetic significance of the intestinal pattern. The unique pattern of piscivorous *Hexagrammos* and *Agrammus* (Hexagramminae; see above) is an adequate example.

Intestinal pattern is determined by intestine length, volume and shape of the peritoneal cavity and developmental mechanism. The pattern complexity is dual in nature, both quantitative and directional. As such, it can be measured by the numbers of loops and/or by the directional changes that a loop displays. For instance, the more loops a pattern is composed of, the more complex it is. Alternatively, if loop a is the only loop, a pattern with a dextral-winding loop a is more complex than a pattern with a straight loop a. With equal volume of the peritoneal cavity, a species with a long intestine is likely to have a pattern more complex than a species with a short intestine. For example, chaetodontids have an oval, small peritoneal

cavity and a long intestine which generally leads to complex patterns. High complexity does not normally correlate with high in-group variation in intestinal pattern. Conversely, intestinal patterns are generally consistent as examplified by cyprinoids, mugilids, chaetodontids, kyphosids, blenniids, and acanthurids (Mok, 1977, 1978). It is not true that a long intestine is always associated with a complex pattern, because the size and shape of the peritoneal cavity also correlate with complexity. In most pleuronectiforms, for example, the peritoneal cavity ends in front of the first haemal spine, and a dextral-winding loop a occurs. But in some soleid species (e.g., *Heteromycteris japonicus* and *Trinectes maculatus*) the intestine is long, and the right secondary peritoneal cavity (the posterior extension of the cavity on the right side of the haemal spines) makes room for the intestine (also see Ochiai, 1966). Loop a of these species, is straight and without the dextral winding tendency. It seems generally true that fishes with a long peritoneal cavity tend to have a simple pattern, e.g., *Ammodytes personatus* (Ammodytidae), *Atherina bleekeri* (Atherinidae) and *Trichiurus haumela* (Trichiuridae) (Suyehiro, 1942).

Differences in the patterns may sometimes be found in two groups with similar determinant factors. For instance, soleids have either sinistral or dextral coiling loop a within the right secondary body cavity which is the shared determinant factor. Conversely, specialized patterns have been observed in groups that differ in certain determinant factors (e.g., shape and volume of the acanthurine and zancline peritoneal cavity). These phenomena suggest that intestinal pattern is governed by an additional determinant factor, the developmental mechanism, which may enhance the phylogenetic significance of intestinal pattern.

Members of numerous groups traditionally considered as monophyletic share specialized intestinal patterns: osteoglossomorphs, homalopterids, atherinoids, hexagrammines, chaetodontids (not including pomacanthids), kyphosids (including girellids and scorpids), mugilids, ophioblennines, salariines (according to the taxonomic scheme of Norman, 1957), acanthurids (including *Zanclus*) and mon-

acanthids (Mok, 1978). Their sharing of the specialized character indicate that intestinal pattern reveals congruent evidence.

In summary, the low conspecific variation, non-random variation in groups with complex patterns, and resemblance of intestinal patterns among members of phylogenetically related groups suggest that intestinal patterns provide valuable information for the understanding of phylogenetic relationships. The present classification of the intestinal patterns is an attempt to set up an information system for detailed comparisons. The criteria that I adopt for this classification are a few among others which are applicable to the study of intestinal patterns.

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条鰭類の腸型の分類

Hin-Kiu Mok

条鰭類の 596 種について腸型を調査，分類し，個体変異，成長に伴う変異，各型の出現，相互関係を検討した．腸型は種内変異性が低く，複雑な型をもつグループでは変異に定向性があり，単系の種間では類似している．これらのことは魚類の腸型が系統関係についての有意な情報を提供することを示している．