

Certain Lateral-Line Canals of the Head in Cyprinid Fishes, with Particular Reference to the Derivation of North American Forms

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Abstract In all native American cyprinids the supraorbital and infraorbital lateral-line canals of the head are separate. American forms differ in this feature from tropical cyprinid groups but agree with the leuciscines of temperate Eurasia. Within the leuciscine cyprinids, particularly close resemblances in head canal patterns between Eurasian and American genera are shown by *Leucaspius* and *Notemigonus*, by *Tribolodon* and *Lavinia*, and in the *Phoxinus-Moroco-Chrosomus* complex.

Various ways of classifying the fishes of the family Cyprinidae have been suggested, e.g., by Günther (1868), Regan (1911), Nichols (1938), Tretiakov (1946), Kryzanovsky (1947), Nikolsky (1954), and Banarescu (1968a), but phylogenetic relationships within the family remain obscure. The lateral-line canal system of the head is one of the characteristics that has been used in cyprinid classification, notably by Tretiakov (1946). Nevertheless, papers that deal with the canal configuration of the cyprinid head on a broad comparative basis are few; the most extensive are those of Illick (1956) and Reno (1969), both on North American forms. The present paper is concerned with certain aspects of the canal system that seem to provide leads for the investigation of the derivation of native North American cyprinids. The aspects under consideration are the presence or absence of connections between (1) the supraorbital and infraorbital canals and (2) the preopercular and infraorbital canals.

The cyprinid names used in the present paper are those in the literature or on the bottles of specimens examined. Where some question regarding the use of a generic name is known to the author, the name has been placed in quotation marks.

The names of the canals and the methods of investigation are those of Illick (1956). The canal connecting the lateral line of the body with the one passing around the lower border of the eye is considered a part of the in-

fraorbital canal. In cyprinids a fine jet of compressed air usually suffices for determining the canal pattern, but removal of the flesh from canal areas sometimes clarifies the configuration. Only one or a few of the larger specimens of available species were usually examined. However, individual and population variations in cyprinid head-canal configuration are well known. As an example of individual variation, one of two available specimens of *Abbottina*, which is listed in Table 1 as having the supraorbital and infraorbital canals separate, has a connection between these two canals on one side of the head. Variation in canal pattern appears to be particularly common in certain species, e.g., *Gobio gobio* (Tretiakov, 1946).

The head-canal configuration in *Carassius* (Illick, 1956), *Barbus*, etc., is here considered to be the basic type in the Cyprinidae, primarily because a very similar pattern occurs in such characins as *Brycon* (Weitzman, 1962). In these genera all of the head canals form a single interconnected system.

Among cyprinids fragmentation of this continuous system has repeatedly occurred, probably in association with various factors. The most easily identified association is that between fragmentation and small adult size. The lateral-line canal system of the head, like that of the body, develops relatively late in ontogeny (Lekander, 1949). In *Carassius auratus* the canal system is still incomplete when the fish attains a length of 6 cm. (Disler, 1960), but

Table 1. Examined Old World cyprinids without and with a break between the supraorbital and infraorbital canals of the head. The species on which the generic listings are based are recorded in the material examined.

| | Southern Asia and Africa | Europe | Japan, China, and Siberia |
|---|-----------------------------|-----------------|------------------------------|
| Genera with a connection between the supraorbital and infraorbital canals | 8 ¹ | 1 ² | 17 ³ |
| Genera with a break between the supraorbital and infraorbital canals | 2 ⁴ | 19 ⁵ | 17 ⁶ |

¹ *Barbus*, *Barilius*, "Chela", *Cyclocheilichthys*, *Danio*, *Esomus*, *Labeo*, and *Rasbora*.

² *Barbus*.

³ *Acheilognathus*, *Carassius*, *Ctenopharyngodon*, *Culter*, *Cyprinus*, *Erythroculter*, *Gnathopogon*, *Hemibarbus*, *Hemiculter*, *Ischikauia*, *Megalobrama*, *Parabramis*, *Paracheilognathus*, *Pungtungia*, *Sarcocheilichthys*, *Tribolodon* (in part, see text), and *Xenocypris*.

⁴ *Amblypharyngodon* and *Rasborichthys*.

