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MSS. intended for publication and books, etc., intended for review should be sent to the responsible editor, Professor J. McKeen Cattell, Garrison-on-Hudson, N. Y.

THE FISH FAUNA OF JAPAN, WITH OBSERVATIONS ON THE GEOGRAPHICAL DISTRIBUTION OF FISHES.*

THE JAPANESE FISH FAUNA.

THE group of islands which constitute the empire of Japan is remarkable for the richness of its animal life. Its variety in climatic and other conditions, its nearness to the great continent of Asia and to the chief center of marine life, the East Indian Islands, its relation to the warm Black current or Kuro Shiwo from the south and to the cold currents from the north, all tend to give variety and richness to the fauna of its seas. Especially is this true in the group of fishes. In spite of the political isolation of the Japanese Empire, this fact has been long recognized and the characteristic types of Japanese fishes have been well known to naturalists.

NUMBERS OF SPECIES OF JAPANESE FISHES.

At present about 900 species of fishes are known from the four great islands which constitute Japan proper, Hondo, Hokkaido, Kiusiu and Shikoku. About 200 others are known from the volcanic islands to the north and south. Of these 1,100 species, about fifty belong to the fresh waters. These are all closely allied to forms found

* Address to the Section of Zoology, Denver Meeting, 1901.

on the mainland of Asia, from which region all of them were originally derived.

FRESH-WATER FAUNAL AREAS.

Two faunal areas of fresh waters may be fairly distinguished, although broadly overlapping. The northern region includes the island of Hokkaido and the middle and northern part of the great island of Hondo. In a rough way, its southern boundary may be defined by Fuji Yama and the Bay of Matsushima. It is characterized by the presence of salmon, trout and sculpins, and northward by sturgeon and brook-lampreys. The southern area loses by degrees the trout and other northern fishes, while in its clear waters abound various minnows, gobies and the famous ayu, or Japanese dwarf salmon, one of the most delicate of food fishes. Sculpins and lampreys give place to minnows, loaches and chubs. Two genera, a sculpin* and a perch,† are confined to this region and seem to have originated in it, but like the other species, form a Chinese stock.

ORIGIN OF JAPANESE FRESH-WATER FISHES.

The question of the origin of the Japanese river fauna seems very simple. All the types are Asiatic. While most of the Japanese species are distinct, their ancestors must have been estrays from the mainland. To what extent river fishes may be carried from place to place by currents of salt water has never been ascertained. One of the most widely distributed of Japanese river fishes is the large hakone dace or chub.‡ This has been repeatedly taken by us in the sea at a distance from any stream. It would evidently survive a long journey in salt water. An allied species§ is found in the midway island of Tsushima, between Korea and Japan.

* *Trachidermis*.

† *Bryttosus*.

‡ *Leuciscus hakonensis* Günther.

§ *Leuciscus jouyi*.

FAUNAL AREAS OF MARINE FISHES.

The distribution of the marine fishes of Japan is mainly controlled by the temperature of the waters and the motion of the ocean currents. Five faunal areas may be more or less clearly recognized, and these may receive names indicating their scope, Kurile, Hokkaido, Nippon, Kiusiu, Kuro Shiwo and Riu Kiu. The first or Kurile district is frankly sub-Arctic, containing species characteristic of the Ochotsk Sea on the one hand, and of Alaska on the other. The second or Hokkaido* district includes this northern island and that part of the shore of the main island of Hondo† which lies to the north of Matsushima and Noto. Here the cold northern currents favor the development of a northern fauna. The herring and the salmon occupy here the same economic relation as in Norway, Scotland, Newfoundland and British Columbia. Sculpins, blennies, rockfish and flounders abound off the rocky shores and are seen in all the markets.

South of Matsushima Bay and through the Inland Sea as far as Kobe, the Nippon fauna is distinctly one of the temperate zone. Most of the types characteristically Japanese belong here, abounding in the sandy bays and about the rocky islands.

About the islands of Kiusiu and Shikoku, the semi-tropical elements increase in number and the Kiusiu fauna is less characteristically Japanese, having much in common with the neighboring shores of China, while some of the species range northward from India and Java. But these faunal districts have no sharp barriers. Northern fishes,‡ unquestionably of Alaskan origin, range as far south as Nagasaki, while certain semi-

* Formerly, but no longer, called Yeso in Japan.

† Called Nippon on foreign maps, but not so in Japan, where Nippon means the whole empire.

‡ *Pleuronichthys cornutus*; *Hexagrammos otakii*; *Ozorth hexagramma*, etc.

tropical* types extend their range northward to Hakodate and Volcano Bay. The Inland Sea, which in a sense bounds the southern fauna, serves at the same time as a means of its extension. While each species has a fairly definite northern or southern limit, the boundaries of a faunal district as a whole must be stated in the most general terms.

The well-known boundary called Blackiston's Line, which passes through the Straits of Tsugaru, between the two great islands of Hondo and Hokkaido, marks the northern boundary of monkeys, pheasants and most tropical and semi-tropical birds and mammals of Japan. But as to the fishes, either marine or fresh water, this line has no significance. The northern fresh-water species probably readily cross it; the southern rarely reach it.

We may define as a fourth faunal area that of the Kuro Shiwo district itself, which is distinctly tropical and contrasts strongly with that of the inshore bays behind it. This warm 'Black Current,' analogous to our Gulf Stream, has its origin in part from a return current from the east, which passes westward through Hawaii, in part from a current which passes between Celebes and New Guinea. It moves northward by way of Luzon and Formosa, touching the east shores of the Japanese islands Kiusiu and Shikoku, to the main island of Hondo, flooding the bays of Kagoshima and Kochi, of Waka, Suruga and Sagami. The projecting headlands reach out into it and the fauna of their rock pools is distinctly tropical, as far to the northward as Tokio.

These promontories of Hondo, Waka, Ise, Izu, Misaki and Awa have essentially the same types of fishes as are found on the reefs of tropical Polynesia. The warmth of the off-shore currents gives the fauna of

Misaki its astonishing richness, and the wealth of life is by no means confined to the fishes. Corals, crustaceans, worms and molluscs show the same generous profusion of species.

A fifth faunal area, closely related to that of the Black Current, is formed by the volcanic and coral reefs of the Riu Kiu Archipelago. This fauna, so far as known, is essentially East-Indian, the genera and most of the species being entirely identical with those of the islands about Java and Celebes.

RESEMBLANCE OF THE JAPANESE AND MEDITERRANEAN FISH FAUNAS.

It has been noted by Dr. Günther that the fish fauna of Japan bears a marked resemblance to that of the Mediterranean. This likeness is shown in the actual identity of genera and species, and in their relation to each other. This resemblance he proposes to explain by the hypothesis that, at some recent period, the two regions, Japan and the Mediterranean, have been united by a continuous shore-line. The far-reaching character of this hypothesis demands a careful examination of the data on which it rests.

The resemblance of the two faunal areas, so far as fishes are concerned, may be stated as follows: There are certain genera* of shore fishes, tropical or semi-tropical, common to the Mediterranean and Japan, and wanting to California, Panama and the West Indies, and in most cases to Polynesia also. Besides these, certain others, found in deeper water (100 to 200 fathoms) are common to the two areas,† and have been rarely taken elsewhere.

* Of these, the principal ones are *Oxyostomus*, *Myrus*, *Pagrus*, *Sparus*, *Macrorhamphosus*, *Cepola*, *Callionymus*, *Zeus*, *Uranoscopus*, *Lepidotrigla*, *Chelidonichthys*.

