THE FISHES OF LAKE LANAO: A PROBLEM IN EVOLUTION[1]

DR. ALBERT W. C. T. HERRE
STANFORD UNIVERSITY, CALIFORNIA

ORGANIC evolution, the development of new forms of life from previously existing stocks, is a fact taken for granted by all scientific men. Yet many fail to recognize that the evolution of new species of animals and plants is a continuous operation not confined to past geological ages, but actually going on during the present era.

Students of lichens have long recognized that the evolutionary development of those strange organisms is now actively in progress in numerous cases. The most marked illustration is the strongly differentiated lichen genus Cladonia. This group contains many polymorphic and intergrading species, each with a host of varieties, which only a little study shows are now in process of evolution. It is therefore no wonder that Cladonia comprises some of the most puzzling forms known to the student of plant life and is perhaps the best example extant of evolution under natural outdoor conditions here and now.

For more than a dozen years it has been my lot to devote a good deal of time to exploring and studying the plateau of Lanao, in the great island of Mindanao. While engaged in a preliminary reconnaissance of the aquatic life of Lake Lanao, for the purpose of helping improve the food supply of the more than 90,000 Marinao living around the lake, I discovered a unique endemic fish fauna.

Lake Lanao is a sheet of open water covering 145 square miles, lying at an elevation of 2,100 feet. For much of its extent the lake is comparatively shallow;

[1] The Cyprinidae of Lake Lanao are described by Herre in the *Philippine Journal of Science*, Vol. 24, 1924, pp. 249–306 and Vol. 29, 1926, pp. 499–502, and in *Copeia* for October, 1932, pp. 140 and 141.

along its northern, eastern and southeastern shores are great areas of shoal water with an average depth of four to ten meters. Along the western shore it is relatively deep and there is deep water from the outlet to the southern shore directly opposite. A half mile from the outlet the lake is 150 feet deep, and this depth increases as one goes toward Bayong, 18 miles away on the southern shore. Near Bayong the lake has a depth of 900 feet, according to the military cable survey.

At the northwest corner of the lake is its outlet, the torrential Agus, which rushes headlong to Iligan Bay 14 miles away. A few kilometers from the sea the Agus leaps over the Maria Cristina Falls, a jump of 65 meters.

Mindanao was originally not less than five rather large islands, which eventually coalesced to form the present great island. Lanao was originally an elevated coral reef on which has been superimposed lava and volcanic ash to a great depth. Lake Lanao was formed when a lava flow dammed up a deep ravine or mountain cañon.

The fish fauna of Lake Lanao comprises one eel (*Anguilla celebesensis*), one species of *Ophicephalus* (*Ophicephalus striatus*), and seventeen or more species of Cyprinidae. The young eels make their way up from the sea to the lake, apparently through underground channels impassable to other fishes. Such channels can be seen at the Maria Cristina Falls, pouring water out through the side of the cañon below the falls, and at Lake Nunuñgan where the outlet of the lake disappears under a mountain, emerging a five hours' march distant. *Ophicephalus striatus* was introduced by man a long, long time ago, just as the Malays have done all over Malaysia in both historic and prehistoric time.

The seventeen species of Cyprinidae thus far described by me from Lake Lanao have all descended from a single parent stock and therefore present a very interesting problem in evolution. It is the purpose of this paper to present a tentative arrangement of the relationships of the Cyprinidae of Lake Lanao, and incidentally

of all the Philippine Cyprinidae belonging to the genus Barbodes, and also to call attention to the remarkable opportunity the fishes of Lanao present to the student of evolution who wishes to investigate a large scale experiment now being conducted in one of the recesses of the laboratory of Dame Nature.

First, it is necessary to consider all the Philippine members of Barbodes occurring outside Lanao, since they are closely related to one another and to the Lanao species.

Barbodes binotatus Cuv. and Val. is unquestionably the ancestor of all the Philippine species of Cyprinidae here considered. It is a fish of very wide distribution in the Malayan Archipelago, occurring from Sumatra and Singapore to Lombok and Borneo, and on into the southern Philippines. In the ancient land bridge now called the Sulu Archipelago it found a home in Tawi Tawi and Basilan and reached Mindanao, spreading over the whole of the latter island with the exception of the isolated plateau of Lanao.

Barbodes binotatus occurs in Mindanao from sea-level to an altitude of over a thousand meters in Bukidnon. It is a powerful swimmer, able to ascend mountain torrents, but is prevented from reaching the Lanao plateau by impassable waterfalls.

In the days when Sunda Land occupied a large part of what is now the South China Sea and Borneo and Sumatra were the outlying fringes of this great body of land, Palawan and the Calamianes were a part of what we now call Borneo. By this land bridge *Barbodes binotatus* migrated northward along the eastern shore of the China Sea. Later on when Sunda Land sank and the northern spur of land narrowed greatly and became the detached islands of Balambangan, Balabac, Palawan, Culion, Busuanga and Mindoro, the parent stock of *Barbodes binotatus* was cut off and isolation was free to work.

On Palawan, and perhaps elsewhere, *Barbodes binotatus* variety *palavanensis* became differentiated. From it in turn arose the following species:—(1) *Barbodes ivis* (Seale), occurring on the islands of Balabac, Palawan and Busuanga; (2) *Barbodes manguaoensis* (A. L. Day) and (3) *Barbodes bantolensis* (A. L. Day), both known only from Lake Manguao in northern Palawan; and (4) *Barbodes hemictenus* Jordan and Richardson, known only from Northern Mindoro.

In Mindanao with its heavy rainfall, great rivers, and great range *Barbodes binotatus* was undifferentiated over the greater part of the island. The peninsula of Zamboanga, without large streams and with little connection with the rest of the island, developed the closely related species *Barbodes quinquemaculatus* (Seale and Bean), thus far known only from the vicinity of the town of Zamboanga and the near-by island of Basilan. *Barbodes montanoi* (Sauvage) is another very closely related and doubtful species which may not be different from *B. binotatus*. It was obtained by the celebrated traveler Montano in 1880, from the Simulao River, an eastern tributary of the Agusan River, Mindanao, but has not been collected since although I looked for it in the Agusan Valley.

When the Lanao mountain ravine was dammed long ago it is self evident that the Cyprinid ancestor of the Lanao fishes of to-day was imprisoned in the headwaters of the stream. Gradually the mountain stream changed to a large lake with a great diversity of conditions, but of course there were always swift tributary mountain brooks and creeks, in which conditions would remain relatively uniform. Manifestly the changing conditions in the lake, with all its varied assortment of environments, imposed new demands upon the parent stock of fishes and eventually various new forms of more or less permanence or fixity appeared, some of which survived while others may have disappeared. To me, at least, it seems that this state of flux or transition for certain groups now living in the lake is still in existence.

It is not possible to say with absolute finality whether *Barbodes binotatus* or *Barbodes quinquemaculatus* dwelt in the fluvial system which was converted into Lake Lanao. The two species are very close, but a study of their distribution seems to indicate that a variety or rather geographical race of *B. binotatus* was the original inhabitant. I have previously indicated (*Philippine Journal of Science,* vol. 24, 1924, p. 291) that specimens from the coastal streams of Lanao, Misamis and Bukidnon differ in color and general form from those collected elsewhere.