⁵ *Abramis*, *Acanthalburnus*, *Alburnoides*, *Alburnus*, *Aspius*, *Blicca*, *Chalcalburnus*, *Chondrostoma*, *Gobio*, *Leucaspis*, *Leuciscus*, *Pelecus*, *Phoxinus*, *Rhodeus*, *Rutilus*, *Scardinius*, *Squalius*, *Tinca* and *Vimba*.

⁶ *Abbottina*, *Acanthorhodeus*, *Aphyocypris*, *Aristichthys*, *Biwia*, *Elopichthys*, *Hemigrammocypripis*, *Hypophthalmichthys*, "Moroco", *Ochetobius*, *Opsariichthys*, *Phoxinus*, *Pseudogobio*, *Pseudoperilampus*, *Pseudorasbora*, *Tribolodon* (in part, see text), and *Zacco*.

in many cyprinids it is completed at a considerably smaller size. In the smallest members of various cyprinid groups, e.g., *Notropis bifrenatus* (Harrington, 1955), "*Hybopsis*" *crameri* (Reno, 1969), *Iotichthys* (Illick, 1956), and *Leucaspis* (Disler, 1960), the canals in the adult are represented by a number of separate segments. In such fishes it appears that the invaginations prerequisite to the formation of canals between these segments (Lekander, 1949) have failed to develop. (Sometimes a canal develops but lies superficial to the bone in which it is normally enclosed.) The canal system in such species not only appears incomplete but tends to be variable in its adult representation, e.g., in "*Hybopsis*" *crameri* (Illick, 1956; Reno, 1969). The same phenomenon of apparently incomplete development associated with variability of adult representation occurs in *Phoxinus phoxinus* (Lekander, 1949), though factors other than size may be involved here.

There seems to be a general pattern in the way an originally interconnected head-canal system becomes fragmented in various cyprinids. The sections of the canal system that are the last to form in *Carassius* (Disler, 1960) are the areas in which breaks tend to occur in the fragmented representation, i.e., the median section of the supratemporal commis-

sure, the links (1) between the circumorbital and pterotic parts of the infraorbital canal and (2) between the mandibular and preopercular parts of the mandibulopreopercular canal, and the connections (1) between the supraorbital and infraorbital canals and (2) between the mandibulopreopercular and infraorbital systems. Thus, as the translation of Disler (1971: 294) states: "In canal structure the adult *Leucaspis* is similar not to the adult *Abramis* and *Rutilus*, but to their young."

A reduced head-canal system is often associated with an incomplete lateral line on the body. This association occurs, for example, in the following cyprinids, none of them of large adult size: *Iotichthys* and *Notropis bifrenatus* in North America; *Leucaspis*, *Phoxinus*, and *Rhodeus* in Europe; *Aphyocypris* and *Hemigrammocypripis* in eastern Asia; and *Amblypharyngodon* and *Rasborichthys* in south-east Asia. Since the same sort of reduction in lateral-line canal configuration occurs in various cyprinid lineages it follows that similar fragmentation patterns in the canal system of the head may have evolved independently.

A connection between canals that in a particular group are normally separated seems to have evolved less frequently than fragmentation. Thus, some specimens of *Hybopsis*, a complex in which the supraorbital and in-

fraorbital canal are normally separated, have connections between the two systems (Reno, 1969). An apparently redeveloped connection between the preopercular and infraorbital canals is discussed below.

The great majority of native North American cyprinids have complete lateral lines on the sides and are not dwarfed forms. In none of them is a connection regularly developed between the supraorbital and infraorbital canals. The consistency of this interruption suggests that the characteristic was already stabilized in the stock (or stocks) that entered North America and that the relationships of American cyprinids should be looked for among Old World forms with such an interruption.

Old World cyprinids display a geographic pattern (Table 1) in respect to the presence or absence of a gap between the supraorbital and infraorbital canals. With the exception of two genera made up of relatively small forms with incomplete lateral lines on the body, all southeast Asian and African cyprinids have the supraorbital and infraorbital canals connected; the tropical cyprinids are therefore dismissed from further consideration here. Among the more northern forms there is a mixture of cyprinids with and without such a connection. Among the European forms examined, most of the genera with such a gap fall into the leuciscine and abramidine sections of Günther (1868), but *Tinca*, *Gobio*, and *Rhodeus* also have this interruption. Regan (1911, p. 29) states that the aberrant *Tinca* "seems to be nearer to *Barbus* than to *Leuciscus*." *Gobio* has been allocated to a separate gobionine group by Berg (1949; see also Taranetz, 1938; Ramaswami, 1955; and Banarescu and Nalbant, 1965). Among Günther's group Rhodeina (Acheilognathinae of Banarescu, 1968a) *Rhodeus*, *Acanthorhodeus*, and *Pseudoperilampus* have the lateral line on the body incomplete and the supraorbital and infraorbital canals separate, but in *Acheilognathus* and *Paracheilognathus* the lateral line of the body is complete and there is usually a connection between the supraorbital and infraorbital canals of the head. Within the Rhodeina the development of a break between

