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UNBRANCHED DORSAL-FIN RAYS AND SUBFAMILY CLASSIFICATION IN THE FISH FAMILY CYPRINIDAE

BY WILLIAM A. GOSLINE

ABSTRACT. Few known characters separate major cyprinid lineages. The number of unbranched dorsal-fin rays is useful in this regard to the extent that the Cyprininae almost always have 4, whereas all other cyprinid subfamilies have 3 as a basal number. Unbranched dorsal ray counts are given for various cyprinids and related forms. An attempt is made to divide the Cyprinidae into its major phylogenetic components. Five subfamilies are recognized: Rasborinae, Cyprininae, Gobioninae, Acheilognathinae, and Leuciscinae. Problems regarding the limits of the Leuciscinae in Eastern Asia are discussed.

As has been noted repeatedly (e.g., by Sagemehl, 1891; Regan, 1911; Ramaswami, 1955), major groups within the large family Cyprinidae are not readily differentiable. In cyprinid classification there has been a tendency to chip off small groups of specialized forms from the central mass of species and to recognize such groups as subfamilies (see, for example, Berg, 1940). Here, the viewpoint of Kryzanovsky (1947) is adopted, namely that the primary division of the Cyprinidae, i.e., into subfamilies, should be between the main phylogenetic units. Such a classification provides a more meaningful basis for comparison between the smaller groups of cyprinids and for zoogeographic analysis. The difficulty lies in working out certain of these major units. The first part of this paper adds some new data that seem to be of assistance here. The second part is a discussion of cyprinid subfamilies. Most of the discussion is devoted to the Leuciscinae, particularly to problems raised by certain East Asian forms.

The subfamily classification adopted throughout the paper is presented at the beginning of the second part. Except in the word ostariophysine, the informal ending *ine* is used here in writing of

groups at the subfamily level, e.g., the cyprinines make up the subfamily Cyprininae. For groups of presumably related genera at the various possible taxonomic levels below subfamily the informal termination *in* is used, e.g., the cultrin group of genera within the Leuciscinae.

Unbranched Dorsal-Fin Rays

The study of relationships within the Cyprinidae is infested with convergent characters. It has become clear that many of the features once used for distinguishing groups within the Cyprinidae, e.g., the cultrate abdominal keel, or a pharyngeal dentition specialized for plant feeding, developed repeatedly among independent lineages. A search for features that are sound phylogenetic indicators seems at best to lead to characters of value in some cyprinid groups but not others. For these reasons it appears advisable to accumulate and evaluate as many features of potential phylogenetic significance as possible. The number of unbranched dorsal-fin rays seems to be a character of this type that has not previously been used.

Though the number of branched rays in the median fins of cyprinids has long been utilized as a means of distinguishing groups (for example, by Günther, 1868), the number of unbranched fin rays has received little attention. A principal reason that the unbranched rays have been neglected lies in the relatively great difficulty in counting them. Though the posterior unbranched fin rays usually present no problem in this regard, the anteriormost ray is generally represented by a pair of small splints buried in the flesh at the front of the fin base. Furthermore, this first ray undergoes various stages of rudimentation. Sometimes only one member of the splint pair is present (in which event it is here considered half a ray), and sometimes the anteriormost of the expected rays seem to have disappeared completely. In large specimens the first unbranched ray is ascertainable by dissection, but for small cyprinids a reliable unbranched ray count can only be obtained from cleared and stained specimens. An attempt to count unbranched rays on radiographs was abandoned. The x-rayed fish must lie exactly flat on its side; otherwise the small first ray is obscured by the supporting pterygiophore.

In the Cyprinidae the construction of the dorsal and anal fin is very much alike. There is variation in the number of unbranched rays in both fins. However, that of the dorsal is greater and appears more significant systematically than that of the anal, which will not be considered further.

The unbranched dorsal fin rays diminish in size from back to front. The posterior two are normal rays (or spines) in possessing the usual dorsal fin ray musculature. Their sideways movements are restricted by lateral expansions of the upper ends of the first two pterygiophores, with the posteriormost unbranched ray propped against the second pterygiophore and the penultimate unbranched ray against the first. Unbranched rays ahead of the last two lack musculature. They ride over the dorsal surface of an anterior projection from the first pterygiophore. It is in the number of these small anterior rays that the variation occurs.

Three preliminary points regarding the unbranched dorsal fin rays may be made. One is that they ossify relatively early in ontogeny, i.e., before the branched rays bifurcate. A second is that in the counts of unbranched rays recorded in the literature, one is never sure whether the small first ray has been included. Branched fin rays counts appear more reliable even though the question of how the last ray has been treated arises. Third, no particular effort has been made here to determine the variability of unbranched dorsal ray number within species. Usually (see Appendix) only a single count for a species was recorded, and such counts were based on one or two specimens. When within-species variability was suspected, further material was investigated if available; thus, the counts for *Orthodon macrolepidotus* were based on four skeletons from a single lot. In general, it is the stability rather than the variation in unbranched dorsal fin ray counts of cyprinids that seems notable. Available specimens of Cobitidae and Catostomidae (see Appendix) showed greater variation between species in the number of unbranched dorsal rays than within the subfamilies of Cyprinidae.