With the formation of the lake and the isolation of the entire plateau, *Barbodes binotatus* disappeared and in its stead appeared *Barbodes tumba* Herre. This well-marked species occurs in mountain streams and lakes all over the Lanao plateau, with the single exception (whether real or apparent is not yet determined) of Lake Lanao itself. I have obtained it from all the other lakes of the plateau, from tributaries of the great lake as far up as fish can ascend, and in the boiling waters of the Agus, outlet of Lake Lanao.

As Lake Lanao attained maturity, various offshoots from *Barbodes tumba* arose, each with special adaptations for a particular environment.

One set of species took up life in the clear blue surface water about the great forests of *Potamogeton* lying offshore in depths of 5 to 15 meters. Here they fed, reproduced and swam about in great schools in the open spaces well offshore. A study of thousands of specimens seems to show the following named species to form a direct line of succession from *Barbodes tumba,* all living under the conditions outlined above: *Barbodes amara* Herre; *Barbodes lanaoensis* Herre; *Barbodes lindog* Herre; *Barbodes disa* Herre. *Barbodes lindog* is the culmination of this series, and from it arose *B. disa* on the one hand, and on the other the singular *Spratellicypris palata* (Herre).

Barbodes tumba has also given rise directly to at least one species which has become habituated to life at a

greater depth than the other Cyprinidae of Lake Lanao. Consequently it is rarely seen except after great storms at the height of the rainy season, or in midwinter. When the waves are rolling unusually high it approaches the surface and may be caught in the little gill nets used by all Marinao fishermen to catch Cyprinidae from the lake. This deep water inhabitant is *Barbodes baoulan* Herre, the most highly prized food fish of the Lanao plateau.

In shallow muddy bays, where the water is a mat of vegetation, a real lacustrine jungle, several other species have developed. The species living in such places are usually blackish or black, or dusky bronze. It is very noticeable that life in such a habitat causes most species of fish to be highly melanistic. The swampy lowland lakes of Cotabato Province, Mindanao, afford excellent illustrations of this. *Glossogobius giurus,* which well deserves its Tagalog name of Bia ng puti (usually written Biang puti) or "White goby," develops such marked melanism in Lake Buluan and the adjacent Liguasan Marsh that its blackened condition makes it difficult to recognize at a casual glance.

Another line of evolution from *B. tumba* has given us the pot-bellied little *Barbodes sirang* Herre, which is often entirely black in life. The maximum size of this species, 60 mm., is half or two thirds that of the next smallest Cyprinidae of Lake Lanao. I discovered *B. sirang* on my last visit to the lake, in July, 1931, and know nothing of its habits.

A line of development entirely distinct from those already mentioned has given us *Barbodes flavifuscus* Herre, from which has arisen *Barbodes katolo* Herre. With their very large, clumsy looking heads these two species are markedly different from all those previously named. The evidence is not conclusive, but I believe that *Barbodes flavifuscus* is an offshoot from *Barbodes amara.* Certainly I can not place it elsewhere with our present knowledge.

From *Barbodes katolo* have come two closely related genera, *Cephalokompsus* Herre and *Ospatulus* Herre. *Cephalokompsus* is distinguished by the possession of a continuous postlabial groove on the lower jaw, which is not interrupted beneath the chin as in *Barbodes* and most genera of Cyprinidae. The only species is *Cephalokompsus pachycheilus* Herre.

Ospatulus is separated from other genera by its truncate mandible, which is much shorter than the upper jaw. There are two species, *O. truncatulus* Herre and *O. palaemophagus* Herre.

Barbodes clemensi Herre is a large, thick, robust fish which occurs in the lakes of the Lanao plateau, particularly in Lake Lanao, where it, too, sports about in the groves of *Potamogeton* along with *Barbodes lanaoensis* and *Barbodes lindog*. It is a handsome fish, dark green above and yellow beneath, with a golden or brassy luster on its sides. Its size and color at once distinguish it from the various fishes whose lines of descent have already been traced. Adult specimens will average 175 to 200 mm., standard length.

Associated with *B. clemensi* by its color and general appearance, and attaining a still larger size so that it is easily the largest of Philippine Cyprinidae, is *Barbodes manalak* Herre, which occurs only in Lake Lanao, as far as yet known. Adult specimens measure from 190 to more than 250 mm., standard length, and are very bulky for their length.

There is a strong probability that *Barbodes clemensi* and *Barbodes manalak* arose directly from *Barbodes binotatus*, but it is also possible that they developed from *Barbodes tumba* without any connection whatever with the lines culminating in *B. lindog* or *B. katolo*.

The most remarkable of all the Lanao Cyprinidae has taken to life in the boiling eddies and swirling mad torrent of the Agus, the outlet of Lake Lanao. This fish is *Mandibularca resinus* Herre, a genus and species set apart from all other Cyprinidae by the development of

the mandible. The lower jaw has become an extraordinary elongated, upward curved, spatula shaped, fleshless organ. It is so strange that Dr. David Starr Jordan said it might almost be made the type of a new family. This species, which is fully as large as *Barbodes clemensi,* probably occurs also in Lake Lanao, but thus far I have only seen specimens from the rapids and whirlpools of the Agus, some caught by myself and some by Marinao anglers.

The origin of *Mandibularca resinus* is not very difficult to trace, as now and then one finds individuals of *Barbodes clemensi* in which the lower jaw suggests the singular development so characteristic of *Mandibularca.*

Barbodes tras Herre is a peculiar Cyprinid which apparently is not very closely related to any of the other species thus far known from the lake, yet its structure suggests that it too is an offshoot from *Barbodes flavifuscus.* However this may be, it has evolved in a way entirely distinct from any of the others mentioned.

While working out the above-named forms, I have encountered many anomalous individuals which can not be placed with any certainty. Some are apparently hybrids, others seem to be valid species but more and better material is needed to determine their status. Some individuals, especially those belonging to the highly melanistic *katolo* group, seem to be in a state of flux with a commingling of the characters of several species.

I feel that the Cyprinidae of Lake Lanao present to the zoologist, within a limited and sharply isolated area, a miniature illustration of what certain Cladonias present on a world-wide scale.

From the outline given it can be seen that the fishes of the Lanao plateau present a highly interesting problem to the student of evolution, one which would well repay an intensive study. Something has been presented here from the unfashionable view-point of the field naturalist, in the hope that some modern technician might take up the study of the Lanao Cyprinidae.

It would seem that here we have an experiment being conducted before our eyes on a scale unapproachable by man. Let one of the "new" biologists leave his laboratory and apply his methods to the fishes of Lanao; perhaps he might then make a real contribution to the study of evolution. By spending six months on the shores of the lake he could obtain with great ease all the material he could handle, as the Marinao fishermen bring in thousands of fish on market day, often many canoe loads of each of the commoner species.

By studying several thousand fresh specimens of each of the ten most abundant species, and studying all the specimens obtainable of the rarer species and all the anomalous individuals, he could do much toward unraveling the phylogeny of the more puzzling forms and could perhaps place in their proper sequence the doubtful cases and those forms which seem to be examples of hybridism.

With the foundation indicated, his statistical analysis of species would have real value and would throw light upon the evolution of so many species from one parent species.

