Minnows First, Then Trout

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ABSTRACT

In the past two decades there has been a dramatic change in the practice of classifying organisms based on a rigorous, new methodology called cladistics, which defines relationships based on the distribution of shared derived characters. This approach, coupled with new information, has led to changes in our concepts of the relationships of major fish groups. These changes should be reflected in newer classifications and lists. For many purposes it is desirable to list related taxa together so that it is easy to make comparisons among them. The order in which taxa are listed is important as an indication of relatedness. Some variations in arrangement are equivalent and interchangeable; others imply relationships that are contrary to available evidence and must be rejected.

In my recent book *Inland Fishes of New York State* (Smith 1986), I listed the minnows and their relatives, the suckers and catfishes, before the trouts and salmons. This follows several taxonomic works (Rosen 1973; Fink and Weitzman 1982; Lauder and Liem 1983) and was used by J. Nelson (1984) in his revision of *Fishes of the World*, but it is contrary to the arrangement given in *A List of Common and Scientific Names of Fishes from the United States and Canada* (Robins et al. 1980) published by the American Fisheries Society. Some people have questioned the reasons for such a radical departure from a long-established order of sequence. Even though most fishery workers may not be especially interested in the nuances of zoological classification, it appears that an explanation is in order.

Most scientists are aware that it is conventional in biological studies to list families, and often genera as well, in phylogenetic sequence beginning with the most primitive and working up to the most advanced. There is, of course, a very good reason for choosing this approach over some other, say a simple alphabetical listing, which might be clear-cut and more convenient. As biologists, we are interested in the evolution of organisms, and it is generally accepted that a phylogenetic order reflects the course of evolution. More to the point, however, is the fact that the more closely species are related, the more they look alike and the more similarities they share. There is a very real advantage to having accounts of similar (= related) species close together in order to make comparisons easier. This is true whether our interest is in the basic identification of species or in the subtleties of life history or habitat requirements and population management. As fishery biologists we certainly want darters listed with other darters and the bullheads listed with the madtoms and other catfishes. It follows, then, that we would want to have any general fish book arranged by families and, as long as we have come that far, to have the families in the same manner (like-with-like). We can also extend this reasoning to higher, more inclusive categories such as suborders, orders, and classes.

There is a common, but erroneous, notion that the data necessary to establish the interrelationships of these higher categories have been well known and understood for many years. Therefore, their arrangement in textbooks and faunal works is so well established as to be fixed and unchanging. Actually, the reverse is true: the relationships of the higher categories of fishes are quite poorly understood. Moreover, they are being studied intensively by systematists, and our ideas about them are changing rapidly. The higher classification of fishes is anything but stable these days.

Why this current interest in classification? Like other fields, systematics has its fads and trends which change with the times. As in other sciences, there is also a cyclical aspect to systematics, and this is well illustrated by the history of the subdiscipline that deals with the classification of fishes at the family level and above. In the late 1800s, Theodore Gill redefined many of the families that we still use today. His work was sound and much of it was adopted by Jordan and his coworkers during the period that culminated with publication of *Fishes of North and Middle America* (Jordan and Evermann 1896–1900). For the next 65 years, however, scant attention was paid to higher classification; instead, other aspects of systematics, such as geographic variation and the differentiation of subspecies, commanded the efforts of ichthyological classifiers. By the 1950s it had become obvious that the higher classification of fishes was outmoded and unsatisfactory in many ways. In 1966 awareness of this sad state of affairs led to the publication of a Bulletin of the American Museum entitled *Phyletic Studies of Teleostean Fishes, with a Provisional Classification of Living Forms* by Greenwood, Rosen, Weitzman, and Myers. This marked the beginning of a resurging interest in higher classification that, two decades later, still continues to gather momentum.

A major factor in the present dynamism of fish classification is the evolution of the practice of classification itself from a rather nebulous artform to a rigorous and clearly defined methodology. At first glance the act of classification appears simple. Groups of similar things are classified together, and these groups are arranged into larger, more inclusive groups and so

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on, until there is a complete system of successively more inclusive categories. At first, the fact that organisms could be so arranged was taken as evidence of the orderly hand of the Creator. Not until Darwin's time did it become apparent that such arrangements were one of the best documentations of organic evolution. Be that as it may, as we accumulated more and more information about organisms, the classifiers were surprised to find that their problems had become more, rather than less, acute. Slowly it became clear that the basic problem lay in determining what could be accepted as reliable evidence of relationship. Repeatedly, attempts to base classifications on overall similarity produced paradoxical results. Perhaps the most discouraging thing of all was that different workers, using the same data, frequently came up with different classifications. Obviously the trouble lay with the methodology.