In cyprinids there seem to be two modal unbranched dorsal-fin ray counts: 4 in the Cyprininae, and 3 in the other cyprinid subfamilies (see Appendix).The basic count of 4 in the Cyprininae is relatively stable. Counts of 3 or 5 occur rarely. The only specimen examined with 5 unbranched dorsal rays *(Labiobarbus cuvieri)* showed an incipient duplication in the first pterygiophore and may be aberrant. Counts of 3 in cyprinines seem to result from the loss of the usual first ray. In one cleared and stained specimen of *Amblypharyngodon mola* there was a very small anterior fourth ray, but in a second specimen I could find only 3. Again, most species of *Barbus* examined had 4 unbranched dorsal-fin rays, but one of two specimens of *B. maculatus* had 3 as did the only cleared and stained specimen of *B. perince*. *Amblypharyngodon mola, Barbus maculatus,* and *B. perince* are relatively small

cyprinines, and a size factor may be involved. However, the single large available specimen of *Rohteichthys,* apparently a perfectly good cyprinine genus, also had only 3 unbranched rays. Finally, in *Garra taeniata* the first two of the 4 unbranched rays were very small, suggesting the possibility of modification in the unbranched rays of hill-stream cyprinines.

In cyprinids other than the Cyprininae a count of 4 is rare except among the Leuciscinae of western North America. In the Old World, then, the distinction between 4 and 3 unbranched rays is of some assistance in separating members of the Cyprininae from other subfamilies. Thus, *Hemibarbus* has sometimes been placed in the Cyprininae, but Banarescu and Nalbant (1973) removed it to the Gobioninae; *Leptobarbus,* also included at times in the Cyprininae, has been allocated by Gosline (1975) to the Rasborinae. The 3 unbranched dorsal rays in both *Hemibarbus* and *Leptobarbus* provides additional evidence against their inclusion in the Cyprininae.

Dorsal spines are most strongly developed in the Cyprininae, but also occur in at least some members of all cyprinid subfamilies except the Rasborinae. Dorsal spines and their associated features appear to show two different trends of development in cyprinids. In the Cyprininae with dorsal spines, the four unbranched rays are graduated in size, closely appressed to one another, and move together. The other trend is best developed in certain of the East Asian leuciscines of the cultrin group. In the members of this group with a dorsal spine (and in some without) the 3 unbranched dorsal rays are not graduated in size. Rather, the first is reduced to a pair of blunt knob-like structures more or less separated by an interspace from the second unbranched ray. At its most extreme development (in *Hemiculter leucisculus)* this pair of anterior knobs becomes rather firmly attached to the first pterygiophore and retains very little independent movability.

The cyprinid subfamilies with a basal count of 3 unbranched dorsal rays seem to differ from one another in both the amount and direction of variation. The limited material available suggests a stability in the unbranched ray counts of the Gobioninae and Acheilognathinae (see Appendix). The Rasborinae is the only subfamily with a frequent count of 2. In the Leuciscinae the number of unbranched rays varies from 2 to 5½. Leuciscines from western North America appear to show greater variability and generally higher counts than members of the same subfamily from Eurasia .

Discussion of Cyprinid Subfamilies

As a basis for discussion, the subfamily classification adopted here is summarized below in synoptic form. No attempt will be made to compare this classification with preexisting ones, as this would involve a review of much of the cyprinid taxonomic literature. Such a review up to 1970 is available in Hensel (1970). Since 1970 one complete subfamily classification has appeared, namely that summarized in Banarescu (1972). Suffice it to say that, except in the reduction in the number of subfamilies usually recognized, the classification presented below is not very radical. It does, however, differ in greater or lesser detail from previous classifications.

Synoptic Key to the Subfamilies of Cyprinidae

1a. Lateral line, when complete, extending along the lower half of the caudal peduncle in adults; uppermost infraorbital bone (the dermosphenotic) in direct contact with the supraorbital (except in small species of *Rasbora*). RASBORINAE (of Gosline, 1975)

1b. Lateral line, when complete, passing along the middle of the caudal peduncle or at least rising to near the middle posteriorly; uppermost infraorbital bone rarely in contact with supraorbital.

2a. Anal fin usually with 5 or 6 branched rays (7 in a few genera, more than 7 in *Rohtee*).

3a. Scales with basal radii (Chu, 1935); unbranched dorsal rays almost always 4 (see above). Each of the following features is frequently present: a rostral barbel, a dorsal spine, and 3-rowed pharyngeal teeth. CYPRININAE (including Barbinae, Garrinae, and Schizothoracinae, auctorum; also *Tinca*)

3b. Scales without basal radii; unbranched dorsal rays 3. No rostral barbel; a dorsal spine and 3-rowed pharyngeal teeth present only in *Hemibarbus*. GOBIONINAE (of Banarescu and Nalbant, 1973)

2b. Anal fin usually with 7 or more branched rays (rarely 6) in Old World forms. (In America a count of 6 branched rays frequently occurs in the Leuciscinae, the only native subfamily represented there.)

4a. Ripe females with a long ovipositor; breeding males usually with a pair of tubercle-bearing plates on the tip of snout (Okada, 1934; Nakamura, 1969); anal fin originating below the dorsal fin. ACHEILOGNATHINAE (= Rhodeinae, auctorum)

4b. No long ovipositor; no tubercle-bearing plates on the tip of snout; anal fin usually originating behind the dorsal fin. LEUCISCINAE (including Abraminae or Abramidinae, Chondrostominae, Cultrinae, Elopichthyinae, Hypophthalmichthyinae, and Xenocyprininae, auctorum)

The five cyprinid subfamilies recognized here vary greatly in size and diversity. Two of intermediate size, the Rasborinae and Gobioninae, seem to form coherent groups and have been dealt with recently (by Gosline, 1975, and by Banarescu and Nalbant, 1973, respectively). They will not be discussed further.