† Among these are *Beryx*, *Helicolenus*, *Lotella*, *Netastoma*, *Centrolophus*, *Hoplostethus*, *Aulopus*, *Chlorophthalmus*, *Lophotes*.

* As *Halichoeres*, *Tetrapturus*, *Callionymus*, *Arisopopus*, etc.

SIGNIFICANCE OF RESEMBLANCE.

The significance of these facts can be shown only by a fuller analysis of the fauna in question, and those of other tropical and semi-tropical waters. If the resemblances are merely casual, or if the resemblances are shown by other regions, the hypothesis of shore continuity would be unnecessary or untenable. It is tenable if the resemblances are so great as to be accounted for in no other way.

Of the genera regarded as common, only two* or three are represented in the two regions by identical species, and these have a very wide distribution in the warm seas. Of the others, nearly all range to India, to the Cape of Good Hope, to Australia or to Brazil. They may have ranged farther in the past; they may even range farther at present. At the most, but two† are confined to the two districts in question. As equally great resemblances exist between Japan and Australia or Japan and the West Indies, the case is not self-evident, without fuller comparison. I shall, therefore, ask your attention to a somewhat fuller analysis of the evidence bearing on this and similar problems, with a view to the conclusions which may be legitimately drawn from the facts of fish distribution.

DIFFERENCES BETWEEN JAPANESE AND MEDITERRANEAN FISH FAUNAS.

We may first, after admitting the alleged resemblances and others, note that differences are equally marked. In each region are a certain number of genera which we may consider as autochthonous. These genera are represented by many species or by many individuals in the region of their supposed origin, but are more scantily developed elsewhere. Such genera in Mediterranean waters are *Crenilabrus*, *Labrus*, *Spicara*, *Pagellus*, *Mullus*, *Boopis*, *Spondylosoma*,

* *Beryx*, *Hoplostethus* and perhaps *Macrorhamphosus*.

† *Lepadogaster*, *Myrus*.

Oblata. None of these occurs in Japan nor have they any near relatives there. Japanese autochthonous types, as *Pseudoblennius*, *Duymæria*, *Anoplus*, *Histioporus*, *Monocentrus*, *Oplegnathus*, *Plecoglossus*, range southward to the Indies or to Australia, but all of them are totally unknown to the Mediterranean. The multifarious genera of Gobies of Japan show very little resemblance to the Mediterranean fishes of this family, while blennies, labroids, scaroids and scorpenoids are equally diverse in their forms and alliances. To the same extent that likeness in faunæ is produced by continuity of means of dispersion, is it true that unlikeness is due to breaks in continuity. Such a break in continuity of coast-line, in the present case, is the Isthmus of Suez, and the unlikeness in the faunas is about what such a barrier should produce.

SOURCES OF FAUNAL RESEMBLANCES.

There are two main sources of faunal resemblances; first, the absence of barriers permitting the actual mingling of the species; second, the likeness of temperature and shore configuration favoring the development of the same or analogous types. If the fish faunæ of different regions have mingled in recent times, the fact would be shown by the presence of the same species in each region. If the union were of a remote date, the species would be changed, but the genera might remain identical.

In case of close physical resemblances in different regions, as in the East Indies and West Indies, like conditions would favor the lodgment of like types, but the resemblance would be general, the genera and species being unlike. Without doubt, part of the resemblance between Japan and the Mediterranean is due to similarity of temperature and shores. Is that which remains sufficient to demand the hypothesis of a former shore-line connection?

EFFECTS OF DIRECTION OF SHORE LINE.

We may first note that a continuous shore-line produces a mingling of fish-faunas only when not interrupted by barriers due to climate. A north and south coast-line, like that of the East Pacific, however unbroken, permits great faunal differences. It is crossed by the different zones of temperature. An east and west shore-line lies in the same temperature. In all cases of the kind which now exist on the earth (the Mediterranean, the Gulf of Mexico, the Caribbean Sea, the shores of India), even species will extend their range as far as the shore-line goes. The obvious reason is because such a shore-line rarely offers any important barrier to distribution, checking dispersion of species. We may, therefore, consider the age and nature of the Isthmus of Suez and the character of the faunas it separates.

NUMBERS OF GENERA IN DIFFERENT FAUNAS.

For our purposes, the genera must be rigidly defined, a separate name being used in case of each definable difference in structure. The wide-ranging genera of the earlier systematists were practically cosmopolitan, and their distribution teaches us little. Using the modern definition of genus, we find in Japan 483 genera of marine fishes; in the Red Sea, 225; in the Mediterranean, 231. In New Zealand 150 are recorded; in Hawaii, 171; 357 from the West Indies, 187 from the Pacific coast of tropical America, 300 from India, 450 from the East-Indian islands and 427 from Australia.

Of the 483 genera ascribed to Japan, 156 are common to the Mediterranean also, 188 to the West Indies and Japan, 169 to the Pacific coast of the United States and Mexico. With Hawaii Japan shares 90 genera, with New Zealand 62; 204 are common to Japan and India, 148 to Japan and the Red Sea, most of these being found

in India also. 200 genera are common to Japan and Australia.

AFFINITIES OF JAPANESE FAUNA.

From this, it is evident that Japan and the Mediterranean have much in common, but apparently not more than Japan shares with other tropical regions. Japan naturally shows most likeness to India, and next to this to the Red Sea. Proportionately less is the resemblance to Australia, and the likeness to the Mediterranean seems much the same as that to the West Indies, or to the Pacific coast of America.

But, to make these comparisons just and effective, we should consider not the fish fauna as a whole; we should limit our discussion solely to the forms of equatorial origin. From the fauna of Japan we may eliminate all the genera of Alaskan-Aleutian origin, as these could not be found in the other regions under comparison. We should eliminate all pelagic and all deep-sea forms, for the laws which govern the distribution of these are very different from those controlling the shore fishes, and most of the genera have reached a kind of equilibrium over the world.

SIGNIFICANCE OF RARE FORMS.

We may note also, as a source of confusion in our investigation, that numerous forms found in Japan and elsewhere are very rarely taken, and their real distribution is unknown. Some of these will be found to have, in some unexpected quarter, their real center of dispersion. In fact, since these pages were written, I have taken in Hawaii representatives of three* genera which I had enumerated as belonging chiefly to Japan and the West Indies. Such species may inhabit oceanic plateaus, and find many halting places in their circuit of the tropical oceans. We have already discovered that

* *Antigonia*, *Etelis*, *Emmelichthys*.

Madeira, St. Helena, Ascension and other volcanic islands constitute such halting places. We shall find many more such, when the deeper shore regions are explored, the region between market-fishing and the deep-sea dredgings of the *Challenger* and the *Albatross*. In some cases, no doubt, these forms are verging on extinction and a former wide distribution has given place to isolated colonies.

The following table shows the contents, so far as genera are concerned, of those equatorial areas in which trustworthy catalogues of species are accessible. It includes only those fishes, of stationary habit, living in less than 200 fathoms. It goes without saying that considerable latitude must be given to these figures, to allow for errors, omissions, uncertainties and differences of opinion.

DISTRIBUTION OF SHORE FISHES.