In 1966, a book entitled *Phylogenetic Systematics*, based on a 1950 work by a German entomologist named Willi Hennig, described a set of basic principles that made other systematists sit up and take notice. Over the next few years Hennig's concepts were hotly debated and refined and gradually came to be accepted, in a somewhat modified form, under the formal name "cladistics" (from the Greek word for branch). For a concise and thorough treatise on the subject of classification the reader should consult Patterson (1982), Janvier (1984), and ultimately Nelson and Platnick's 1981 masterpiece *Systematics and Biogeography: Cladistics and Vicariance*.

It is important to note that one cannot classify a single entity or two entities. All that can be said about two items is that they are different. In this sense any classification would be meaningless. With three or more units, however, it is possible to determine that two are closer to each other than either is to the third, and this can be represented by a branching diagram that can be reflected in a classification.

One of the problems that seems to plague many classifiers is the temptation to expect too much of a classification. It is easy to expect a classification to reflect both time and overall structural change when, in fact, it can do neither of these effectively. Morphological changes proceed in different directions in different lineages and, therefore, cannot be represented on a two-dimensional diagram or a linear classification. Cladists avoid this problem by considering only the sequence of branching, and this can be illustrated fully on two dimensional diagrams. Cladistic classifications are straightforward reflections of such branching diagrams.

Another major difficulty of many older classifications is that they tried to classify organisms on the basis of overall similarity. Organisms are mosaics of general (primitive) and advanced (derived) features. If we try to use all of their characteristics at once, we face impossible confusion. However, if we limit ourselves to derived features that occur in only a few groups, the situation is much improved. In fact, *only* shared derived characters are of use in classification. Primitive features and unique derived features (specializations that occur in only one lineage) are of no help at all. Each branch of the diagram must have one or more unique derived features that are shared by all its subdivisions and only by them. We must also remember, however, that a feature that is a derived character for a large, inclusive group will be a primitive character for all of the subgroups within that line. For example, the presence of a backbone is a derived character that serves to unite all vertebrates. When it comes to classifying catfish, cats, and catbirds, however, the presence of a vertebral column is uninformative because it is a primitive feature that is present in all three groups. To finish the diagram we must find a derived feature that is shared by two of the three units. In this case, the presence of limbs unites cats and catbirds, but not catfish, which have fins.

Sometimes it is difficult to determine which condition is derived and which is primitive. Why, for example, do we think that limbs are more derived than fins? Could it not have been the other way around? This is indeed a problem and perhaps the major source of difficulty in formulating cladistic classifications. Often such problems can be resolved by examining the condition of the character in groups that are not part of the same line. This is called outgroup comparison and it is one of the most useful techniques in cladistics.

Consider the anal spines of centrarchid fishes. Black bass and sunfishes have three anal spines; rock bass, fliers, and crappies have five or more. Which is the derived condition? When we look at many other non-centrarchid spiny-rayed fishes (such as grunts, snappers, groupers, etc.), we find that the overwhelming majority have three anal spines. Hence, we are justified in assuming that three is the primitive number for centrarchids as well. As for the question of fins being primitive, we find that the jawless vertebrates like the lampreys, are an outgroup (as indicated by their lack of jaws) and they have fins, not limbs.

Another problem is convergent evolution—similar structures arising independently in separate lineages. Usually these convergences can be recognized by adequate morphological or ontogenetic study but in the absence of such studies it may not be possible to make a final determination. In such cases the classifier indicates a lack of resolution by a branching point with three or more lines coming together.