The Cyprininae are a very large subfamily with a number of readily differentiable, specialized offshoots that have frequently been recognized as separate subfamilies or families. The problems raised by the separate cyprinoid families (see Ramaswami, 1957) are not discussed. That the various cyprinids included here in the Cyprininae are interrelated is indicated by a number of features held in common. The presence of four unbranched dorsal rays, discussed above, is one such feature. Only the area of confusion between the Cyprininae and Leuciscinae is taken up below (with reference to *Squaliobarbus, Ctenopharyngodon,* and *Mylopharyngodon).*

The remaining cyprinids are here included in the two subfamilies Acheilognathinae and Leuciscinae. The Acheilognathinae are a small group of specialized forms, whereas the Leuciscinae are a very large and diverse group. The question immediately arises of why the Acheilognathinae are recognized as a separate subfamily whereas an equally distinctive group such as the Hypophthalmichthyinae (auctorum) is here included in the Leuciscinae. The answer lies less in morphological distinctiveness than in relationships. *Hypophthalmichthys* seems quite clearly to be an offshoot of the cultrin group of Leuciscinae (see below), whereas the relationship of the Acheilognathinae is not apparent, at least to this author. Kryzanovsky (1947), presumably on the basis of embryonic similarities, placed the Acheilognathinae with the Cyprininae. To Regan (1911) the osteology of adult acheilognathines suggested the Leuciscinae. However, in the development of an ovipositor and in scale characters (Chu, 1935) the Acheilognathinae are closely resembled by the *Sarcocheilichthys*-group of Gobioninae. The obviously specialized acheilognathines thus appear to have an *incertae sedis* status within the Cyprinidae, and, at least until their relationships can be determined, it seems best to recognize them as a separate subfamily.

The remainder of the subfamily discussion deals with the Leuciscinae. Except for the transfer of *Tinca* to the Cyprininae, the broad interpretation of the Leuciscinae adopted here is essentially that of Kryzanovsky (1947). The subfamily contains at least three major adaptive radiations. One is the leuciscin-abramadin-chodrostomin group most diversely represented today in Europe, but also with a few genera in Eastern Asia and *Notemigonus* in North America. Another (possibly more than one), which contains American forms, also includes members of the *Phoxinus*-group in Eurasia and possibly *Tribolodon* as well (see, for example, Gosline, 1974). A third adaptive radiation is represented by the cultrin-xenocyprinin group of cyprinids and its relatives in Eastern and Southeastern Asia. These three adaptive radiations are here included in a single subfamily primarily because of difficulties in establishing clear limits between them. The following discussion takes up some of the Eurasian, primarily East Asian, aspects of this problem.

The adaptive radiations represented by the leuciscin-abramadin-chondrostomin group primarily of Europe and by the cultrin-xenocyprinin cyprinids of Asia have been recognized as separate subfamilies at least three times (Nikolsky, 1954; Banarescu, 1967; Gosline, 1974). There are a number of features indicating that the two groups evolved separately. All members of the leuciscin-abramadin-chondrostomatin radiation show two reduction characters: they never have more than two rows of pharyngeal teeth, and there is no connection between the supraorbital and infraorbital sensory canals on the head (Gosline, 1974). In the cultrin-xenocyprinin group by contrast there are usually three rows of pharyngeal teeth (but sometimes two or one), and in some members the supraorbital and infraorbital canals are connected (though in others they are not). In dorsal fin structure, however, the cultrin-xenocyprinin group shows greater specialization than the leuciscin-abramadin-chondrostomin section of the Leuciscinae. In the latter the number of both the unbranched and branched dorsal rays is variable: the unbranched rays are usually 3, but may be 4, and the number of branched rays may be as low as 6 but is usually more than 7. In the cultrin-xenocyprinin section there are always 3 unbranched (see Appendix) and 7 branched dorsal rays (Banarescu, 1967); furthermore, in the numerous members with a dorsal spine as well as in some without, the first unbranched ray is specialized as a pair of knob-like structures more or less separated by an interspace from the second unbranched ray (see above). Other groups of Leuciscinae infrequently have a dorsal spine, and at least in the American *Lepidomeda* which does,

the first unbranched dorsal ray is normally developed. Finally, there are in some members of the cultrin-xenocyprinin group certain other specializations that do not seem to occur in the leuciscin-abramadin-chondrostomin section, namely, a three-lobed swim bladder (Tchang, 1931) and an opening in the suspensorium (Gosline, 1975).

In a number of respects the leuciscin-abramidin-chondrostomin adaptive radiation in Europe appears to parallel that of the cultrin-xenocyprinin group in East and Southeast Asia. At one end of the spectrum in both radiations are pelagic forms with cultrate abdomens, upturned mouths, and long, somewhat downwardly-directed pectorals—*Pelecus* in Europe and *Macrochirichthys* in Southeast Asia. (*Pelecus* seems to belong with the leuciscins, though Banarescu [1967] included it with his Cultrinae.) At the other extreme are round-bellied forms with small downturned mouths and pharyngeal teeth specialized for plant feeding (Chu, 1935)—*Chondrostoma* in Europe and *Xenocypris* in Eastern Asia.