A. Japan and the Mediterranean.

Genera * chiefly confined to these regions.	2
Genera of wide distribution.....	77
Total of common genera.....	79
Total in both regions.....	399
Genera above included, found in all equatorial regions.....	55
Genera † found in most equatorial regions.....	11
Genera more or less restricted.....	13
	79

B. Japan and the Red Sea.

Genera ‡ chiefly confined to these two regions.....	2
Genera of wide distribution.....	109
Total genera common.....	111
Total in both regions.	424

* *Lepadogaster*, *Myrus*; *Lophotes*, thus far recorded from Japan, the Mediterranean and the Cape of Good Hope is bassalian and of unknown range. *Beryx*, *Trachichthys*, *Hoplostethus*, etc., are virtually cosmopolitan as well as semi-bassalian.

† In this group we must place *Cepola*, *Callionymus*, *Pagrus*, *Sparus*, *Beryx*, *Zeus*, all of which have a very wide range in Indian waters.

‡ *Cryptocentrus*, *Asterropteryx*. The range of neither of these genera of small shore fishes is yet well known.

C. Japan and Hawaii.

Genera * chiefly confined to these regions	3
Genera of wide distribution.....	79
Total genera common.....	82
Total in both regions.....	396

D. Japan and Australia.

Genera chiefly confined to these regions..	13
Genera of wide distribution (chiefly East-Indian).....	122
Total genera common.....	135
Total in both regions.....	533

E. Japan and Panama.

Genera † chiefly confined to these regions	2
Genera of wide distribution.....	89
Total genera common.....	91
Total in both regions.....	499

F. Japan and the West Indies.

Genera ‡ chiefly confined to these regions	5
Genera of wide distribution.....	108
Total genera common.....	113
Total in both regions.....	520

G. The Mediterranean and the Red Sea.

Genera confined to the Suez region.....	0
Genera of wide distribution (chiefly Indian).....	40
Total genera common.....	40
Total in both regions.....	295

H. West Indies and the Mediterranean.

Genera chiefly confined to the equatorial Atlantic.....	11
Genera of wide distribution.....	59
Total.....	70
Total in both regions.....	373

I. West Indies and Panama.

Genera chiefly confined to equatorial America.....	68
Genera of wide distribution.....	101
Total genera common.....	169
Total in equatorial America.....	376

J. Hawaii and Panama.

Genera chiefly confined to the regions in question.....	3
Genera § of wide distribution.....	74
Total genera common.....	77
Total in both regions.....	323

* *Pikea*, *Eumycterias*, *Engyprosopron*.

† *Bairdiella*, *Aboma*. The occurrence of *Bairdiella acanthodes* in Japan needs verification.

‡ *Scombrops*, *Polymixia*, *Pseudopriacanthus*, *Antigonia*, *Chaunax*. All these genera are semi-bassalian.

§ *Sectator*, *Chaenomugil*, *Garmannia*.

K. Hawaii and the East Indies.

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Genera of wide distribution in the equatorial Pacific.....	123
Genera† confined to Hawaii and the West Indies	1

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Genera in the Red Sea.....	191
Genera in India.....	280
Genera in Japan (exclusive of northern forms).....	334
Genera in Australia.....	344
Genera in New Zealand.....	108
Genera in Hawaii.....	144
Genera about Panama.....	256
Genera in West Indies.....	299

EXTENSION OF INDIAN FAUNA.

From the above tables it is evident that the warm-water fauna of Japan, as well as that of Hawaii, is derived from the great body of the fauna of the East Indies and Hindostan; that the fauna of the Red Sea is derived in the same way; that the fauna of the Mediterranean bears no especial resemblance to that of Japan, rather than to other elements of the East Asiatic fauna in similar conditions of temperature, and no greater than is borne by either to the West Indies; that the faunas of the sides of the Isthmus of Suez have relatively little in common, while those of the two sides of the Isthmus of Panama show large identity of genera, although few species are common to the two sides. Of the 255 genera recorded from the Panama region, 179, or over 70 per cent., are also in the West Indies; while 68, or more than 30 per cent. of the number, are limited to the two regions in question.

THE ISTHMUS OF SUEZ AS A BARRIER
TO DISTRIBUTION.

With the aid of the above table, we may examine further the relation of the fauna

* *Holotrachys*, *Cirrhitops*, *Perkinsia*.

† *Malacanthus*.

of Japan to that of the Mediterranean. If a continuity of shore-line once existed, it would involve the obliteration of the Isthmus. With free connection across this isthmus, the fauna of the Red Sea must have been once practically the same as that of the Mediterranean. The present differences must be due to later immigrations to one or the other region, or to the extinction of species in one locality or the other, through some kind of unfitness. In neither region is there evidence of extensive immigration from the outside. The present conditions of water and temperature differ a little, but not enough to explain the difference in faunæ. The Red Sea is frankly tropical and its fauna is essentially Indian, much the same, so far as genera are concerned, as that of Southern Japan. The Mediterranean is at most not more than semi-tropical and its fishes are characteristically European. Its tropical forms belong rather to Guinea than to the East Indies. With the Red Sea the Mediterranean has very little in common, not so much, for example, as has Hawaii. Forty genera of shore fishes (and only fifty of all fishes) are identical in the two regions, the Mediterranean and the Red Sea. Of those, every one is a genus of wide distribution, found in nearly all warm seas. Of shore fishes, only one genus in seven is common to the two regions. Apparently, therefore, we cannot assume a passage across the Isthmus of Suez within the lifetime of the present genera. Not one of the types alleged to be peculiar to Japan and the Mediterranean is thus far known in the Red Sea. Not one of the characteristically abundant Mediterranean types* crosses the Isthmus of Suez, and the distinctive Red Sea and Indian types† are equally

* As *Crenilabrus*, *Labrus*, *Symphodus*, *Pagellus*, *Spondyllosoma*, *Sparisoma*.

† As *Chætodon*, *Lethrinus*, *Sphærodon*, *Abudefduf*, etc.

wanting in the Mediterranean. The only genera which could have crossed the Isthmus are certain shallow-water or brackish-water forms, sting-rays, torpedoes, sardines, eels and mullets, widely diffused through the East Indies and found also in the Mediterranean. The former channel if one ever existed, had, therefore, much the same value in distribution of species, as the present Suez Canal.

GEOLOGICAL EVIDENCE OF SUBMERSION OF THE ISTHMUS OF SUEZ.

Yet, from geological data, there is strong evidence that the Isthmus of Suez was submerged in relatively recent times. The recognized geological maps of the Isthmus show that a broad area of post-Pliocene or Pliocene deposits constitutes the Isthmus and separates the nummulitic hills of Suez from their fellows about thirty miles to the eastward. The northern part of the Isthmus is alluvium from the Nile, and its western part is covered with drifting sands. The Red Sea once extended farther north than now and the Mediterranean farther to the southeast. Assuming the maps to be correct, the Isthmus must have been open water in the late Pliocene or post-Pliocene times.

Admitting this as a fact, the difference in the fish fauna shows that the waters over the submerged area must have been so shallow that rock-loving forms did not and could not cross it. Moreover, the region must have been overspread with silt-bearing fresh waters from the Nile. To such fishes as *Chaetodon*, *Holocentrus*, *Thalassoma*, of the Red Sea, or to *Crenilabrus*, *Boops* and *Zeus*, of the Mediterranean, such waters would form a barrier as effective as the sand-dunes of to-day.

CONCLUSIONS AS TO THE ISTHMUS OF SUEZ.