With these principles in mind, let us return to the original problem of arranging the families of freshwater fishes from eastern North America. Lampreys and jawed fishes are united by the presence of a notochord. Lampreys stand alone as a distinct line, not because they have only primitive features (they are, in fact, quite specialized), but because all of the other fishes are united into a single group by having jaws. Lampreys, therefore, stand as a line separate from (a "sister group" of) all the rest of the fishes (Fig. 1). Without going into detail here, it has been shown that there are shared, derived features for each successive branch on our diagram: lampreys lack the derived features of sturgeons and the rest of the fishes, gars lack the derived features that unite bowfins and teleosts, and all teleosts have certain derived features that demonstrate their cohesiveness. When we get to the higher teleosts, we find that minnows, suckers, and catfishes have a specialization of the vertebral column called the Weberian apparatus (a modification of the first four of five vertebrae that connect the swim bladder to the inner ear for sound transmission) that is so uniquely complex that it serves to unite them as a clear-cut group. This is a classic example of a shared, derived character. It unequivocally unites the minnows,

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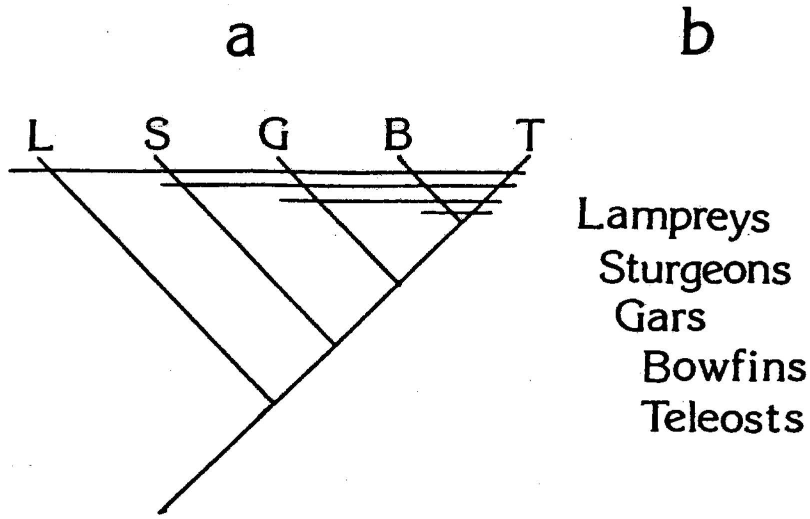

Figure 1. A.—Branching diagram showing the relationships of selected groups of fishes. B.—Classification based on that diagram. L—lampreys, S—sturgeons, G—gars, B—bowfins, T—teleosts. Horizontal bars indicate the distribution of the derived characters that define the branches.

catfishes, and suckers (and several other groups as well). Its presence by itself, however, tells us nothing about their interrelationships.

Now let us consider the relationship between this minnow-sucker-catfish lineage (the Ostariophysi) and other fish families that occur in the northeastern United States. The Ostariophysi lack several features that are present in both salmonids and higher fishes. First, higher fishes have a specialization of the caudal fin supports (the presence of paired stegural outgrowths of the first uroneural). Second, they have acellular bone in some parts of the skeleton, and finally, in salmonids and higher fishes the first vertebra articulates with three bones of the skull, the basioccipital and the two exoccipitals, and in the ostariophysans and lower fishes it articulates with only the unpaired basioccipital. From these features we can conclude that the ostariophysans form a branch equivalent to another line that includes the trouts and the higher teleosts. We say the ostariophysans are the sister group of all the more advanced teleosts. At present these are the only features known that can be used to analyze the relationships of these three lineages. If future studies reveal additional information it might become necessary to revise our classification. It is a basic tenet of systematics that any classification is a hypothesis to be tested. All we are justified in saying is that this hypothesis has been tested and cannot be rejected at this time. Classifications can never be proven.

This, however, is not the end of the story. Once we have gathered enough data to permit the construction of a branching diagram, it is a relatively simple matter to derive a classification, which is a list that reflects the sequence of the branching. In Figure 1 we compare the branching diagram with the resulting classification. We could make this a complete classification by naming each branch:

Agnatha
Gnathostomes
  Chondrostei
  Neopterygii
    Ginglymodi
    Halecostomi
    Halecomorphi
    Teleostei

Lampreys
Sturgeons
Gars
Bowfins
Teleosts

Such a list provides a great deal more information than a simple list of the tips of the branches, but the list alone does reflect the sequence of the branches.