Though there seems little doubt that the leuciscin-abramidin-chondrostomin group in Europe and the cultrin-xenocyprinin cyprinids of Asia represent separate adaptive radiations, both are provisionally included here in the subfamily Leuciscinae for two reasons. First, the only diagnostic characters I can find for the leuciscin-abramadin-chondrostomin group, i.e., the pharyngeal teeth in one or two rows and the discontinuity in the head canal system, are derivative reduction features that also occur in some of the cultrin-xenocyprinin group. The second reason has to do with the difficulties of assigning certain members to either stock. The problem of the European *Pelecus* has already been noted. In Western and Central Asia there appear to be a number of enigmatic genera, e.g., *Capoetobrama,* that may present problems of allocation, but neither the fishes from this area nor much of the literature regarding them (some of it cited in Banarescu, 1973) are available to me. Finally, there is the question of the affinities of certain East Asian forms, notably *Elopichthys* and its relatives. *Elopichthys,* and to a lesser extent *Opsariichthys* (see below), suggest that the cultrin stock may have given rise to leuciscin-like fishes on several occasions. In any event, it seems impossible to circumscribe, let alone define, a monophyletic leuciscin group of Leuciscinae at the present time.

In Eastern Asia there are a number of small groups of specialized cyprinids that can best be taken up in relation to the cultrin adaptive radiation of the Leuciscinae. The groups, allocated to various subfamilies in the past, that will be dealt with here are: (1) *Aphyocypris, Hemigrammocypris,* and *Tanichthys;* (2) *Hypophthalmichthys* and *Aristichthys;* (3) *Opsariichthys* and *Zacco;* (4) *Elopichthys, Ochetobius,*

and *Luciobrama;* and (5) *Squaliobarbus, Ctenopharyngodon,* and *Mylopharyngodon.* The first three of these groups appear to represent specialized offshoots of the cultrin radiation. The relationships of the last two groups are more questionable, though in quite different respects.

Aphyocypris and *Hemigrammocypris* are dubiously separable genera, to which *Tanichthys* appears to be allied. The group, which may contain additional genera, is made up of small East Asian fishes that show various features of miniaturization (Karaman, 1972) such as the usually incomplete lateral line and, in *Tanichthys,* the loss of the fleshy bridge that normally separates the two nostrils (Weitzman and Chan, 1966). As with so many cyprinids of reduced size, the affinities of the three genera are less than clear. Sometimes they have been placed with the Rasborinae and sometimes with the Leuciscinae. Features that point in the direction of a leuciscine rather than a rasborine allocation are: the absence of contact between the dermosphenotic and supraorbital bone (examined in *Aphyocypris;* see Gosline, 1975), the absence of barbels, the absence of a symphyseal knob on the chin, the presence of a cultrate abdomen behind the pelvic fins in *Aphyocypris* and *Hemigrammocypris,* and the reduction of the first unbranched dorsal-fin ray in *Aphyocypris (Phoxiscus) kikuchii* to a short, double-lobed shield-like structure (see above). Within the Leuciscinae, the construction of the first unbranched dorsal ray of *Aphyocypris kikuchii* just mentioned and the three rows of pharyngeal teeth in *Hemigrammocypris* indicate a cultrin allocation, although in the presence of well-developed basal radii on their scales *Aphyocypris* and *Hemigrammocypris* differ from typical cultrins (Chu, 1935).

Hypophthalmichthys and *Aristichthys* are two well-known genera widely used in fish culture that have usually been assigned a separate subfamily Hypophthalmichthyinae. They differ from other cyprinids in a number of notable respects, most or all of which seem to be associated with their use of phytoplankton and zooplankton, respectively, as a food source. They have a suprabranchial organ (Fang, 1928) and long gill rakers arranged in *Hypophthalmichtys* to form a reticulum. There are two large openings in each lightly-constructed pharyngeal bone (Chu, 1935). The large gill covers are attached to one another by a fold that is nearly free from the isthmus. The supraorbital bone is loosely attached to the skull, and the parasphenoid has a large ventrally-projecting process. (These features seem to me to be at least as distinctive as those of *Psilorhynchus,* a genus placed in a separate cyprinoid family by Ramaswami [1952] and others.)

The genetic isolation of *Hypophthalmichthys* and *Aristichthys* does not seem to be as great as their morphological peculiarities might suggest. Viable hybrid offspring from crosses between *Hypophthalmichthys molitrix* and each of the following cyprinids have been reported: *Aristichthys nobilis, Ctenopharyngodon idella, Parabramis pekinensis,* and *Megalobrama terminalis* by Makeyeva and Sukanovna (1966); *Cyprinus carpio* by Makeyeva (1967); and *Abramis brama orientalis* by Ryabov (1973). Very similar results were obtained using *Aristichthys nobilis* as one parent.

Morphologically there seem to me to be clear indications of a cultrin derivation for *Hypophthalmichthys* and *Aristichthys* (see also Kryzanovsky, 1947, in this regard). Aside from a number of more or less general resemblances between *Hypophthalmichthys, Aristichthys,* and the cultrins, *Hypophthalmichthys* has one feature that appears to be diagnostic for the cultrin stock, namely a three-lobed swim bladder (Tchang, 1931). It seems relevant to provide here a preliminary evaluation of this character.