THE ENDEMIC FISH FAUNA OF LAKE LANAO, AND THE EVOLUTION OF HIGHER TAXONOMIC CATEGORIES [1]

GEORGE SPRAGUE MYERS
Stanford University

Received January 25, 1960

INTRODUCTION

The present paper is concerned only incidentally with speciation. Its purpose is to point out some striking but neglected features of lake-fish evolution that illustrate the rapid origin of genera and still higher categories going on at the present time. I have selected the Lanao fishes as an example for several reasons. First, I have examined the fishes myself. Second, the Lanao fishes are in a recognizable stage of what has been called "explosive" evolution. Third, the age of the lake can be determined geologically, and its relative youth cannot be in serious dispute. Fourth, the remarkable zoogeographical situation of Lanao and of Mindanao Island excludes any reasonable possibility that more than one still existing species could have given rise to the 18 endemic species and four endemic genera now inhabiting the lake. The endemic Lanao fish fauna is without parallel, so far as known, in demonstrating explosive specific and generic evolution from a known and still existing ancestral species.

I am deeply indebted to my long-time friend and colleague, Dr. Albert W. Herre, discoverer and describer of the Lanao fish fauna, for many discussions regarding Lake Lanao and its fishes, extending through a period of 30 years. The late Professor Bailey Willis of Stanford, well known for his geological researches on four continents, did me the honor of employing his extensive first-hand knowledge of Philippine geology to prepare the brief geological account of Lake Lanao quoted below. Finally I must present my best thanks to my present graduate student, Mr. Angel Alcala, Instructor in Zoology at Silliman University, Dumaguete, Oriental Negros, for making further collections of Lanao fishes for Stanford. Mr. Alcala was working under National Science Foundation Grant G4381, made to Dr. Walter C. Brown for herpetological research in the Philippines.

THE LAKE

Lake Lanao lies at an altitude of approximately 2,100 feet in the midst of a volcanic area in central Mindanao, the largest island of the southern Philippines. Its exact area is in dispute, Herre giving it 375 square kilometers, and others as many as 900. The late Professor Bailey Willis, who had given much attention to Philippine geology, as well as to that of the African Rift Valley and its lakes, investigated what was known of the geological history of Lake Lanao and prepared the following statement for me:

"The island of Mindanao has risen from the ocean gradually and unequally since the Miocene. It now consists of plateaus, hill country, swamps, and volcanoes. The streams were initially small and isolated from each other. The headwaters were, and are, generally swift and the lower courses estuarine.

"A north-central region was built up by basalt flows to a plateau, on which a small system of rivers developed. Some of them flowed southwesterly to Illana Bay, others northwesterly to Iligan Bay. The divide between them ranged from southwest to northeast.

[1] Abstract published in: Proc. XVth Internat. Congr. Zool., 151–152, 1959.

"Volcanoes were built up across the southwesterly flowing streams and they were dammed. Their headwaters gathered in the basin thus formed until they overflowed a low pass in the divide at Camp Keithly and discharged into Iligan Bay on the north coast.

"The impounded waters constitute Lake Lanao. The basin is probably shallow, 200 to 300 feet, perhaps, where deepest. The outlet at Camp Keithly plunges over a fall into a short canyon, indicating an age of 10,000 years, more or less. The principal tributaries to the lake enter from the southeast, from young but dormant volcanoes, and may at times have brought in quantities of ash."

While I have no specific reason to doubt Dr. Willis's estimate of the age of Lake Lanao, 10,000 years seems to be a very short time for the evolution of the Lanao fish fauna. When I brought up this question, Dr. Willis replied that the length of the canyon worn by the Agus River indicated a very brief erosional period. The possibility remains that more than one volcanic damming has been involved in the history of Lake Lanao, but the relative youth of the lake cannot be seriously doubted. The geology of the Lanao Plateau obviously needs more geological investigation.

The Fishes

Dr. A. W. Herre collected fourteen species of the Lanao fishes and described them formally in 1924, without mentioning the peculiar evolutionary features concerned. Before the publication of his 1924 paper, he had prepared an account of the zoogeography of Philippine freshwater fishes, in which he implicitly recognized the autochthonous nature of the Lanao fish fauna. However, this distributional paper was not published until considerably later (Herre, 1928). Dr. Herre visited the lake upon later occasions, adding two more species in 1926 and two in 1932.

After Dr. Herre joined the Stanford Museum staff in 1928, I urged upon him the value of preparing an account of the evolutionary features of the Lanao fauna. This resulted in the proposal of a new genus for one remarkable Lanao species (Herre and Myers, 1931) and, finally, in Herre's well-known paper of 1933. Since that time, nothing of importance has been published on these fishes save for Dr. Brooks' review of 1950.

This history is important because of the destruction of Herre's earlier material when the Bureau of Science was dynamited and its collections totally destroyed by Japanese troops in February, 1945, during the battle of Manila. The only sizable collection of Lanao fishes presently available is that in the Natural History Museum of Stanford University. This consists of a few specimens obtained by exchange from the Bureau of Science before World War II; the excellent collection made by Dr. Herre in 1931, including the types of two of his species; and a small collection made at my request in 1959 by Mr. Alcala. Two of the endemic genera (*Mandibularca* and *Spratellicypris*) and the majority of the species are represented. The only other collection of Lanao fishes known to exist in any museum is a small one obtained in 1908 by Dr. Hugh M. Smith and Dr. Paul Bartsch, and now in the U. S. National Museum. This collection was not reported upon *in extenso* until long after Herre's work was completed (Fowler, 1941). I am unable to accept some of Fowler's identifications and have not considered them in the present paper. Two of Herre's endemic genera (*Cephalakompsus* and *Ospatulus*) are known only from the destroyed types.

I have examined the Stanford collection and have had much unpublished information from Dr. Herre. Despite the unavailability of several of the described species, I am convinced that most if not all of the species described by Herre are distinct, some of them remarkably so. Unfortunately, little ecological information

is on record. Most of the
tained from the lake have
from the native fishermen
extensively fished, and
endemic forms are high
foodfishes by the local Mo

The endemic forms are
the Cyprinidae, the larg
primary fresh-water fishe
species flock consists of 13
of the genus Dr. Herre ca
better called *Puntius* (see
Beaufort, 1916) but in m
easily distinguished from t
genus *Barbus* (Myers,
more species are placed in
Spratellicypris (1), *Man*
Ospatulus (2), and *Cephal*
all of them obviously imme
from stocks of *Barbus* wi
Other still undescribed spe
bly present in the lake.
endemic predators are pr
striata, perhaps introduced
one diadromus eel (*A*
besensis). Eels of this gro
to be able to ascend rapids
impassable to other fishes.
American black bass
salmoides), a voracious pr
to have been introduced in

Derivation of the Cyprinidae

Herre (1928 and 1933)
some of the distributional
Philippine Cyprinidae, and
lished a general study of the
of the fresh-water fishes
(Myers, 1951). The esse
as follows:

Central and southern
with Cyprinidae, but the
of North Borneo is relativ

[2] It is difficult to see why such
should have been considered. I
as a measure for increasing
it is clearly unsound. Scientific
the unique nature of the ende
fauna, it becomes a crime!

is on record. Most of the collections obtained from the lake have been purchased from the native fishermen. The lake is extensively fished, and some of the endemic forms are highly prized as foodfishes by the local Moros.