We are led, therefore, to these conclusions:

1. There is no evidence, derivable from the fishes, of the submergence of the Isthmus of Suez.

2. If the isthmus was submerged in Pliocene or post-Pliocene times, the resultant channel was shallow and muddy, so that ordinary marine fishes or fishes of rock bottoms, or of deep waters, did not cross it.

3. It formed an open water to brackish-water fishes only.

4. The types common to Japan and the Mediterranean did not enter either region from the other, by way of the Red Sea.

5. As most of these are found also in India or Australia or both, their dispersion was probably around the south coast of Africa or by the Cape of Good Hope.

THE CAPE OF GOOD HOPE AS A BARRIER TO FISHES.

The fishes of the Cape of Good Hope are not well enough known for close comparison with those of other regions. Enough is known of the Cape fauna to show its general relation to those of India and Australia. The Cape of Good Hope lies in the South Temperate zone. It offers no absolutely impassable barrier to the tropical fishes from either side. It bears a closer relation to either the Red Sea or the Mediterranean than they bear to each other. It is, therefore, reasonable to conclude that the transfer of tropical shore fishes of the Old World between the Atlantic and Pacific, in recent times, has taken place mainly around the southern point of Africa. To pelagic and deep-sea fishes the Cape of Good Hope has offered no barrier whatever. To ordinary fishes it is an obstacle, but not an impassable one. This the fauna itself shows. It has, however, not been passed by many tropical species, and by these only as the result of thousands of years of struggle and point-to-point migration.

RELATIONS OF JAPAN TO MEDITERRANEAN
EXPLAINABLE BY PRESENT CONDITIONS.

We may conclude that the resemblance of the Mediterranean fish fauna to that of Japan or India is no more than might be expected, the present contour of the continents being permanent for the period of duration of the present genera and species. The imagined removal of barriers on any large scale would necessitate much closer resemblances than those which actually exist.

THE ISTHMUS OF PANAMA AS A BARRIER
TO DISTRIBUTION.

Conditions in some regards parallel with those of the Isthmus of Suez exist in but one other region—the Isthmus of Panama.

IDENTITY OF GENERA ON TWO SHORES OF
THE ISTHMUS OF PANAMA.

Here the first observers were very strongly impressed by the resemblance of forms. Nearly half the genera found on the two sides of this isthmus are common to both sides. Taking those of the Pacific shore for first consideration, we find that three fourths of the genera of the Panama fauna occur in the West Indies as well.

This identity is many times greater than that existing at the Isthmus of Suez. Moreover, while the Cape of Good Hope offers no impassable barrier to distribution, the same is not true of the southern part of South America. The subarctic climate of Cape Horn has doubtless formed a complete check to the movements of tropical fishes for a vast period of geologic time.

UNLIKENESS OF SPECIES ON THE SHORES OF
THE ISTHMUS OF PANAMA.

But curiously enough, this marked resemblance is confined chiefly to the genera and does not extend to the species on the two shores.

Of 1,400 species of fishes recorded from tropical America north of the Equator, only about 70 are common to the two coasts. The number of shore fishes common is still less. In this 70 are included a certain number of cosmopolitan types which might have reached either shore from the Old World.

A few others invade brackish or fresh waters and may possibly have found their way, in one way or another, across the Isthmus of Nicaragua. Of fishes strictly marine, strictly littoral, and not known from Asia or Polynesia, scarcely any species are left as common to the two sides. This seems to show that no waterway has existed across the isthmus within the lifetime, whatever that may be, of the existing species. The close resemblance of genera shows apparently with almost equal certainty that such a waterway has existed, and within the period of existence of the groups called genera. How long a species of fish may endure unchanged no one knows, but we know that in this regard great differences must exist in different groups. Assuming that different species crossed the Isthmus of Panama in Miocene times, we should not be surprised to find that a few remain to all appearances unchanged; that a much larger number have become 'representative' species, closely related forms retaining relations to the environment to those of the parent form, and, finally, that a few species have been radically altered.

This is exactly what has taken place at the Isthmus of Panama with the marine shore fishes. Curiously enough, the movement of genera seems to have been chiefly from the Atlantic to the Pacific. Certain characteristic genera* of the Panama region have not passed over to the Pacific. On the

**Hoplopagrus*, *Xenichthys*, *Xenistius*, *Xenocys*, *Microdesmus*, *Cerdale*, *Cratinus*, *Azevia*, *Microlepidotus*, *Orthostoechus*, *Isaciella*, etc.

other hand, most of the common genera* show a much larger number of species on the Atlantic side. This may be held to show their Atlantic origin.

Of the relatively small number of genera which Panama has received from Polynesia, few† have crossed the Isthmus to appear in the West Indian fauna.

GÜNTHER ON THE ISTHMUS OF PANAMA.

The elements of the problem at Panama may be better understood by a glance at the results of previous investigations.

In 1869 Dr. Günther, after enumerating the species examined by him from Panama, reaches the conclusion that nearly one third of the marine fishes on the two shores of tropical America will be found to be identical. He enumerates 193 such species as found on the two coasts; 59 of these, or 31 per cent. of the total, being actually identical. From this he infers that there must have been, at a comparatively recent date, a depression of the Isthmus and intermingling of the two faunas.‡

OBSERVATIONS IN 1885.

In an enumeration of the fishes of the Pacific coast in 1885,§ the present writer showed that Dr. Günther's conclusions were based on inadequate data.

In my list, 407 species were recorded from the Pacific coast of tropical America—twice the number enumerated by Dr. Günther. Of these, 71 species, or $17\frac{1}{2}$ per cent., were found also in the Atlantic. About 800 species are known from the Caribbean and adjacent shores, so that out of the total

* *Hæmulon*, *Anisotremus*, *Gerres*, *Centropomus*, *Galeichthys*, *Hypoplectrus*, *Mycteroperca*, *Ulaema*, *Stellifer*, *Micropogon*, *Bodianus*, *Microspathodon*.

† Among these are perhaps *Teuthis* (*Acanthurus*), *Itisha*, *Salarias*, *Myripristis*, *Thalassoma*. Some such which have not crossed the Isthmus are *Cirrhit*es, *Sebastops*is and *Lophiomus*.

‡ 'Fishes of Central America,' 1869, 397.

§ *Proc. U. S. Nat. Mus.*, 1885, 393.

number of 1,136 species, but 71, or 6 per cent. of the whole, are common to the two coasts. This number does not greatly exceed that of the species common to the West Indies and the Mediterranean, or even the West Indies and Japan. It is to be noted also that the number 71 is not very definitely ascertained, as there must be considerable difference of opinion as to the boundaries of species, and the actual identity in several cases is open to doubt.

This discrepancy arises from the comparatively limited representation of the two faunæ at the disposal of Dr. Günther. He enumerates 193 marine or brackish-water species as found on the two coasts, 59 of which are regarded by him as specifically identical, this being 31 per cent. of the whole. But in 30 of these 59 cases, I regard the assumption of complete identity as erroneous; so that taking the number 193, as given, I would reduce the percentage to 15. But these 193 species form but a fragment of the total fauna, and any conclusion based on such narrow data is certain to be misleading.

Of the 71 identical species admitted in our list, several (*e. g.*, *Mola*, *Thunnus*) are pelagic fishes common to most warm seas. Still others (*e. g.*, *Trachurus*, *Carangus*, *Diodon* sp.) are cosmopolitan in the tropical waters. Most of the others (*e. g.*, *Gobius*, *Gerres*, *Centropomus*, *Galeichthys* sp., etc.) often ascend the rivers of the tropics, and we may account for their diffusion, perhaps, as we account for the dispersion of fresh-water fishes on the isthmus, on the supposition that they may have crossed from marsh to marsh at some time in the rainy season.