Finally, let us consider only the section of the diagram that deals with the ostariophysans, the trouts, and the perches (as a representative of higher teleosts) (Fig. 2). Minnows and suckers are united by the presence of a Weberian apparatus and must be placed

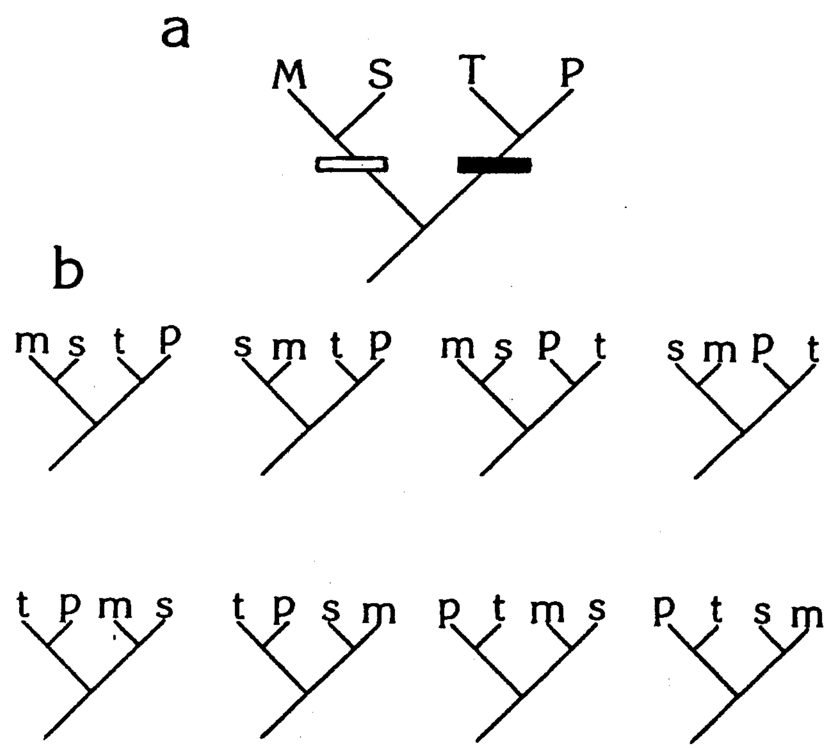

Figure 2. A.—Branching diagram showing the relationships of minnows (m), suckers (s), salmonids (t), and perches (p). B.—These eight diagrams are all equivalent and reflect the same relationships.

on the same branch. The trouts and the perches share several derived specializations and they belong on the other branch (Fig. 2a).

Note that there are several possible arrangements that reflect this branching sequence as shown in Figure 2b. This is because a simple dichotomy implies nothing regarding the sequence of the two branches. A on the left and B on the right means exactly the same thing as B on the left and A on the right. Normally, in a general classification we simply list the smallest groups first, but this is frequently reversed if we are especially interested in some intermediate group rather than the most advanced lineage.

What we cannot do, however, is place one lineage in the middle of another one. In Figure 3, arrangements in Row A are legitimate and reflect branching diagrams that are exactly equivalent to each other. Arrangements in Row B, however, imply branching diagrams that are incorrect because they do not indicate that the trouts and the perches (see Fig. 3) are on a line that is the sister group of the ostariophysans. Therefore, minnows must either come before both the trouts and the perches or after them but they cannot come between them. For general works such as regional guide books or the AFS checklist, it is more appropriate to place the minnows first because they have fewer specializations. If, however, we were treating mainly minnows we might choose to place the higher form first just to indicate their relationships and then get them out of the way. In this sense we would be following the rule of listing the smaller branch (i.e., the one with the fewer names) first.

Many aspects of the relationships among the higher (more inclusive) groups of teleost fishes are still in doubt. Here are just a few examples: Are the pikes and pickerels really related to the salmonids? What are the nearest relatives of the sculpins? Are there two families of topminnows or only one? What are the nearest relatives of the suckers? Consequently, we can expect to see many more changes in fish classification during the next few years, as such problems are taking advantage of new techniques and different viewpoints. The classical Linnaean hierarchy—kingdom, phylum, class, order, family, genus, and species will come to have less and less importance as branching sequences are emphasized more and more.

References

Fink, W. L., and S. H. Weitzman. 1982. Relationships of the stomiform fishes (Teleostei), with a description of *Doplophas*. Bull. Mus. Comp. Zool. 150:31–93.

Greenwood, P. H., D. E. Rosen, S. Weitzman, and G. S. Myers. 1966. Phyletic studies of Teleostean fishes, with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist. 131(4):341–353.