The endemic forms are all members of the Cyprinidae, the largest family of primary fresh-water fishes. The large species flock consists of 13 known species of the genus Dr. Herre called *Barbodes*, better called *Puntius* (see Weber and de Beaufort, 1916) but in my opinion not easily distinguished from the widespread genus *Barbus* (Myers, 1960). Five more species are placed in four genera, *Spratellicypris* (1), *Mandibularca* (1), *Ospatulus* (2), and *Cephalakompsus* (1), all of them obviously immediately derived from stocks of *Barbus* within the lake. Other still undescribed species are probably present in the lake. Two non-endemic predators are present, *Channa striata*, perhaps introduced by man, and one diadromus eel (*Anguilla celebesensis*). Eels of this group are known to be able to ascend rapids and waterfalls impassable to other fishes. The North American black bass (*Micropterus salmoides*), a voracious predator, is said to have been introduced in recent years.[2]

Derivation of the Mindanao Cyprinidae

Herre (1928 and 1933) has outlined some of the distributional history of the Philippine Cyprinidae, and I have published a general study of the zoogeography of the fresh-water fishes of the region (Myers, 1951). The essential facts are as follows:

Central and southern Borneo teems with Cyprinidae, but the cyprinid fauna of North Borneo is relatively depauperate. Cyprinids have entered the Philippines from North Borneo in two widely different directions, through the Palawan-Calamianes chain to Mindoro, and through the Sulu chain to Mindanao. Cyprinids got no farther. The family is absent in the rest of the Philippines, and in Celebes. The Palawan-Mindoro cyprinids do not concern us here.

That Cyprinidae reached Mindanao via a sweepstakes route, across a series of salt-water gaps, is unlikely. My own studies (Myers, 1938, 1949, 1951) indicate that fresh-water fishes are less likely to cross such gaps, especially a series of them, than any terrestrial animals, although they must have done so (probably only once, across a very narrow barrier) at Lombok Strait (Myers, 1951). The Lombok crossing, if not by the hand of man, was almost certainly by means of a local cyclone (Darlington, 1938; Myers, 1951), for the salt-water gap at Lombok Strait, although probably broader now than in the Pleistocene, cannot have been bridged very recently (see Bruun and Kiilerich, 1957). Nor is it likely that hurricane (typhoon) winds could have aided the fishes invading Mindanao. The typhoon tracks shown by Dickerson (1928: 40) are all westerly in direction. Finally, fresh-water fishes are not well adapted to raft-dispersal across seas!

The obvious conclusion is that fresh-water fishes entered Mandanao across a dry-land filter bridge, through the Sulu chain. Just what lowering of sea-level occurred there during the Pleistocene, or what elevations or depressions of the Sulu chain may have occurred, is not known. The region is a volcanic, unstable one.

That few or no remains of the cyprinid migration are to be found today on the islands of the Sulu Archipelago is not too surprising. Dr. Herre fished the largest island, Jolo. He found the streams small and without Cyprinidae, but believes that relatively recent volcanic activity has wiped out the fresh-water fishes of the island (Herre, 1928).

[2] It is difficult to see why such an introduction should have been considered. Ecologically, and as a measure for increasing food production, it is clearly unsound. Scientifically, in view of the unique nature of the endemic Lanao fish fauna, it becomes a crime!

Quite clearly, then, North Borneo itself, together with the Sulu Archipelago, acted as a filter bridge to limit the access of fresh-water fishes to Mindanao. Only three genera of Cyprinidae reached Mindanao (*Barbus, Rasbora,* and *Nematabramis*) and these three are still the dominant cyprinid genera in the streams of North Borneo. Probably only one species of each genus reached Mindanao.

The cyprinid fauna of Mindanao Island outside the Lanao Plateau is very small. There is a single endemic *Rasbora* (*R. philippina*) confined to the western part of the island and closely related to a North Borneo species (Brittan, 1954: 127–131). There are two species of *Nematabramis* (*N. alestes* and *N. verecundus*), very closely allied to each other and to the species of North Borneo (Herre, 1953). Finally, there are four nominal species of *Barbus* (or *Puntius*). *Barbus binotatus* is widespread in Mindanao, and, according to Herre (1953: 123), has been erroneously reported from Lake Lanao by Fowler. *Barbus montanoi* is a doubtful form known only from the type from the Agusan River drainage, eastern Mindanao. *Barbus quinquemaculatus* from the Zamboanga Peninsula is probably a geographical subspecies of *B. binotatus*. *Barbus cataractae* (see Fowler, 1941: 797), also from the Zamboanga Peninsula, is probably a localized variant of *B. binotatus*. After examining the evidence, I suspect that there are really only three well-established cyprinid species in Mindanao outside the Lanao Plateau, one *Rasbora,* one *Nematabramis,* and one *Barbus,* each possibly represented on the island by several subspecies.

Nature of the Lanao Fish Fauna

Barbus binotatus is the commonest, most widespread, and probably the most variable cyprinid of Sundaland (see Weber and de Beaufort, 1916). It ranges from Siam to Singapore, and throughout Sumatra, Java, and Borneo. It is one of the three cyprinids that have been able to cross Wallace's Line at Lombok Strait; the others are forms of *Rasbora* (Brittan, 1954). *Barbus binotatus* exists in most or all of the lowland streams of Mindanao. It exhibits innumerable local races throughout its range.

With no other large endemic lake fish fauna is it possible with such certainty to identify the ancestral species. Lake Lanao was clearly formed rather rapidly, by volcanic action. The ill defined races of *Barbus binotatus* surrounding the Lanao Plateau form the only local source of invasions. Multiple invasions by dissimilar species of *Barbus* or other cyprinid genera are ruled out, unless one wishes to postulate a series of aerial invasions from Borneo, which dropped fishes only on the Lanao Plateau without colonizing the remainder of Mindanao!

Nor are any cyprinids known from Borneo or elsewhere which parallel or are similar to the strange Lanao genera *Mandibularca* and *Spratellicypris*. The same may be true of the genera *Cephalakompsus* and *Ospatulus,* but the types and only known specimens of these two genera were destroyed in Manila.

We are thus forced to the conclusion that *Barbus binotatus* alone gave rise to at least 18 species on the Lanao Plateau, including four new genera. All of the species that I have examined give evidence of derivation from *Barbus binotatus* or at least a close relative. Two or three of the species are only slightly differentiated from *binotatus* and occur both in the lake and its tributary streams. The most distinctive species are known only from the lake itself. *Mandibularca* occurs only in highly turbulent water at the outlet. One or two of the species are said by local fishermen to inhabit only the deeper waters of the lake, while others are found only in the shallow *Potamogeton* beds. *Barbus binotatus* is not known to occur on the plateau, nor are any of the lake species known from below María Cristina Falls, 65 meters in

height, in the Agus River
the lake.

The Supralimital Spe

In 1936, in connection w
fishes from Lake Tangan
pointed out (perhaps for
some of the general fea
evolution in large lakes t
world—the African lak
Baikal, and Lanao. Brook
reviewed the subject of
ancient lakes, including La
is not an ancient lake
speaking, and the particu
wish again to stress are
to ancient lakes nor recogni

In Lake Lanao, the pec
different lower jaw modific
in the genera *Mandibularca*
cypris (and probably in
well) are approached nowh
very large family Cyprini
generally distributed throug
Africa, and North America
many remarkable specializati
words, the jaw modificati
Lanao cyprinids transcend
limits of all the 1,500 to 2,0
cyprinid species in the wor
of a better term I am callin
limital specializations.

That peculiar supralimit
tions are not confined to La
common and general feature
tion of endemic fish faunas i
is easily demonstrated. Th
scaleless cyprinid *Sawbwa*
Lake in Burma (Annandal
highly modified species of
Titicaca, the extraordinar
cichlid genera of Nyasa and
and many of the cottoids of
all transcend, in one way
(often strongly and in ma
istics) the limits of speciali
large, widespread, and varie
which they belong.