the supraorbital and infraorbital canals does not seem to be closely related to size, for the specimens of *Acheilognathus* and *Paracheilognathus* available to me at least are smaller than those of *Acanthorhodeus* which have such a gap. Again, the presence or absence of this particular break within the schizothoracine cyprinids (Disler, 1960) does not seem to be size-related, and the same is true among gobionine genera (Ramaswami, 1955).

Günther's (1868) Abramidina also contains some Old World genera with a break between the supraorbital and infraorbital canals and others with a junction between these two canals. However, an examination of Günther's abramidine genera suggests, not a transition of canal pattern within a related group of fishes as in the Rhodeina, but rather that his Abramidina is made up of two quite different cyprinid types. Aside from certain small forms that probably belong with this group (*Rasboraichthys*, *Aphyocypris*, and *Hemigrammocypripis*), the Asiatic members ("*Chela*", *Culter*, *Erythroculter*, *Hemiculter*, *Ischikauia*, *Megalobrama*, and *Parabramis*) all have the supraorbital canal continuous with the infraorbital canal. By contrast, all of the European members examined (*Abramis*, *Alburnoides*, *Blicca*, *Chalcalburnus*, *Leucaspis*, *Pelecus*, and *Vimba*) have a break between the two canals. The canal configurations of *Abramis* and *Leuciscus* are almost identical, which suggests that the European Abramidina are close to the Leuciscina, but that Günther's Asiatic abramidines are not. Regan (1911, p. 29) made about the same point: Günther's "Rasborina and Daniona should be united and some of the Abramidina should be added to this group, some to the Leuciscina." Nikolsky (1954) unites Günther's European Abramidina with the Leuciscina and places the Asiatic members in a separate subfamily Cultrinae; Nikolsky's arrangement, which differs in certain respects from that of Banarescu (1967), will be accepted here.

The native American cyprinids have usually been placed with the abramidine-leuciscine group that dominates the European cyprinid fauna. The supraorbital-infraorbital canal configuration corroborates such a placement,

which will be accepted here. However, a caveat on this matter may be noted. First, there are a large number of non-leuciscine cyprinids, particularly in northeast Asia (see below), that have the same separation of suborbital and infraorbital canals as American forms. Second, some American native cyprinids possess features such as barbels and/or fin spines that do not occur in the Eurasian leuciscine-abramidines.

As compared to Europe or North America, cyprinid interrelationships in northeast Asia appear to be very complex. Northeast Asia differs from the other two geographic areas in that the leuciscine-abramidine group does not dominate the cyprinid fauna, and appears indeed to make up only a small part even of those forms with the supraorbital and infraorbital canals separate (Table 1). Thus *Elopichthys* (with *Ocherobius*) and *Hypophthalmichthys* (with *Aristichthys*) seem to represent highly specialized cyprinid groups without close relatives. *Acanthorhodeus* and *Pseudoperilampus* are rhodeines. *Abbottina*, *Pseudogobio*, *Pseudorasbora* and *Biwia* were placed among the gobionines by Banareescu and Nalbant (1965). *Zacco* and *Opsariichthys* were considered members of the Danionae by Banareescu (1968b). *Hemigrammocyppris* and *Aphyocypris* have the abdomen cultrate behind the pelvis and presumably belong with *Rasbora*, which Banareescu (1967) includes in the Cultrinae. Only *Tribolodon*, "*Moroko*," and *Phoxinus*, among the northeast Asian cyprinids examined, seem to show leuciscine relationships, and it is only these genera that will be considered further below.