In certain cyprinids, usually midwater forms, the posterior chamber of the swim bladder, instead of having a rounded terminal wall, develops a projection of one sort or another. In such rasborines as *Barilius guttatus* and *Rasbora dusonensis* this projection takes the form of a small knob-like tip on the posterior end of the second chamber. In the leuciscin *Pelecus,* the projection resembles a short, tail-like appendage that is not constricted basally (personal observations). However, in a number of members of the cultrin stock, a constriction at the base of such a projection results in a small, posterior, third lobe in the swim bladder. Tchang (1931) reported a three-lobed swim bladder from the following Chinese cyprinids: *Parosteobrama pellegrini, Culter erythropterus, C. brevicauda, Parabramis pekinensis, Chanodichthys mongolicus, Parapelecus machaerensis, Hemiculter* sp., *Xenocypris* sp., and *Hypophthalmichthys molitrix.*

The third lobe is never large and may vary from well-developed through small to absent within a single genus, e.g., *Culter.* Its absence is therefore of no systematic significance, but its presence appears to be. Tchang (1931) did not find a third lobe in the swim bladder of the other Chinese cyprinids he examined. I have found in the literature no records of such a lobe in cyprinids outside the cultrin stock and did did not find a third lobe in specimens of the following non-Chinese midwater genera: *Abramis, Alburnus, Notemigonus,* and *Pelecus* among leuciscins; *Barilius, Engraulicypris, Nematabramis,* and *Rasbora* among rasborines.

Opsariichthys and *Zacco* are nest-building cyprinids (Nakamura, 1969) and in this respect differ from most or all members of the cultrin stock. In both genera the anal fin rays are long, with those of the male the longer and bearing breeding tubercles (Okada, 1934). There are also large breeding tubercles on the face. *Zacco barbatus* differs from other members of the cultrin stock (except *Squaliobarbus,* see below) in having a maxillary barbel. In the reduction of the lateral-line canal system on the head *Zacco* and *Opsariichthys* resemble the leuciscins rather than the cultrins. However, the beak-like jaw of *Opsariichthys* is more cultrin than leuciscin, and the three rows of pharyngeal teeth seem to exclude *Opsariichthys* and *Zacco* from the leuciscins. Finally, both genera possess one character that is known elsewhere only among the cultrin cyprinids, namely, the opening in the suspensorium between the symplectic and metapterygoid (Gosline, 1975). On balance, *Opsariichthys* and *Zacco* seem to this author to be specialized genera closest to the cultrin series of Leuciscinae, but with indications of affinity with the *Tribolodon*-American section of the subfamily (see also Makeyeva and Ryabov, 1973).

Elopichthys, Ochetobius, and *Luciobrama* are peculiar, elongate cyprinids of Eastern Asia. (Howes has a paper in preparation on *Luciobrama,* a genus I have not seen.) Suffice it to say here that the three genera appear to me to be related and to belong to the Leuciscinae. They have 9 to 12 branched anal rays and terminal mouths. In certain features they appear to belong with the cultrin section of the Leuciscinae and in others with the leuciscin section. The dorsal fin is leuciscin. All of the groups of East Asian genera previously discussed have the typical cultrin count of 3 unbranched and 7 branched dorsal rays. However the branched dorsal ray count of *Elopichthys* and *Ochetobius* is 9 or 10, and that of *Luciobrama* is 8 (according to Lin, 1935a). *Elopichthys* has 4 unbranched dorsal rays, a count unknown in cultrins but one that occurs in a number of leuciscins (see Appendix). On the other hand, the pharyngeal teeth of *Elopichthys* and *Ochetobius* are in three rows, though only in a single row in *Luciobrama*. The scales of *Elopichthys* and *Ochetobius* are modified in a way that is neither leuciscin nor cultrin, though the scales of *Luciobrama* are less peculiar (Chu, 1935). On the basis of their external characters I see no way of determining whether these three genera belong with the leuciscin or with the cultrin side of the Leuciscinae.

A final group of East Asian cyprinids to be considered comprises the genera *Squaliobarbus, Ctenopharyngodon,* and *Mylopharyngodon.* With these the problem is whether they belong with the cultrin stock

of the Leuciscinae or with the Cyprininae. (There is no question of an affinity with the leuciscin side of the Leuciscinae. *Squaliobarbus* has three-rowed pharyngeals. All three genera have the supraorbital and infraorbital canals of the head connected. Finally, *Ctenopharyngodon* and *Mylopharyngodon* have radiating striations on the outer surface of the opercle, another character frequently present in the Cyprininae and in the cultrin group, but undeveloped in the leuciscin section of the Leuciscinae.) *Squaliobarbus, Ctenopharyngodon,* and *Mylopharyngodon,* are all monotypic genera containing large and well-known food fishes native to China and the Amur region. In the following discussion these genera will be considered in relation to the various characters that seem to distinguish the Cyprininae from the cultrin stock of the Leuciscinae.

In the Cyprininae (as in the Rasborinae) there are frequently two well-separated barbels on each maxillary—one at or near its tip and the second (rostral) barbel well forward along the maxillary. In the cultrin *Zacco barbatus* and in some American Leuciscinae barbels are present near or at the end of the maxillary, but there is no rostral barbel. *Ctenopharyngodon* and *Mylopharyngodon* have no barbels, but in *Squaliobarbus* there is usually a small maxillary barbel and sometimes a minute rostral barbel as well.