One illustration will s
Percomorphi form the larg

and Borneo. It is one
inids that have been able
s Line at Lombok Strait;
rms of *Rasbora* (Brittan,
binotatus exists in most
vland streams of Minda-
s innumerable local races
ange.
r large endemic lake fish
sible with such certainty
ancestral species. Lake
ly formed rather rapidly,
on. The ill defined races
notatus surrounding the
form the only local source
Multiple invasions by dis-
of *Barbus* or other
are ruled out, unless one
ulate a series of aerial
Borneo, which dropped
he Lanao Plateau without
remainder of Mindanao!
y cyprinids known from
where which parallel or are
strange Lanao genera
and *Spratellicypris*. The
rue of the genera *Cephala-*
spatulus, but the types and
specimens of these two
estroyed in Manila.
s forced to the conclusion
notatus alone gave rise to
cies on the Lanao Plateau,
new genera. All of the
have examined give evi-
tion from *Barbus binotatus*
ose relative. Two or three
are only slightly differen-
notatus and occur both in
ts tributary streams. The
ve species are known only
itself. *Mandibularca* occurs
y turbulent water at the
or two of the species are
fishermen to inhabit only
waters of the lake, while
ound only in the shallow
beds. *Barbus binotatus* is
occur on the plateau, nor
e lake species known from
Cristina Falls, 65 meters in

height, in the Agus River which drains the lake.

The Supralimital Specializations

In 1936, in connection with a report on fishes from Lake Tanganyika, I briefly pointed out (perhaps for the first time) some of the general features of fish evolution in large lakes throughout the world—the African lakes, Titicaca, Baikal, and Lanao. Brooks (1950) has reviewed the subject of speciation in ancient lakes, including Lanao, but Lanao is not an ancient lake, geologically speaking, and the particular features I wish again to stress are neither limited to ancient lakes nor recognized by Brooks.

In Lake Lanao, the peculiar but quite different lower jaw modifications evolved in the genera *Mandibularca* and *Spratellicypris* (and probably in *Ospatulus* as well) are approached nowhere else in the very large family Cyprinidae, which is generally distributed throughout Eurasia, Africa, and North America, and exhibits many remarkable specializations. In other words, the jaw modifications of some Lanao cyprinids transcend the familial limits of all the 1,500 to 2,000 non-Lanao cyprinid species in the world. For want of a better term I am calling these supralimital specializations.

That peculiar supralimital specializations are not confined to Lanao, but are a common and general feature of the evolution of endemic fish faunas in large lakes, is easily demonstrated. The remarkable scaleless cyprinid *Sawbwa* of the Inlé Lake in Burma (Annandale, 1918), the highly modified species of *Orestias* in Titicaca, the extraordinarily modified cichlid genera of Nyasa and Tanganyika, and many of the cottoids of Lake Baikal, all transcend, in one way or another (often strongly and in many characteristics) the limits of specialization of the large, widespread, and varied families to which they belong.

One illustration will suffice. The Percomorphi form the largest order of bony fishes, containing nine thousand species or more. Within the order, many families are defined by relatively few characteristics, of which dentition is often of considerable importance. The fresh-water percomorphs of the family Cichlidae form a large family of perhaps 700 species, distributed throughout Africa, Syria, Madagascar, southern India, and tropical America. Their dental characteristics are generally rather uniform, the modifications usually of small degree. Yet in some of the endemic cichlid genera of Lake Tanganyika, the dental modifications (especially the great, double pointed, heavy-based teeth of *Perissodus* and the utterly strange leaf-like teeth of *Plecodus*) far transcend the limits of dental modification not only of the family Cichlidae, but also of the order Percomorphi and of the entire class of bony fishes. Nothing remotely like them exists. Nor are dental characters the only ones involved. Specializations of the pelvic fins for bottom living (genera *Asprotilapia, Enantiopus*), which elsewhere are considered to be taxonomically of great importance, occur. Indeed, some of the Nyasa and especially the Tanganyika cichlids have come to resemble closely such diverse percomorph families as the Blenniidae (*Telmatochromis*), Girellidae (*Tropheus*), and certain European Percidae (*Asprotilapia*), representing a radiative divergence, and convergence towards different families, entirely unknown elsewhere in the entire gigantic order Percomorphi.

Both *Perissodus* and *Plecodus*, as well as certain other African lake cichlids, might easily be held to represent monotypic families, as has indeed been done with the Comephoridae and (by some) the Cottocomephoridae of Lake Baikal. The late Dr. David Starr Jordan, when shown the jaw of the Lanao genus *Mandibularca*, remarked that a family might well be set up for this genus alone. While I cannot quite agree with this opinion, Jordan's remark is indicative of the situation.

It may be noted that supralimital specializations in fishes are not confined to lake faunas. Any specialization peculiar to one species or genus is, in a sense, a supralimital specialization. However, the general or perhaps the invariable occurrence of extreme and unique specializations in the fishes of lakes that have existed long enough to have produced considerable endemic fish faunas, is notable. Still more notable is the fact that species possessing striking supralimital specializations form a much higher percentage of older lake faunas than they do of stream faunas in general.

The reason for this seems obvious. Most fresh-water fishes inhabit streams and are adapted to life in running water. When lakes are formed, only species already adapted to the slow moving, quiet backwaters are able to take immediate and full advantage of an extensive still-water environment. This extensive new environment usually provides many biotypes not represented in streams, and, in addition, geographical barriers (especially in larger lakes) which may either be present originally or develop with the evolution of the lake itself. The inability of biologists, who are terrestrial animals, to envision these subaquatic facts has greatly hindered studies of fish evolution in lakes.

Stages of Lake Fish Evolution

It is possible to point out sequential steps in the evolution of lake fish faunas, using different existing large lakes as examples; it seems worthwhile to do so. I have specifically refrained from any attempt to evaluate the probably numerous instances in which a relatively small or recent lake has obviously permitted the evolution of one or a few species, sometimes of diverse groups. One such lake is Lake Waccamaw in North Carolina (Hubbs and Raney, 1946). Another is Bear Lake, on the Utah-Idaho boundary, in which three distinct coregonids have evolved (Snyder, 1919). The coregonids have been especially prone to apparent endemism in northern glacial and alpine lakes, but doubt as to the real distinctiveness of many such forms in Postglacial lakes has often been expressed.

In the North American Great Lakes, which have become generally available to fishes only since the geologically recent retreat of glaciation, the coregonids of the "lake herring" (*Leucichthys*) type have experienced a burst of evolution, but many of the endemic species and races are still difficult to separate (Koelz, 1929), if indeed they are really distinct. The fauna is still too young to show anything very definite in the way of supralimital specializations, but the development of species flocks of coregonids is evident. Except for the "lake herrings," no other group of fishes so well preadapted to very cold, still water was present, and this one gained ascendancy.

A similar situation, but probably of greater age because of the greater distinctiveness of the species, is seen in the athernids (*Chirostoma*) of Lake Chapala and other lakes in Mexico (Regan, 1906–1908; Jordan and Hubbs, 1919; Alvarez, 1950) and the cichlids (Meek, 1907; Regan, 1906–1908) of Lakes Nicaragua and Managua. Supralimital specializations among the Cyprinodontidae are clearly foreshadowed in the dwarf, deep-bodied species of *Orestias* in Lake Titicaca (Tchernavin, 1944), which are unlike any of the non-Titicaca *Orestias*.