A different interruption in the canal system of the head that is almost always present in native American cyprinids is that between the upper end of the preopercular canal and the infraorbital canal (Illick, 1956). By contrast, in *Carassius*, etc. (Ramaswami, 1955), as well as in most European leuciscines, the preopercular canal extends upward through an anterodorsal projection of the opercle and on to a junction with the infraorbital canal. A gap of varying size between these two canals develops repeatedly in cyprinids, notably in small forms with incomplete lateral lines on

the body. It is therefore possible that the various degrees of development of this gap in American cyprinids (Illick, 1956) have all evolved from a single American ancestral type with a relatively complete preopercular canal, e.g., *Notemigonus*. But as already noted, the majority of American cyprinids have a complete lateral line on the body and are not dwarf forms, and it is also possible that the different representations of the preopercular canal-system are independently traceable to two or more origins among Eurasian cyprinids. The data presented below provide some circumstantial evidence for the second alternative.

In occasional specimens of *Notemigonus* and *Lavinia*, but not elsewhere among native American cyprinids, the preopercular and infraorbital canals are connected (Illick, 1956). When such a connection occurs, it is quite different structurally in the two genera: in *Notemigonus* the preopercular canal passes upward through the anterodorsal opercular extension; in *Lavinia* it passes superficial to this extension.

In most specimens of *Notemigonus* the preopercular canal, after passing upward through the opercular extension, ends blindly, i.e., fails to form a connection with the infraorbital canal. The only Old World leuciscine I have examined that duplicates this particular condition is *Leucaspis*. However, unlike *Notemigonus*, *Leucaspis*, as previously noted, contains small fishes with an incomplete lateral line on the body and a fragmented head-canal configuration: its infraorbital and supratemporal canals are both incomplete (Disler, 1960).

Most specimens of *Lavinia*, like many other American cyprinids, have the preopercular canal ending blindly at the top of the preopercle. In the lack of a canal in the opercle *Lavinia* differs from all European leuciscine genera examined except *Phoxinus*. In the presence of a preopercular canal extending across the surface of the opercle in some specimens but not others *Lavinia* closely approximates the condition in the northeast Asian *Tribolodon*. In *T. taczanowskii* the preopercular canal extends upward across the opercle (T. Uyeno, personal communication) to a junction with the infraorbital canal

(Nakamura, 1963, 1969), but in *T. ezoe* and *T. hakonensis* it ends blindly at the top of the preopercle. The most satisfactory explanation of this variability in *Lavinia* and *Tribolodon* seems to be that a connection between the preopercular and infraorbital canals is sometimes redeveloped across the top the opercle. To my knowledge such a redevelopment does not occur elsewhere among leuciscine cyprinids. It may have evolved independently in *Lavinia* and *Tribolodon*. Nevertheless, even the potentiality for such a redevelopment suggests the possibility of some relationship between the two genera.

In some American cyprinids the preopercular canal does not even extend to the top of the preopercle (Illick, 1956), resembling in this respect the Eurasian leuciscines *Phoxinus* and "*Moroco*." This type of head-canal reduction occurs repeatedly in small species with an incomplete lateral line, e. g., *Notropis bifrenatus* (Harrington, 1955), and it may be that *Phoxinus* and the "*Chrosomus*"-type of American cyprinid belong in this category. However, "*Moroco*," sometimes placed in the synonymy of *Phoxinus*, e. g., by Berg (1949) and Banarescu (1964), is made up of somewhat larger fishes with complete lateral lines on the body, but it still has an abbreviated *Phoxinus*-like preopercular canal.

To summarize briefly, the parallels in lateral-line canal configuration between *Notemigonus* and *Leucaspis*, between *Lavinia* and *Tribolodon*, and between "*Chrosomus*" and *Phoxinus* suggest that American cyprinids may have had at least three separate derivations from Eurasian forms.

So far as distinguishing American cyprinids from Eurasian leuciscines is concerned, American forms can be separated by the use of lateral-line canal features discussed above from all but *Tribolodon*, *Phoxinus*, and "*Moroco*."

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Eurasian Cyprinids Examined

The names used below are those on the

bottles; no effort has been made to check identifications. Numbers following the names are University of Michigan Museum of Zoology catalog numbers. The final figure in each entry is the standard length in mm of the largest specimen in the particular lot.