In the Cyprininae the features of the individual scales are better differentiated than in the Leuciscinae (Chu, 1935). In cyprinines the circuli between the apical radii are more or less modified as compared to the circuli on the rest of the scale (though not in *Schizothorax*). In the Leuciscinae the circuli are usually more or less continuous around the scale (though not in *Elopichthys* and *Ochetobius*). In *Squaliobarbus, Ctenopharyngodon,* and *Mylopharyngodon* the circuli are of the leuciscine type. In the Cyprininae basal radii seem to be consistently present; in the Leuciscinae they may be present or absent (Chu, 1935). In *Ctenopharyngodon* and *Mylopharyngodon* basal radii are present; in *Squaliobarbus* they are absent.

Squaliobarbus, Ctenopharyngodon, and *Mylopharyngodon* all have 8 branched anal rays, which is a fairly typical number for leuciscines but is greater than that in any cyprinine except *Rohtee.*

Cyprinines generally have 4, rarely 3, unbranched dorsal rays. Old World leuciscines usually have 3, sometimes 4, unbranched dorsal rays. *Squaliobarbus* and *Mylopharyngodon* have 3 unbranched rays. *Ctenopharyngodon* also seems to have 3 as a basal number, but anteriorly there is sometimes a half-ray present giving a variation in count from 2½to 3½. The number of branched dorsal rays in *Squaliobarbus,*

Ctenopharyngodon, and *Mylopharyngodon* is 7. This is the constant count for cultrins, but also occurs in the Cyprininae and other subfamilies.

Most of the skeletal features of *Ctenopharyngodon* and *Mylopharyngodon* (no skeleton of *Squaliobarbus* is available) suggest the Cyprininae rather than the Leuciscinae. Cyprinine features in the skull include: an ethmoid region that is considerably broader than the vomer, the exoccipitals expanded on the posterior face on the skull, and the vagus nerve exiting from a horizontally elongate slit in the exoccipital. The cultrin species nearest to *Ctenopharyngodon* and *Mylopharyngodon* in these respects is *Hypophthalmichthys molitrix.*

Sagemehl (1891) pointed out that in certain of the fishes here included in the Cyprininae part of the M. dilatator operculi extends forward between the frontal and the pterotic to an attachment on the roof of the orbital cavity. This character holds for all of the few cyprinine skeletons available: *Barbus, Carassius, Cyprinus,* and *Labeo.* In *Ctenopharyngodon* and *Mylopharyngodon,* as in skeletons of cyprinids other than the Cyprininae, the M. dilatator operculi does not penetrate into the orbital cavity.

Regan (1911) called attention to the broad, indented anterior border of the cleithrum of cyprinids of the *Barbus*-group. This feature, though characteristic of the Cyprininae, does not occur in all of them. Thus, the anterior end of the cleithrum of the cyprinine *Garra* is relatively narrow and is rounded anteriorly. In both cyprinines and leuciscines, aside from certain specialized forms, there seems to be a relationship between the width of the chest region and the breadth and configuration of the anterior border of the cleithrum. Thus, in the relatively compressed cyprinine *Hampala* the anterior rim is relatively short and little indented. In most of the Leuciscinae the anterior end of the cleithrum is far narrower, and its oblique anterior border is straight or convex. However, in such relatively robust leuciscines as *Gila robusta* the anterior end of the cleithrum is broader and somewhat concave. In *Squaliobarbus, Ctenopharyngodon,* and *Mylopharyngodon* the concavity in the moderately broad cleithrum is about as in *Hampala* or *Gila robusta.*

In all cyprinines so far as known the second and third vertebrae are fused. In the Leuciscinae the second and third vertebrae are usually, though not always, separate (see, for example, Chranilov, 1927). In *Ctenopharyngodon* and *Mylopharyngodon* the second and third vertebrae are fused.

To summarize for morphological features, the occasional presence of

two pairs of barbels in *Squaliobarbus* and most of the skeletal characteristics of *Ctenopharyngodon* and *Mylopharyngodon* suggest cyprinine affinities. The fins and scales of these three genera, by contrast, are those of the cultrin Leuciscinae.

There are two other types of information that bear on the affinities of the three genera. First, *Mylopharyngodon* is said to have pelagic eggs (Nikolsky, 1954), and *Ctenopharyngodon* spawns pelagically in large rivers (Lin, 1935). This is a common type of reproduction in cultrins. Some of the Indian cyprinines migrate up large rivers, but I have been unable to find records of where they spawn.

Makeyeva and Sukhanovna (1966) obtained viable hybrids between *Ctenopharyngodon* and the cultrin genera *Hypophthalmichthys, Aristichthys,* and *Megalobrama.* Ryabov (1973) was unsuccessful in his attempt to cross *Ctenopharyngodon* with the leuciscin *Abramis.* Kobayashi and Mizumoto (1950) raised hybrids from a cross between *Ctenopharyngodon* and *Cyprinus* but reported that up to 86 percent of the offspring were "anomalous in shape."