A clearly more advanced stage is represented by Lake Lanao, in which a single ancestral species of cyprinid has given rise to a species flock, five members of which have become so distinct as to be referable to four endemic genera. Their supralimital specializations have been mentioned above. The excellent work of Mr. Greenwood on the Cichlidae of Lake Victoria shows that the Victoria cichlids are in a state more or less comparable to that of the Lanao cyprinids, although evolution is proceeding on a far grander scale. The species flocks are much larger

and there are four disti
genera (Greenwood, 1956.
ancestral types are eithe
identifiable. However,
endemics of families o
dominant one are absent.

A much older stage is
the fishes of Lake Nyasa
(1950: 135) estimates
mately 500,000 years old.
264) gives evidence poin
age. As in all other larg
can lakes, the cichlids (T
Fryer, 1959) are dominan
the greatest of all know
among lake fishes—over
the widespread genus *Ha*
addition, there are over 7
belonging to 20 endemic
of which exhibit remark
specializations. Howeve
families have entered the
lished endemic species,
endemic genus (Wor
Jackso , 1959). Most
drained by physiographic
they attain any age such
and it alone remains t
evolutionary stage of its
same is true of the tw
fish faunas, those of
Baikal.

Lake Tanganyika is a
years old and may be evo
1950: 148). Its fish fa
1953) indicates a mu
tionary stage than tha
being especially notable
comparable size and ge
imity of these two inm
lakes. The cichlids ar
they are fewer in numb
in Nyasa, but the vast
to endemic Tanganyika
group that could be
flock" is formed by t
Lamprologus, a genus a
the Congo.[3] Several

[3] The interesting possi
that Lamprologus is an au
yika genus which has colon

and there are four distinctive endemic genera (Greenwood, 1956, 1959), but the ancestral types are either lost or unidentifiable. However, as in Lanao, endemics of families other than the dominant one are absent.

A much older stage is represented by the fishes of Lake Nyasa, which Brooks (1950: 135) estimates to be approximately 500,000 years old. Fryer (1959: 264) gives evidence pointing to greater age. As in all other large Central African lakes, the cichlids (Trewavas, 1935; Fryer, 1959) are dominant. They present the greatest of all known species flocks among lake fishes—over 100 species of the widespread genus *Haplochromis*. In addition, there are over 70 cichlid species belonging to 20 endemic genera, several of which exhibit remarkable supralimital specializations. However, fishes of other families have entered the lake and established endemic species, but only one endemic genus (Worthington, 1933; Jackson, 1959). Most large lakes are drained by physiographic evolution before they attain any age such as that of Nyasa, and it alone remains to represent the evolutionary stage of its fish fauna. The same is true of the two still older lake fish faunas, those of Tanganyika and Baikal.

Lake Tanganyika is at least 1,500,000 years old and may be even older (Brooks, 1950: 148). Its fish fauna (Poll, 1946; 1953) indicates a much later evolutionary stage than that of Nyasa, this being especially notable because of the comparable size and geographical proximity of these two immense Rift Valley lakes. The cichlids are still dominant; they are fewer in number of species than in Nyasa, but the vast majority belong to endemic Tanganyika genera. The only group that could be called a "species flock" is formed by the 19 species of *Lamprologus*, a genus also represented in the Congo.[3] Several of the endemic genera, as has already been noted, are morphologically worthy of familial or subfamilial groupings, and several have come to resemble quite different families of Percomorphi. In non-cichlid fishes, Tanganyika has had time to develop, in addition to a number of endemic species belonging to non-endemic genera, two endemic genera of Clupeidae, two of Bagridae, two of Clariidae, one of Cyprinodontidae (representing a distinctive subfamily; Myers, 1936) and one (*Luciolates*) of Centropomidae (Worthington and Ricardo, 1937; Poll, 1953). Evolution of some of these must have been accomplished in the face of strong competition by the entrenched Cichlidae.

Lake Baikal is the oldest of all, perhaps as much as 75,000,000 years old; its southern basin is Paleocene or possibly even late Cretaceous in age. However, the present lake basin was enlarged and deepened as late as the Pleistocene (Brooks, 1950: 33), and it is doubtful that even the most distinctive Baikal fishes arose prior to the Mid-tertiary. The Cottidae and their derivatives are dominant in Baikal; species of no other fish families are endemic to the lake (Taliev, 1955). The absence of non-cottoid endemics is notable; it is probably due to the poverty of the Siberian fish fauna. The 26 endemic cottoid species belong to nine endemic genera, eight referred by Taliev to two endemic subfamilies of the Cottidae and one genus with two species to the endemic family Comephoridae.

Other lake fish faunas might be fitted into the sequence, but this seems unnecessary.[4]

In all the larger endemic lake-fish faunas, from the youngest to the very

[3] The interesting possibility presents itself that Lamprologus is an autochthonous Tanganyika genus which has colonized the Congo basin.

[4] Some other lakes, with the families to which the dominant endemics belong, are: Lake Biwa, Japan (Cyprinidae); the Celebes lakes (Atherinidae, usually); various Mexican lakes (Atherinidae); the African lakes George, Albert, etc. (Cichlidae); various Central Asiatic lakes, such as Lop Nor, Koko Nor, etc. (Cyprinidae or Cobitidae); Utah Lake (Catostomidae).

oldest, a single family group, preadapted over other stream fishes for lake life, has gained dominance over all others and has retained it. This accounts for my former belief (Myers, 1936) that access to lakes dominated by a single fish family must have been restricted. Access was restricted in Lake Lanao, but probably this has only rarely been true in other lakes. Moreover, in all except the youngest lake fish faunas, supralimitally specialized forms are evident and continue to become more striking until some of them, in the older lakes, could be or are accepted by taxonomists as distinct families.

One other important point should be made. The greater richness in genera and species of the older lake fish faunas, insofar as the dominant family is concerned, compared to the fluviatile fauna of the same family in the same region, is always striking. The Lanao cyprinid fauna dwarfs the cyprinid fauna of Mindanao outside the lake. More than half the African species and far more than half the African genera of the large family Cichlidae are endemics in the lakes of East Central Africa. The greater part of the North American forms of *Leucichthys* are lake endemics. Probably the same is true of Mexican atherinids of the genus *Chirostoma*. The forms of *Orestias* in Lake Titicaca are more numerous than those in the rest of the Andean Altiplano. The cottoid genera of Baikal comprise over three-fourths of the known genera of fresh-water cottoids in the world.

Isolated Endemics

Whether the strange little mastacembelid-like *Chaudhuria caudata* (Annandale, 1918) of the Inlé Lake, sole representative of the family Chaudhuriidae, and the possibly even stranger *Indostomus paradoxus* (Prashad and Mukerji, 1929) of the Indawygi Lake, sole representative of the family Indostomidae, are to be considered as vastly modified relicts of autochthonous lake-fish families, is unknown. If so, they would be the ultimate examples of lake fish specialization, but neither species has any known close relatives, and both may be mere survivors of once widely distributed families. The two genera and three known species of the strange family Adrianichthyidae, from Lake Posso and Lake Lindu in Celebes (see Weber and de Beaufort, 1922), which are undoubtedly derivatives of the family Cyprinodontidae, likewise have no known close relatives by which to judge their exact origin. I would suspect them to be derivatives of the subfamily Oryziatinae, members of which are still widely distributed in fresh waters from India and Japan to Timor, and which have given rise, in India, to the remarkable fish *Horaichthys*. Isolated lake-fish endemics are not too rare, often in lakes in which fishes of another family have become dominant, but the endemic nature of the genus or higher category represented by them is sometimes in doubt. The cottid *Triglopsis* in the American Great Lakes is an example. Perhaps some of these isolated endemics are relicts of previous cycles of lake-fish evolution in the same basins, cycles which were terminated by great changes in the basin itself.