In very few cases are representatives of any species from opposite sides of the Isthmus exactly alike in all respects. These differences in some cases seem worthy of specific value, giving us 'representative species' on the two sides. In other cases, the distinctions are very trivial, but in

most cases they are appreciable, especially in fresh specimens.

Further, I expressed the belief that "fuller investigation will not increase the proportion of common species. If it does not, the two faunas show no greater resemblance than the similarity of physical conditions on the two sides would lead us to expect."

This conclusion must hold so far as species are concerned, but the resemblance in the list of genera is too great to be accounted for in this way.

OBSERVATIONS OF DR. GÜNTHER.

In 1880* Dr. Günther expressed his views in still stronger language, claiming a still larger proportion of the fishes of tropical America to be identical on the two sides of the continent. He concluded that "with scarcely any exceptions the genera are identical, and of the species found on the Pacific side, nearly one half have proved to be the same as those of the Atlantic. The explanation of this fact has been found in the existence of communications between the two oceans by channels and straits which must have been open till within a recent period. The isthmus of Central America was then partially submerged, and appeared as a chain of islands similar to that of the Antilles; but as the reef-building corals flourished chiefly north and east of these islands and were absent south and west of them, reef fishes were excluded from the Pacific shores when the communications were destroyed by the upheaval of land."

CONCLUSIONS OF EVERMANN AND JENKINS.

This remark led to a further discussion of the subject on the part of Dr. B. W. Evermann and Dr. O. P. Jenkins. From their paper on the fishes of Guaymas† I make the following quotations:

* 'Introduction to the Study of Fishes,' 1880, p. 280.

† *Proc. U. S. Nat. Mus.*, 1891, pp. 124-126.

"The explorations since 1885 have resulted, (1) in an addition of about one hundred species to one or other of the two faunæ; (2) in showing that at least two species that were regarded as identical on the two shores* are probably distinct; and (3) in the addition of but two species to those common to both coasts.†

"All this reduces still further the percentage of common species.

"Of the one hundred and ten species obtained by us, 24, or less than 21 per cent., appear to be common to both coasts. Of these 24 species, at least 16, from their wide distribution, would need no hypothesis of a former waterway through the isthmus to account for their presence on both sides. They are species fully able to arrive at the Pacific shores of the Americas from the warm seas west. It thus appears that not more than eight species, less than 8 per cent. of our collection, all of which are marine species, require any such hypothesis to account for their occurrence on both coasts of America. This gives us, then, 1,307 species that should properly be taken into account when considering this question, not more than 72 of which, or 5.5 per cent., seem to be identical on the two coasts. This is very different from the figures given by Dr. Günther in his 'Study of Fishes.'

"Now, if from these 72 species, admitted to be common to both coasts, we subtract the 16 species of wide distribution—so wide as to keep them from being a factor in this problem—we have left but 56 species common to the two coasts that bear very closely upon the waterway hypothesis. *This is less than 4.3 per cent. of the whole number.*"

"But the evidence obtained from a study

* *Citharichthys spilopterus* and *C. gilberti*.

† *Hæmulon steindachneri* and *Gymnothorax castaneus* of the west coast probably being identical with *H. schranki* and *Gymnothorax funebris* of the east coast.

of other marine life of that region points to the same conclusion."

"In 1881, Dr. Paul Fischer discussed the same question in his 'Manual de Conchyliologie,' pp. 168-169, in a section on the Molluscan Fauna of the Panamic Province, and reached the same general conclusions. He says: 'Les naturalistes Américiens se sont beaucoup préoccupés des espèces de Panama qui paraissent identiques avec celles des Antilles, ou qui sont représentatives. P. Carpenter estime qu'il en existe 35. Dans la plupart des cas, l'identité absolue n'a pu être constatée et on a trouvé quelques caractères distinctifs, ce qui n'a rien d'étonnant, puisque dans l'hypothèse d'une origine commune, les deux races pacifique et atlantique sont séparées depuis la période Miocène. Voici une liste de ces espèces représentatives ou identiques.' Here follows a list of 20 species. 'Mais ces formes semblables,' he says, 'constituent une infime minorité (3 per cent.).'"

"These facts have a very important bearing upon certain geological questions, particularly upon the one concerning the cold of the Glacial period.

"In Dr. G. Frederick Wright's recent book 'The Ice Age in North America,' eight different theories as to the cause of the cold are discussed. The particular theory which seems to him quite reasonable is that one which attributes the cold as due to a change of different parts of the country, and a depression of the Isthmus of Panama is one of the important changes he considers. He says: * "Should a portion of the Gulf Stream be driven through a depression across the Isthmus of Panama into the Pacific, and an equal portion be diverted from the Atlantic coast of the United States by an elevation of the sea-bottom between Florida and Cuba, the consequences would necessarily be incalculably great, so that the mere existence of such a possible cause

* P. 409.

for great changes in the distribution of moisture over the northern hemisphere is sufficient to make one hesitate before committing himself unreservedly to any other theory; at any rate, to one which has not for itself independent and adequate proof."

"In the Appendix to the same volume Mr. Warren Upham, in discussing the probable causes of glaciation, says, 'The quaternary uplifts of the Andes and Rocky Mountains and of the West Indies make it nearly certain that the Isthmus of Panama has been similarly elevated during the recent epoch. * * * It may be true, therefore, that the submergence of this isthmus was one of the causes of the Glacial period, the continuation of the equatorial oceanic currents westward into the Pacific having greatly diminished or wholly diverted the Gulf Stream, which carries warmth from the tropics to the northern Atlantic and northwestern Europe."

"Any *very* recent means by which the fishes could have passed readily from one side to the other would have resulted in making the fish-faunas of the two shores practically identical; but the time that has elapsed since such a waterway could have existed has been long enough to allow the fishes of the two sides to become *practically distinct*. That the molluscs of the two shores are almost wholly distinct, as shown by Dr. Fischer, is even stronger evidence of the remoteness of the time when the means of communication between the two oceans could have existed, for 'species' among the molluscs are probably more persistent than among fishes.

"Our present knowledge, therefore, of the fishes of tropical America justifies us in regarding the fish faunas of the two coasts as being essentially distinct, and believing that there has not been, at any comparatively recent time, any waterway through the Isthmus of Panama."

It is thus shown, I think, conclusively,

that the Isthmus of Panama could not have been depressed for any great length of time in a recent geological period.

CONCLUSIONS OF DR. HILL.

These writers have not, however, considered the question of generic identity. To this we may find a clue in the geological investigations of Dr. Robert T. Hill.

In a study of 'The Geological History of the Isthmus of Panama and Portions of Costa Rica,' Dr. Hill uses the following language:

"By elimination we have concluded that the only period of time since the Mesozoic within which communication between the seas could have taken place is the Tertiary period, and this must be restricted to the Eocene and Oligocene epochs of that period. The paleontologic evidence upon which such an opening can be surmised at this period is the occurrence of a few California Eocene types in the Atlantic sides of the tropical American barrier, within the ranges of latitude between Galveston (Texas) and Colon, which are similar to others found in California. There are no known structural data upon which to locate the site of this passage, but we must bear in mind, however, that this structure has not been completely explored.