Abbottina rivularis, 70314, China, 78; *Abramisa brama*, 186345, Romania, 138; *Acanthalburnus microlepis*, 174615, USSR, 101; *Acanthorhodeus macropterus*, 174622, USSR, Far East, 97; *Acheilognathus intermedia*, 142975, Japan, 78; *Alburnoides bipunctatus*, 185352, Poland, 78; *Alburnus filippi*, 174613, USSR, 103; *Amblypharyngodon mola*, 187844, Bangladesh, 60; *Aphyocypris chinensis*, 167397, China, 36; *Aristichthys nobilis*, uncataloged material, Thailand (introduced), 134; *Aspius aspius*, 174607, USSR, 140; *Barbus barbus*, 185022, Romania, 109; *B. javanicus*, 155756, Indonesia, 134; *B. maculatus*, 155609, Indonesia, 110; *B. orphoides*, 155750, Indonesia, 121; *Barilius zambezensis*, 189153, Zambia, 89; *Biwia zezera*, 187576, Japan, 45; *Blicca bjorkna*, 174616, USSR, 174; *Carassius auratus*, 186094, Madagascar (introduced), 128; *Chalcalburnus chalcoides*, 174611, USSR, 144; *Chela bacaila*, 187849, Bangladesh, 90; *Chondrostoma nasus*, 174608, USSR, 116; *Ctenopharyngodon idella*, uncataloged material, Thailand (introduced), 131; *Culter alburnus*, 66530, China, 106; *Cylocheilichthys enoplos*, 181248, Cambodia, 170; *Cyprinus carpio*, 141496, Utah (introduced), 141; *Danio devaria*, 187873, Bangladesh, 55; *Elopichthys bambusa*, 100644, China, 171; *Erythroculter erythropterus*, 100646, China, 132; *Esomus goddardi*, 192970, Thailand, 60; *Gnathopogon japonicus*, 142962, Japan, 91; *Gobio gobio*, 185000, Romania, 81; *Hemibarbus barbus*, 142963, Japan, 119; *Hemiculter nigromarginis*, 158509, China, 149; *Hemigrammocypis rasborella*, uncataloged material, Japan, 41; *Hypophthalmichthys microlepis*, 100653, China, 184; *Ischikauia steenackeri*, 142967, Japan, 227; *Labeo lunatus*, 189110, Zambia, 139; *Leucaspis delineatus*, 185043, Romania, 61; *Leuciscus bergi*, 174603, USSR, 149; *L. cephalus*, 185043, 187; *L. leuciscus*, 159290, Czechoslovakia, 145; *Megalobrama hoffmani*, 100652, China, 173; *Moroco percunurus*, 188854, Japan, 73; *M. steindachneri*,

142951, Japan, 104; *Ochetobius elongatus*, 100649, China, 116; *Opsariichthys bidens*, 64240, China, 119; *Parabramis* (sp. ?), 167398; China, 155; *Paracheilognathus rhombeus*, 70307, China, 64; *Palecus cultratus*, 174621, USSR, 230; *Phoxinus phoxinus*, 173695, France, 17, 185045, Romania, 54, and 17606, western Siberia, 52; *Pseudogobio rivularis*, 64239, China, 95; *Pseudoperilampus typus*, 142949, Japan, 60; *Pseudorasbora parva*, 142944, Japan, 61; *Pungtungia nerzi*, 187583, Japan, 117; *Rasbora lateristriata*, 157141, Indonesia, 71; *Rasborichthys altior*, 193382, Singapore, 46; *Rhodeus sericeus*, 185114, Romania, 68; *Rutilus rutilus*, Romania, 129; *Sarcocheilichthys variegatus*, 142937, Japan, 90; *Scardinius erythrophthalmus*, 185032, Romania, 133; *Squalius muticellus*, 174844, Italy, 78; *Tinca tinca*, 159277, Canada (introduced), 230; *Tribolodon hakonensis*, 186882, Japan, 241; *Vimba vimba*, 185033, Romania, 173; *Xenocypris* (sp. ?), 167399, China, 172; and *Zacco platypus*, 187570, Japan, 96.

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頭部側線感覚管からみたアメリカ産コイ科魚類の
祖先型について William A. Gosline

アメリカのコイ科魚類においては頭部側線感覚管系の
眼上管と眼下管は分離しており連絡していない。こ
の点でアメリカ産のコイ科魚類はアジア・アフリカの

熱帯産のものと異なるが、ユーラシアのウグイ亜科の
ものと似ている。特にアメリカの *Notemigonus* はユ
ーラシアの *Leucaspis* と、*Lavinia* はウグイ属 *Tri-*
bolodon と、*Chrosomus* はアブラハヤ属 *Moroco* や
Phoxinus と酷似している。