New Areas, New Groups

What has happened, in the normal course of evolution, when one or more representative of an animal group not hitherto represented in the fauna has suddenly gained access to a large area replete with numerous available and unoccupied biotopes, seems to be clear. If the invaders are unable to withstand the competition of the older fauna, they disappear. If they can overcome competition, or especially if there is little or none, rapid or tachytelic evolution occurs, evolution that was impossible in their old home, where better balanced ecological conditions and a balanced fauna held evolutionary divergence more tightly in check. New genera, often utterly unlike their ancestors in one or more striking characteristics, appe
rapidity. The rapid proli
boscideans, and their
supralimital specialization
vasion of America, is a c

The same sort of evo
pened time and again whe
were colonized. The s
specializations of the Ga
and (whatever their ance
been) especially those of
birds in Hawaii, are well k
Island evolution of this
fish evolution, is often s
the original colonizers
biotopes totally unoccup
arrived.

However, the situatio
what in lakes. The
founders of evolutionar
lakes must contend not
same types of problems
island or continent colo
dition, they must face t
a flowing to a still-wat
and, in many instance
depth, pressure, and s
new or inimical to the
seems possible that grad
salinity in a closed la
eventually check the ev
fresh-water fish groups
(Myers, 1938; 1949).

The tachytelic evolutio
in part at least repres
evolution in Simpson's
point out in a really st
genera, families, or eve
gories of different anim
evolved. If they could
lakes and use their supr
izations in other lakes o
some undoubtedly have
many existing lake fis
become the founders of la
ing new groups at new
Terrestrial groups are
limited in their ability
ranges as are lake anima
has so ably pointed out

ing characteristics, appear with great rapidity. The rapid proliferation of proboscideans, and their development of supralimital specializations after their invasion of America, is a case in point.

The same sort of evolution has happened time and again when island groups were colonized. The supralimital bill specializations of the Galápagos finches, and (whatever their ancestors may have been) especially those of the drepanidid birds in Hawaii, are well known instances. Island evolution of this kind, like lake-fish evolution, is often striking, because the original colonizers found abundant biotopes totally unoccupied when they arrived.

However, the situation differs somewhat in lakes. The colonizers and founders of evolutionary dynasties in lakes must contend not only with the same types of problems that confront island or continent colonizers. In addition, they must face the change from a flowing to a still-water environment, and, in many instances, problems of depth, pressure, and salinity, perhaps new or inimical to them. In fact, it seems possible that gradually increasing salinity in a closed lake basin might eventually check the evolution of some fresh-water fish groups very severely (Myers, 1938; 1949).

The tachytelic evolution of lake fishes, in part at least representing quantum evolution in Simpson's sense, seems to point out in a really striking way how genera, families, or even higher categories of different animal groups have evolved. If they could get out of their lakes and use their supralimital specializations in other lakes or in streams, as some undoubtedly have done in the past, many existing lake fishes could easily become the founders of large and flourishing new groups at new adaptive levels. Terrestrial groups are not usually as limited in their ability to escape their ranges as are lake animals. As Simpson has so ably pointed out, the tachytelic evolution of new superior groups has seldom left a fossil record because of the speed with which events progressed, and, we may add, because of the probable localization of those events.

It seems probable that events of the sort I have been discussing account for the almost unbelievably rich fauna of characid fishes of the greatest of all rivers, the Amazon. In its present form the Amazon is not an old river. In its lower course it is probably a reversed river; its old structural basin plunges westward. Its Peruvian reaches formed a great lake in relatively recent geological times, and the immense but fluctuating lakes that now line its lower course comprise one of the largest areas of ponded fresh water now existing on earth.

Finally, we cannot forbear to mention the largest of all bodies of still, quiet water, the deep seas. The supralimital specializations exhibited by the highly modified deep-sea descendants of invaders from more turbulent shallow waters have long been the wonder of all zoologists.

It follows that opportunity—the absence of well-adapted competing groups—is extremely important as a factor in the evolution of higher categories. The importance of such a conclusion in relation to the early, rapid evolution of the main animal phyla is obvious.

Summary

1. The endemic fish fauna of Lake Lanao, all belonging to the family Cyprinidae, consisting of a species flock of 13 species and five species referred to four endemic genera, has evolved in a relatively short time, possibly as little as 10,000 years.

2. The distributional facts permit the identification, beyond reasonable doubt, of the single, still-existing, ancestral species that gave rise to the entire endemic fish fauna.

3. Certain specializations of the endemic Lanao genera are paralleled or approached by no others in the large,

widespread family Cyprinidae; because they transcend the morphological limits of all non-Lanao cyprinids, these are termed supralimital specializations.

4. Supralimital specializations are shown to be very characteristic if not invariable features of all large, older, endemic lake-fish faunas; some are so distinctive as to provide characters worthy of family rank.

5. The stages of endemic lake-fish evolution are illustrated by examples, the youngest being the American Great Lakes, the oldest Lake Baikal.

6. A single preadapted fish family represented in the surrounding fluviatile fish fauna assumes dominance in the evolution of large endemic lake fish faunas.

7. The evolution of lake-fish faunas is compared to that of island faunas, and to the evolution of any groups newly admitted to extensive areas where competition is light or absent, and shown to be essentially similar in the relatively rapid production of supralimitally specialized forms.

8. The latter are often capable of becoming the founders of new genera, families, or perhaps even higher categories, at new adaptive levels. They have unquestionably already done so in the older lake-fish faunas, where certain endemic Tanganyika and Baikal genera are worthy of subfamilial or familial rank.

9. It is suggested that the origin of the excessively rich characid fauna of the Amazon River, and of the striking forms and groups of deep-sea fishes, has been due to similar tachytelic or quantum evolution.

10. It follows that opportunity for rapid radiative evolution is of very great importance in the evolution of higher categories, and that such opportunity still may occur from time to time through geological changes.

Literature Cited

Alvarez, J. 1950. Claves para la determinacion de especies en los peces de las aguas continentales Mexicanas. Secretaria de Marina, Dirreción General de Pesca e Industrias Conexas, Mexico: 136 pp.

Annandale, N. 1918. Fauna of the Inlé Lake. Rec. Ind. Mus., 14: 214 pp., 26 pls.

Brittan, M. L. 1954. A revision of the Indo-Malayan fresh-water fish genus *Rasbora*. Inst. Sci. Tech. (Manila), Monograph, 3: 224 pp., 3 maps.

Brooks, J. L. 1950. Speciation in ancient lakes. Quart. Rev. Biol., 25: 30–60, 131–176.

Bruun, A., and A. Kiilerich. 1957. Bathymetrical features of the Bali-Lombok Strait. Marine Research in Indonesia, 3: 1–6.