"Even though it was granted that the coincidence of the occurrence of a few identical forms on both sides of the tropical American region, out of the thousands which are not common, indicates a connection between the two seas, there is still an absence of any reason for placing this connection at the Isthmus of Panama, and we could just as well maintain that the locus thereof might have been at some other point in the Central American region.

"The reported fossil and living species common to both oceans are littoral forms, which indicate that if a passage existed, it must have been of a shallow and ephemeral character.

"There is no evidence from either a geologic or a biologic standpoint for believing that the oceans have ever communicated across the Isthmian regions since Tertiary time. In other words, there is no evidence for these later passages which have been established upon hypothetical data, especially those of Pleistocene time.

"The numerous assertions, so frequently found in literature, that the two oceans have been frequently and recently connected across the Isthmus, and that the low passes indicative of this connection still exist, may be dismissed at once and forever and relegated to the domain of the apocryphal. A few species common to the waters of both oceans in a predominantly Caribbean fauna of the age of the Claiborne epoch of the Eocene Tertiary is the only paleontologic evidence in any time upon which such a connection may be hypothesized.

"There has been a tendency in literature to underestimate the true altitude of the Isthmian passes, which, while probably not intentional, has given encouragement to those who think that this Pleistocene passage may have existed. Maack has erroneously given the pass at 186 feet. Dr. J. W. Gregory states 'that the summit of the Isthmus at one locality is 154 feet, and in another 287 feet in height.' The lowest Isthmian pass, which is not a summit, but a drainage col, is 287-295 feet above the ocean.

"If we could lower the Isthmian region 300 feet at present, the waters of the two oceans would certainly commingle through the narrow Culebra Pass. But the Culebra Pass is clearly the headwater col of two streams, the Obispo flowing into the Chagres, and the Rio Grande flowing into the Pacific, and has been cut by fluvial action, and not by marine erosion, out of a land mass which has existed since Miocene time. Those who attempt to establish Pleistocene inter-oceanic channels through this pass on

account of its present low altitude, must not omit from their calculations the restoration of former rock masses, which have been removed by the general leveling of the surface by erosion."

SUMMARY OF DR. HILL.

In conclusion, Dr. Hill asserts that "there is considerable evidence that a land barrier in the tropical region separated the two oceans as far back in geologic history as Jurassic time, and that that barrier continued throughout the Cretaceous period. The geological structure of the Isthmus and Central American regions, so far as investigated, when considered aside from the paleontology, presents no evidence by which the former existence of a free communication of oceanic waters across the present tropical land barriers can be established. The paleontologic evidence indicates the ephemeral existence of a passage at the close of the Eocene period. All lines of inquiry—geologic, paleontologic and biologic—give evidence that no connection has existed between the two oceans since the close of the Oligocene. This structural geology is decidedly opposed to any hypothesis by which the waters of the two oceans could have been connected across the regions in Miocene, Pliocene, Pleistocene, or recent times."

FINAL HYPOTHESIS AS TO PANAMA.

If we assume the correctness of Dr. Hill's conclusions, they may accord in a remarkable degree with the actual facts of the distribution of the fishes about the Isthmus. To account for the remarkable identity of genera and divergence of species I may suggest the following hypothesis:

During the lifetime of most of the present species, the Isthmus has not been depressed. It was depressed in or before Miocene time, during the lifetime of most of the present genera. The channel formed was relatively shallow, excluding forms inhabiting rocky bottoms at considerable

depths. It was wide enough to permit the infiltration from the Caribbean Sea of numerous species, especially of shore fishes of sandy bays, tide pools and brackish estuaries. The currents set chiefly to the westward, favoring the transfer of Atlantic rather than Pacific types.

Since the date of the closing of this channel, the species left on the two sides have been altered in varying degrees by the processes of natural selection and isolation. The cases of actual specific identity are few, and the date of the establishment as species, of the existing forms, is subsequent to the date of the last depression of the isthmus.

While local oscillations, involving changes in coast-lines, have doubtless frequently taken place and are still going on, our knowledge of the distribution of fishes should render impossible the speculations on the dance of continents, which certain geologists and certain biologists have, at one time or another, used as a convenient means of accounting for glacial phenomena, or for anomalies in distribution. We may be also certain that none of the common genera ever found their way around Cape Horn. Most of them disappear to the southward, along the coasts of Brazil and Peru.

Further, it goes without saying, that we have no knowledge of the period of time necessary to work specific changes in a body of species isolated in an alien sea. Nor have we any data as to the effect on a given fish fauna of the infiltration of many species and genera belonging to another. All such forces and results must be matters of inference.

LAWS GOVERNING DISTRIBUTION OF ANIMALS.

I have elsewhere* had occasion to say that the laws governing the distribution of

* 'Footnotes to Evolution.'

animals are reducible to three very simple propositions.

Each species of animal is found in every part of the earth having conditions suitable for its maintenance, unless:

(a) Its individuals have been unable to reach this region through barriers of some sort; or,

(b) Having reached it, the species is unable to maintain itself, through lack of capacity for adaptation, through severity of competition with other forms, or through destructive conditions of environment; or else,

(c) Having entered and maintained itself, it has become so altered in the process of adaptation as to become a species distinct from the original type.

SPECIES ABSENT THROUGH BARRIERS.

The absence from the Japanese fauna of most European or American species comes under the first head. The pike has never reached the Japanese lakes, though the shade of the lotus leaf in the many clear ponds would suit its habits exactly. The grunt* and porgies† of our West Indian waters and the crenilabri of the Mediterranean have failed to cross the ocean and therefore have no descendants in Japan.

SPECIES ABSENT THROUGH FAILURE TO MAINTAIN FOOTHOLD.

Of species under (b), those who have crossed the seas and not found lodgment, we have, in the nature of things, no record. Of the existence of multitudes of estrays we have abundant evidence. In the Gulf Stream off Cape Cod are every year taken many young fishes belonging to species at home in the Bahamas and which find no permanent place in the New England fauna. In like fashion, young fishes from the tropics drift northward in the Kuro Shiwo to the coasts of Japan, but never finding a

permanent breeding-place and never joining the ranks of the Japanese fishes. But to this there have been, and will be, occasional exceptions. Now and then one among thousands finds permanent lodgment, and by such means a species from another region will be added to the fauna. The rest disappear and leave no trace. A knowledge of these currents and their influence is eventual to any detailed study of the dispersion of fishes.

SPECIES CHANGED THROUGH NATURAL SELECTION.

In the third class, that of species changed in the process of adaptation, most insular forms belong. As a matter of fact, at some time or another almost every species must be in this category, for isolation is a source of the most potent elements in the initiation and intensification of the minor differences which separate related species. It is not the preservation of the most useful features, but of those which actually existed in the ancestral individuals, which distinguish such species. I have elsewhere noted that natural selection must include not only the process of the survival of the fittest, but also the results of the survival of the existing. This means the preservation through heredity of the traits not of the species alone, but those of the actual individuals set apart to be the first in the line of descent in a new environment. In hosts of cases the persistence of characters rests not on any special usefulness or fitness, but on the fact that individuals possessing these characters have, at one time or another, invaded a certain area and populated it. The principle of utility explains survivals among competing structures. It rarely accounts for qualities associated with geographical distribution.

BARRIERS CHECKING MOVEMENT OF FISHES.

The limits of the distribution of individual species or genera must be found in

* *Hæmulon*.