When all available sources of information are brought to bear on *Squaliobarbus, Ctenopharyngodon,* and *Mylopharyngodon* there is still, for this author, no way of ruling out any of three, not necessarily very different, conclusions concerning their affinities: (1) they are cyprinines that have developed cultrin-like characteristics; (2) they are actually intermediate between the Cyprininae and the cultrin Leuciscinae; and (3) they are cultrins with cyprinine-like features. Here, they are provisionally retained in the Leuciscinae, where they have usually been placed.

Speculations Regarding Cyprinoid Evolution

All of the main ostariophysine groups have undergone independent adaptive radiations. In ostariophysines other than the cyprinids these radiations have been accompanied by relatively drastic changes in fundamental bony structures. By contrast, the Cyprinidae, the largest family of fishes, appears to have adapted a single highly specialized structural ground-plan to a great variety of habitats and food sources. It is only in that part of the cyprinoid stock that has developed thigmotactic benthic forms that more notable modifications in morphology have occurred, i.e., in the separate cyprinoid families peripheral to the Cyprinidae (Ramaswami, 1957).

There appear to be no known transitional forms, fossil or living, between the cyprinids and other ostariophysine groups. Regan (1911),

primarily because of resemblances to the characins, postulated the long-jawed *Opsariichthys* as the most primitive cyprinid. Gosline (1973), on the basis of feeding hydrodynamics, concluded that the basal cyprinids were small-mouthed forms, and that the resemblances between *Opsariichthy* and characins were mostly or entirely the result of convergent evolution. The present author is, however, unable to determine which among modern cyprinids most closely approximates the ancestral stock. The paper ends with the presentation of three lines of evidence, the first two of which seem to point in the direction of a cyprinine-like ancestor and the third toward the cultrin section of the Leuciscinae as the modern cyprinid group most closely approximating the ancestral type.

All of the other four subfamilies of Cyprinidae recognized here seem to point back in one way or another toward a *Barbus*-like type of Cyprininae. In the Acheilognathinae it is embryological features that do so (Kryzanovsky, 1947). For the other three subfamilies, cyprinine-like genera (as their names suggest) seem to stand at or near their bases: *Hemibarbus* in the Gobioninae (Banarescu and Nalbant, 1973), *Leptobarbus* in the Rasborinae (Gosline, 1975), and possibly *Squaliobarbus* in the Leuciscinae (see above). Furthermore, some, perhaps all, of the peripheral cyprinoid families appear to have evolved from a cyprinine-like stock.

Zoogeographic evidence suggests again, on balance, a cyprinine rather than a leuciscine-like ancestor for the modern cyprinids. The center of morphological diversity among the modern Rasborinae and Cyprininae is Southern and Southeast Asia; that of the other three subfamilies is China (Banarescu, 1972). One difficulty with any hypothesis based on present diversity is that it may represent an overlay on an earlier distribution pattern of a different type. In this connection the presence of cultrin Leuciscinae in Southeast Asia may be noted (Banarescu, 1967), though there seems nothing to indicate that the Southeast Asian cultrins are not the derivatives of a relatively recent invasion. More striking, however, is the presence of certain old, relict cyprinine types in Europe, e.g., *Tinca* (Obrhelova, 1970). Furthermore, the Chinese catostomid *Myxocyprinus* appears to be an early derivative of the cyprinine stock. In short, there is circumstantial evidence for a former cyprinine development in Eurasian areas now occupied primarily by the leuciscine-gobionine-acheilognathine groups.

The main basis for postulating the cultrin Leuciscinae as nearest to the ancestral cyprinid stock is that in a number of respects they seem to show fewer specializations than the Cyprininae (and Gobioninae)

(see, for example, Alexander, 1966). Most of the features in which the Leuciscinae appear to be relatively generalized, e.g., the retention of separate, more lightly constructed bony elements, seem to be associated with the less benthic mode of life of the Leuciscinae. In effect, the leuciscines seem to be more like normal lower teleostean fishes than the Cyprininae; whether they are more like the ancestral Cyprinidae may prove to be a different matter.

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Appendix

The following species, listed according to the number of unbranched dorsal rays within subfamilies (or families), were examined for the present paper. Numbers in parentheses following the species names are University of Michigan catalog numbers. An *s* following such numbers indicates skeletal material; *c* & *s*, cleared and stained specimens.

RASBORINAE

Two. Brachydanio albolineatus (70703c&s), Engraulicypris argenteus (187330c&s), Esomus danricus (187851c&s), Rasbora argyrotaenia (157134c&s), and R. dusonensis (157133).

Three. Barilius guttatus (195106), Chelaethiops bibie (166632c&s), Danio devario (187878c&s), Leptobarbus hoeveni (181154), and Luciosoma bleekeri (195093).

CYPRININAE

Three. Amblypharyngodon mola (187844c&s) 3 in one specimen and a minute fourth in the other, Barbus maculatus (155761c&s) 3 in one specimen and in the other, B. perince (166643c&s), and Rohteichthys microlepis (155561).