Darlington, P. J. 1938. The origin of the fauna of the Greater Antilles, with discussion of dispersal of animals over water and through the air. Quart. Rev. Biol., 13: 274–300.

Dickerson, R. E., and others. 1928. Distribution of life in the Philippines. Bureau Sci. (Manila), Monograph, 21: 322 pp., 42 pls.

Fowler, H. W. 1941. Fishes of the groups Elasmobranchii . . . Ostariophysi obtained by the . . . Albatross . . . chiefly in the Philippine Islands. U. S. Nat. Mus. Bull., 100 (13): 879 pp.

Fryer, G. 1959. The trophic interrelationships and ecology of some littoral communities of Lake Nyasa with especial reference to the fishes, and a discussion of the evolution of a group of rock-frequenting Cichlidae. Proc. Zool. Soc. London, 132: 153–281, 2 pls.

Greenwood, P. H. 1956. The monotypic genera of cichlid fishes in Lake Victoria. Bull. Brit. Mus. (Nat. Hist.), 3: 295–333.

——. 1959. Evolution and speciation in the *Haplochromis* (Pisces, Cichlidae) of Lake Victoria. Proc. XVth Int. Congr. Zool. London, pp. 147–150.

Herre, A. W. 1924. The Philippine Cyprinidae. Philippine J. Sci., 24: 249–307, 2 pls.

——. 1926. Two fishes from Lake Lanao. Philippine J. Sci., 29: 499–502, 2 pls.

——. 1928. True fresh-water fishes of the Philippines. In: Dickerson, 1928 (which see): 242–247. [This paper was written previous to the publication of Herre's 1924 paper, and some of the fish names do not agree with those of the 1924 paper.]

——. 1932. Five new Philippine fishes. Copeia, 1932: 139–142.

——. 1933. The fishes of Lake Lanao: a problem in evolution. Amer. Nat., 68: 154–162.

——. 1953. Check list of Philippine fishes. U. S. Fish and Wildlife Service, Research Report, 20: 977 pp.

Herre, A. W., and G. S. Myers. 1931. Fishes from southeastern China and Hainan. Lingnan Sci. J., 10: 233–254.

Hubbs, C. L., and E. C. Ra[y] endemic fish fauna of L[ake] North Carolina. Misc. P[ubl.] Univ. Michigan, 65: 30 pp.

Jackson, P. N. B. 1959. clariid catfishes of Nyasal[and] scription of a new genus species. Proc. Zool. Soc[. London] 109-128.

Jordan, D. S., and C. L. Hubb[s] in ichthyology: a monogr[aph] the family of Atherinidae Leland Stanford Jr. Univ. [Pub.] 87 pp., 12 pls.

Koelz, W. 1929. Coregoni[dae] Great Lakes. Bull. U. S. [Bur. Fish.] (2): 297–643.

Meek, S. E. 1907. Synopsis the Great Lakes of N[orth] Columbian Museum, Zool[. Ser.] 97–132.

Myers, G. S. 1936. Repor[t] collected by H. C. Raven ganyika in 1920. Proc. U[. S. Nat. Mus.] 84: 1–15, 1 pl.

——. 1938. Fresh-water fishes zoogeography. Ann. Rep. S[mithsonian Inst.] 1937: 339–364, 3 pls.

——. 1949. Salt-tolerance of groups in relation to zooge[ography] lems. Bijdr. Dierk., 28: 3

——. 1951. Fresh-water f[ishes] Indian zoogeography. Stan[ford Ichth. Bull.] 4: 11–21.

——. 1960. Preface to any fu[ture] of the fishes of the genus [Haplochromis] Ichth. Bull., 7 (4). (In p[ress]

Poll, M. 1946. Revision de l[a faune] logique de Lac Tanganika.

HUBBS, C. L., AND E. C. RANEY. 1946. The endemic fish fauna of Lake Waccamaw, North Carolina. Misc. Publ. Mus. Zool. Univ. Michigan, 65: 30 pp.

JACKSON, P. N. B. 1959. Revision of the clariid catfishes of Nyasaland, with a description of a new genus and seven new species. Proc. Zool. Soc. London, 132: 109-128.

JORDAN, D. S., AND C. L. HUBBS. 1919. Studies in ichthyology: a monographic review of the family of Atherinidae or silversides. Leland Stanford Jr. Univ. Publ., Univ. Ser., 87 pp., 12 pls.

KOELZ, W. 1929. Coregonid fishes of the Great Lakes. Bull. U. S. Bur. Fisher., 27 (2): 297–643.

MEEK, S. E. 1907. Synopsis of the fishes of the Great Lakes of Nicaragua. Field Columbian Museum, Zool. Ser., 7 (4): 97–132.

MYERS, G. S. 1936. Report on the fishes collected by H. C. Raven in Lake Tanganyika in 1920. Proc. U. S. Nat. Mus., 84: 1–15, 1 pl.

——. 1938. Fresh-water fishes and West Indian zoogeography. Ann. Rep. Smithsonian Inst., 1937: 339–364, 3 pls.

——. 1949. Salt-tolerance of fresh-water fish groups in relation to zoogeographical problems. Bijdr. Dierk., 28: 315–322.

——. 1951. Fresh-water fishes and East Indian zoogeography. Stanford Ichth. Bull., 4: 11–21.

——. 1960. Preface to any future classification of the fishes of the genus Barbus. Stanford Ichth. Bull., 7 (4). (In press.)

POLL, M. 1946. Revision de la faune ichthyologique de Lac Tanganika. Ann. Musée du Congo Belge, zool., (1) 4: 145–364, 3 pls., map.

——. 1953. Poissons non Cichlidae. Explor. Hydrobiol. Lac Tanganika (1946–1947), Result. Scientif., 3 (5A): 251 pp., 11 pls.

PRASHAD, B., AND D. D. MUKERJI. 1929. The fish of the Indawygi Lake and the streams of the Myitkyina District (Upper Burma). Rec. Ind. Mus., 31: 161–223, pls. 7–10.

REGAN, C. T. 1906–1908. Biologia Centrali-Americana. Pisces. London: xxxiv + 203 pp., 26 pls.

SIMPSON, G. G. 1953. The major features of evolution. New York: xx + 434 pp.

SNYDER, J. O. 1919. Three new whitefishes from Bear Lake, Idaho and Utah. Bull. Bur. Fisher., 36: 1–9.

TALIEV, D. E. 1955. Bitschki-podkamenschtschiki Baikala (Cottoidei). Akademiia Nauk S.S.S.R., Moskva: 603 pp.

TCHERNAVIN, V. 1944. A revision of the subfamily Orestiinae. Proc. Zool. Soc. London, 114: 140–233.

TREWAVAS, E. 1935. A synopsis of the cichlid fishes of Lake Nyasa. Ann. Mag. Nat. Hist., (10) 16: 65–118.

WEBER, M., AND L. F. DE BEAUFORT. 1916. The Fishes of the Indo-Australian Archipelago. Vol. 3. Leiden: xvi + 455 pp.

——. 1922. *Ibid.* Vol. 4. Leiden: xiv + 410 pp.

WORTHINGTON, E. B. 1933. The fishes of Lake Nyasa (other than Cichlidae). Proc. Zool. Soc. London, 1933: 285–316.

WORTHINGTON, E. B., AND C. K. RICARDO. 1937. The fish of Lake Tanganyika (other than Cichlidae). Proc. Zool. Soc. London, 1936: 1061–1112.