† *Calamus*.

some sort of barrier, past or present. The chief barriers which limit marine fishes are the presence of land, the presence of great oceans, the differences of temperature arising from differences in latitude, the nature of the sea bottom and the direction of oceanic currents. That which is a barrier to one species may be an agent in distribution to another. The common shore fishes would perish in deep waters almost as surely as on land, while the open Pacific is a broad highway to the albacore or the sword-fish.

Again, that which is a barrier to rapid distribution may become an agent in the slow extension of the range of a species. The great continent of Asia is undoubtedly one of the greatest of barriers to the wide movement of species of fish, yet its long shore-line enables species to creep, as it were, from bay to bay, or from rock to rock; till, in many cases, the same species is found in the Red Sea and in the tide-pools or sand-reaches of Japan. In the North Pacific, the presence of a range of half-submerged volcanoes, known as the Aleutian and the Kurile Islands, has greatly aided the slow movement of the fishes of the tide-pools and the kelp. To a school of mackerel or of flying fishes these rough islands would form an insuperable barrier.

TEMPERATURE THE CENTRAL FACT IN DISTRIBUTION.

It has long been recognized that the matter of temperature is the central fact in all problems of geographical distribution. Few species in any group freely cross the frost-line, and except as borne by oceanic currents, few species extend their range far into waters colder than those in which the species is distinctively at home. Knowing the average temperature of the water in a given region, we know in general the types of fishes which must inhabit it. It is the similarity in temperature and physical

conditions, not the former absence of barriers, which chiefly explains the resemblance of the Japanese fauna to that of the Mediterranean or the Antilles. This fact alone must explain the resemblance of the Arctic and Antarctic faunæ.

AGENCY OF OCEAN CURRENTS.

We may consider again for a moment the movements of the great currents in the Pacific as agencies in the distribution of species.

A great current sets to the eastward, crossing the ocean just south of the Tropic of Cancer. It extends between the Gilbert and the Marshall Islands and passes on nearly to the coast of Mexico, touching the Galapagos Islands, Clipperton Island and especially the Revillagigedos. This at once accounts for the number of Polynesian species found on these Islands, about which they are freely mixed with immigrants from the mainland of Mexico.

From the Revillagigedos* the current moves northward, passing the Hawaiian Islands and thence onward to the Ladrões. The absence in Hawaii of many of the characteristic fishes of the Society Islands and the Gilbert Islands is doubtless due to the long detour made by these currents, as the conditions of life in these groups of islands are not very different. Between the Gilbert Islands and Samoa there is also a return current to the west, and northeast of Hawaii is a great spiral current, moving with the hands of the watch, forming what is called Fleurieu's Whirlpool. This does not reach the coast of California. This fact may account for the almost complete distinction in the shore fishes of Hawaii and California.†

* Clarion Island and Socorro Island.

† A few Mexican shore fishes, *Chætodon humeralis*, *Galeichthys dasycephalus*, *Hypsoblennius parvipinnis*, have been wrongly accredited to Hawaii by some misplacement of labels.

The westward current from Hawaii reaches Luzon and Formosa. It is deflected to the northward and, joining a northward current from Celebes, it forms the Kuro Shiwo or Black Stream of Japan, which strews its tropical species in the rock pools along the Japanese promontories as far as Tokio. Then, turning into the open sea, it passes northward to the Aleutian Islands, across to Sitka. Thence it moves southward as a cold current, bearing Ochotsk-Alaskan types southward as far as the Santa Barbara Islands, to which region it is followed by species of Aleutian origin. A cold return current seems to extend southward in Japan, along the East shore perhaps as far as Matsushima. A similar current in the sea to the west of Japan extends still further to the southward, to Noto, or beyond.

It is, of course, not necessary that the movements of a species in an oceanic current should coincide with the direction of the current. Young fishes, or fresh-water fishes, would be borne along with the water. Those that dwell within floating bodies of seaweed would go whither the waters carry the drifting mass. But free-swimming fishes, as the mackerel or flying-fishes, might as readily choose the reverse direction. To a free-swimming fish, the temperature of the water would be the only consideration. It is thus evident that a current which to certain forms would prove a barrier to distribution, to others would be a mere convenience in movement.

In comparing the Japanese fauna with that of Australia, we find some trace of both these conditions. Certain forms are excluded by cross-currents, while certain others seem to have been influenced only by the warmth of the water. A few Australian types on the coast of Chili seem to have been carried over by the cross currents of the South Atlantic.

CENTERS OF DISTRIBUTION.

We may assume, in regard to any species, that it has had its origin in or near that region in which it is most abundant and characteristic. Such an assumption must involve a certain percentage of error or of doubt, but in considering the mass of species, it would represent essential truth. In the same fashion, we may regard a genus as being autochthonous or first developed in the region where it shows the greatest range or variety of species. Those regions where the greatest number of genera are thus autochthonous may be regarded as centers of distribution. So far as the marine fishes are concerned, the most important of these centers are found in the Pacific Ocean. First of these in importance is the East-Indian Archipelago, with the neighboring shores of India. Next would come the Arctic Pacific and its bounding islands, from Japan to British Columbia. Third in importance in this regard is Australia. Important centers are also found in temperate Japan, in California, the Panama region, and in New Zealand, Chili and Patagonia. The fauna of Polynesia is almost entirely derived from the Indies; and the shore-fauna of the Red Sea, the Bay of Bengal and Madagascar, so far as genera are concerned, seems to be not really separable from the Indian fauna generally.

I know of but six genera which may be regarded as autochthonous in the Red Sea, and nearly of these are of doubtful value or of uncertain relation. The many peculiar genera described by Dr. Alcock, from the dredgings of the *Investigator* in the Bay of Bengal, belong to the bathybial or deep water series, and will all, doubtless, prove to be forms of wide distribution.

In the Atlantic, the chief center of distribution is the West Indies; the second is the Mediterranean. On the shores to the northward or southward of these regions occasional genera have found their origin.

This is true especially of the New England region, the North Sea, the Gulf of Guinea and the coast of Argentina. The fish fauna of the North Atlantic is derived mainly from the North Pacific, the differences lying mainly in the lower richness of the North Atlantic. But, in certain groups common to the two regions, the migration must have been in the opposite direction; exceptions that prove the rule.

REALMS OF DISTRIBUTION OF FRESH-WATER FISHES.

If we consider the fresh-water fishes alone we may divide the land areas of the earth into districts and zones, fairly agreeing with those marked out for mammals and birds. The river-basin, bounded by its shores and the sea at its mouth, shows many resemblances, from the point of view of a fish, to an island considered as the home of an animal. The nature of the various barriers limiting species in river-basins I have elsewhere* fully discussed and need not consider it further here. It is evident that, with fishes, the differences in latitude outweigh those of continental areas, and a primary division into Old World and New World would not be tenable.

The chief areas of dispersion of fresh-water fishes we may indicate as follows, following essentially the grouping proposed by Dr. Günther:†

NORTHERN ZONE (ARCTIC AND TEMPERATE).

With Dr. Günther, we may recognize, first the *Northern Zone*, characterized familiarly by the presence of sturgeon, salmon, trout, white-fish, pike, lamprey, stickle-back and other species of which the genera and often the species are identical in Europe, Siberia, Canada, Alaska and most of the United States, Japan and China.

* Science Sketches: 'The Dispersion of Fresh-water Fishes.'

† 'Introduction to the Study of Fishes.'