Four. Albulichthys albuloides (131253), Barbichthys laevis (70661c&s), Barbus barbus (185020c&s), B. belinka (155627c&s), B. cyclolepis (186339c&s), B. douronensis (155565c&s), B. duchesnei (171784c&s), B. meridionalis (186336c&s), B. orphoides (181185c&s), B. schwanefeldi (155620), B. sharpeyi (191585s), B. stigma (187845c&s), B. sumatranus (155622c&s), B. tumba (100576c&s), Carassius langsdorfi (187561c&s), Cirrhinus jullieni (195830), Crossocheilus oblongus (155654c&s), C. reticulatus (193014), Cyclocheilichthys apogon (195565c&s), C. armatus (155738c&s), Cyprinion watsoni (186548c&s), Cyprinus carpio (105533), Epalzeorhynchos frenatus (192622), Garra taeniata (193015), Hampala macrolepidota (155730c&s), Labeo cylindricus (171783c&s), Labiobarbus leptocheilus (195268), L. spilopleura (195393), L. tambra (155567 c&s), Lobocheilus sp. (155650c&s), Mystacoleucas marginatus (155643c&s), Osteochilus hasseltii (155735c&s), O. vittatus (155575), Puntioplites proctozysron (195279), Rohtee cotio (187872), Schizocypris sp. (191583), Schizothorax griseus (158510), Spratellocypris palata (100575) Thynnichthys thynnoides (181252), and Tinca tinca (159287).

Five. Labiobarbus cuvieri (155589c&s).

GOBIONINAE

Three. Abbottina rivularis (64239c&s), Gnathopogon japonicus (142961c&s), Gobio albipunctatus (185111c&s), G. gobio (160941), G. uranoscopus (186334c&s), Hemibarbus barbus (142963), Pseudogobio esocinus (142958), Sarcocheilichthys variegatus (187575c&s), and Squalidus gracilis (187601).

ACHEILOGNATHINAE

Three. Acanthorhodeus macropterus (174622), Acheilognathus cyanostigma (187566c&s), A. intermedia (142974), Rhodeus ocellatus (187569c&s), and R. sericeus (185113c&s).

LEUCISCINAE

Two. Eurasian—Oxygaster oxygastroides (155558c&s); American—Rhinichthys falcatus (136193c&s).

Three. Eurasian—Abramis ballerus (174619), A. brama (184987c&s), Alburnoides bipunctatus (184992), Alburnus alburnus (128832), A. charusini (174614c&s), Aphyocypris kikuchii (194372), Aristichthys nobilis (196224), Aspius aspius (174607), Blicca bjorkna (174617c&s), Chondrostoma nasus (185030), Ctenopharyngodon idella (191772s), Culter alburnus (66530), Erythroculter erythropterus (100646), Hemiculter leucisculus (194461), H. nigromaculatus (158509), Hypophthalmichthys molitrix (187622s), Leucaspius deliniatus (185344c&s), Leuciscus bergi (194603), L. borysthenicus (185112c&s), L. cephalus (185036c&s), L. idus (154354c&s). L. leuciscus (159290), L. souffia (185042c&s), Macrochirichthys macrochirus (155564), Megalobrama hoffmani (100652), Moroco steindachneri (142951), Mylopharyngodon aethiops (187624s), Ochetobius elongatus (100649), Opsariichthys bidens (64240c&s), O. uncirostris (187604s), Parabramis sp. (167398), Paralaubuca harmandi (195277), P. riveroi (181128c&s), P. typus (195683), Phoximus percnurus (188854c&s), Pseudobrama simoni (167376), Rasborichthys altior (193382), Salmostoma bacaila (187849), Scardinius erythrophthalmus (185047c&s), Squalius muticellus (174844c&s), Squaliobarbus curriculus (100643), Toxabramis swinhonis (70316), Vimba vimba (185033), Xenocypris lamperti (100645), Zacco barbatus (194563), Z. pachycephalus (194465), Z. platypus (187607s), and Z. temminckii (187632); American—Lepidomeda albivallis (124980), Nocomis raneyi (193092s), Notemigonus crysoleucas (183950s), Notropis emiliae (146601c&s), Phenacobius uranops (154689c&s), Pimephales promelas (166823c&s), Relictus solitarius (141510c&s), Rhinichthys osculus (181753c&s), and Tiaroga cobitis (162724c&s).

Four. Eurasian—Acanthalburnus microlepis (194615c&s), Elopichthys bambusa (100644), Rutilus rutilus (173708), and Tribolodon hakonensis (187626s); American—Acrocheilus alutaceus (178868s), Gila robusta (182476s), Lavinia exilicauda (178871s), Mylocheilus caurinus (177108), Mylopharodon conocephalus (149598), Pogonichthys macrolepidotus (178870), Ptychocheilus oregonensis (177106s), and Richardsonius balteatus (179591s).

Four to five and a half. American—Orthodon microlepidotus (179936s).

CATOSTOMIDAE

Three. Catostomus catostomus (178868s), and C. commersoni (185205s).

Four. Carpiodes carpio (179903s), Chasmistes brevirostris (180686s),

Hypentelium nigricans (189362s), Ictiobus bubalus (190379s), Minytrema melanops (105853), and Xyrauchen texana (186302s).

Four and a half. Myxocyprinus asiaticus (158507).

Five. Cycleptus elongatus (176970s), and Erimyzon sucetta (182952s)

COBITIDAE

Three. Acanthopsis choirorhynchos (195609c&s), Cobitis aurata (185060c&s), and Nemacheilus barbatula (178593c&s).

Four. Botia modesta (195689c&s), Misgurnus fossilis (185341c&s), and Nemacheilus masyi (195624c&s).

GYRINOCHEILIDAE

Four. Gyrinocheilus aymonieri (195925).

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