Hennig, W. 1966. Phylogenetic systematics. Univ. Illinois Press, Urbana. 263 pp.

Janvier, P. 1984. Cladistics: theory, purpose,

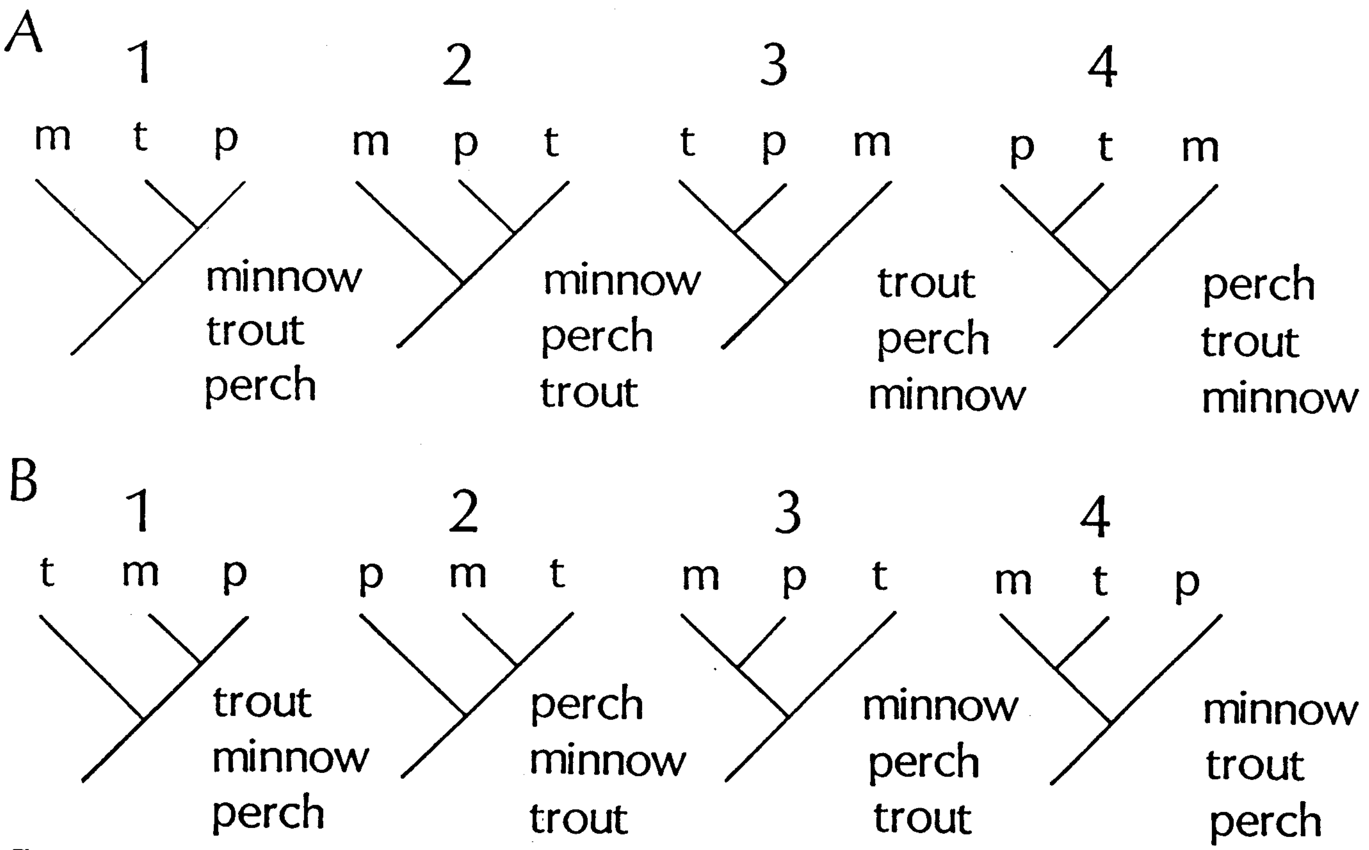

Figure 3. A—Four diagrams, and lists derived from them, that show the correct relationship between minnows (m), salmonids (t), and perches (p). B.—Four diagrams that incorrectly depict the same relationship. Notice that the orders B3 and B4 are identical to orders A1 and A2. This is because branching diagrams convey more information than the lists alone. This would not be true of a list in which the major branches were also named.