This is subject to cross-division into two great districts, the first Europe-Asiatic, the second North American. These two agree very closely to the northward but diverge widely to the southward, developing a variety of specialized genera and species, and both of them passing finally, by degrees, into the Equatorial Zone.

Still another line of division is made by the Ural Mountains in the Old World and by the Rocky Mountains in the New. In both cases the Eastern region is vastly richer in genera and species, as well as in autochthonous forms, than the Western. The reason for this lies in the vastly greater extent of the river basins of China and the Eastern United States, as compared with those of Europe or the Californian region.

Minor divisions are those which separate the Great Lake region from the streams tributary to the Gulf of Mexico; and in Asia, those which separate China from tributaries of the Caspian, the Black and the Mediterranean.

EQUATORIAL ZONE.

The Equatorial Zone is roughly indicated by the tropics of Cancer and Capricorn. Its essential feature is that of the temperature, and the peculiarities of its divisions are caused by barriers of sea or mountains.

Dr. Günther finds the best line of separation into two divisions to lie in the presence or absence of the great group of dace or minnows,* to which nearly half of the species of fresh-water fishes the world over belong. The entire group, now spread everywhere except in the Arctic, South America, Australia and the islands of the Pacific, had its origin in India, from which its genera have radiated in every direction.

The Cyprinoid division of the Equatorial Zone forms two districts, the Indian and the African. The Ancyprinoid division includes South America, south of Mexico, and

* Cyprinidæ.

all the islands of the tropical Pacific lying to the east of Wallace's line. This line, separating Borneo from Celebes and Bali from Lompoe, marks in the Pacific the western limit of Cyprinoid fishes, as well as that of monkeys and other important groups of land animals. This line, recognized as very important in the distribution of land animals, coincides in general with the ocean current between Celebes and Papua, which is one of the sources of the Kuro Shiwo.

In Australia, Hawaii and Polynesia generally, the fresh-water fishes are derived from marine types by modification of one sort or another. In no case, so far as I know, in any island to the eastward of Borneo, is found any species derived from fresh-water families of either the Eastern or the Western Continent. Of course, minor subdivisions in these districts are formed by the contour lines of river basins. The fishes of the Nile differ from those of the Niger or the Congo, or of the streams of Madagascar or Cape Colony, but in all these regions the essential character of the fish fauna remains the same.

SOUTHERN ZONE.

The third great region, the Southern Zone, is scantily supplied with fresh-water fishes, and the few it possesses are chiefly derived from modifications of the marine fauna or from the Equatorial Zone to the north. Three districts are recognized, Tasmanian, the New Zealand and the Patagonian. The fact that certain peculiar groups are common to these three regions has attracted the notice of naturalists.

ORIGIN OF NEW ZEALAND FAUNA.

In a critical study of the fish fauna of New Zealand,* Dr. Gill discusses the origin of the four genera and seven species of fresh-water fishes found in these islands, the principal of these genera (*Galaxias*) being repre-

* 'A Comparison of Antipodal Faunæ,' 1887.

sented by nearly related species in South Australia and in Patagonia.*

According to Dr. Gill, we can account for this anomaly of distribution only by supposing, on the one hand, that their ancestors were carried for long distances in some unnatural manner, as (a) having been carried across entombed in ice, or (b) being swept by ocean currents, surviving their long stay in salt water, or else that they were derived (c) from some widely distributed marine type now extinct, its descendants restricted to fresh water.

On the other hand, Dr. Gill suggests that as 'community of type must be the expression of community of origin,' the presence of fishes of long-established fresh-water types must imply continuity or at least contiguity of land. The objections raised by geologists to the supposed land connection of New Zealand and Tasmania do not appear to Dr. Gill insuperable. It is well known, he says, "that the highest mountain chains are of comparatively recent geological age. It remains, then, to consider which is the more probable, (1) that the types now common in distant regions were distributed in some unnatural manner, by the means referred to; or (2) that they are descendants of forms once wide-ranging over lands now submerged." After considering questions as to change of type in other groups, Dr. Gill is inclined to postulate, from the occurrence of species of the trout-like genus *Galaxias*, in New Zealand, South Australia and South America, that "there existed some terrestrial passage-way between the several regions at a time as late as the close of the Mesozoic period. The evidence of such a connection afforded by congeneric fishes is fortified by analogous representatives among insects, mollusca and even amphibians. The separation of the several areas must have occurred little later than the late Tertiary, inasmuch as the salt-

* *Galaxias*, *Neochanna*, *Prototroctes* and *Retropinna*.

water fishes of corresponding isotherms found along the coast of the now widely separated lands are to such a large extent specifically different. In general, change seems to have taken place more rapidly among marine animals than fresh-water representatives of the same class."

It is not often that I have occasion to differ from Dr. Gill on a question in ichthyology; but, in this case, when one guess is set against another, it seems to me that the hypothesis first suggested, rather than the other, lies in the line of least logical resistance. I think it better to adopt provisionally some theory not involving the existence of a South Pacific Antarctic Continent, to account for the distribution of *Galaxias*. For this view I may give five reasons:

1. There are many other cases of the sort equally remarkable and equally hard to explain. Among these is the presence of species of paddle-fish and shovel-nosed sturgeon,* types characteristic of the Mississippi Valley, in Central Asia. The presence of one and only one of the five or six American species of pike† in Europe; of one of the three species of mud-minnow in Austria,‡ the others being American. Such cases occur all over the globe and must be explained, if at all, on some hypothesis other than that of former land connection.

2. The supposed continental extension should show permanent traces in greater similarity in the present fauna, both of rivers and of sea. The other fresh-water genera of the regions in question are different, and the marine fishes are more different than they could be if we imagine an ancient shore connection. If New Zealand and Patagonia were once united other genera than *Galaxias* would be left to show it.

* *Scaphirynchus* (the shovel-nosed sturgeon) and the paddle-fish (*Polyodon* and *Psephurus*).

† *Esox lucius*.

‡ *Umbra*, the mud-minnow.

3. We know nothing of the power of *Galaxias* to survive submergence in salt water, if carried in a marine current. As already noticed, I have found young and old in abundance of the commonest of Japanese fresh-water fishes in the open sea, at a distance from any river. Thus far this species, the hakone* dace, has not been recorded outside of Japan, but it might well be swept to Korea or China. Two fresh-water fishes of Japanese origin now inhabit the island of Tsushima in the Straits of Korea.

4. The fresh-water fishes of Polynesia show a remarkably wide distribution and are doubtless carried alive in currents. One river-goby† ranges from Hawaii to the Riu Kiu Islands. Another species,‡ originally perhaps from Brazil through Mexico, shows an equally broad distribution.

5. We know that *Galaxias* with its relatives must have been derived from a marine type. It has no affinity with any of the fresh-water families of either continent, unless it be with the Salmonidæ. The original type of this group was marine, and most of the larger species still live in the sea, ascending streams only to spawn.

When the investigations of geologists show reason for believing in radical changes in the forms of continents, we may accept their conclusions. Meanwhile, almost every case of anomalies in the distribution of fishes admits of a possible explanation through 'the slow action of existing causes.' Geologists will attach more weight to biological data, if biologists refrain from insisting on theories which at the best are mere possible explanations, in the incomplete state of our knowledge.

Finally, I may repeat that real causes are always simple when they are once known. All anomalies in distribution

* *Leuciscus hakuensis*.

† *Eleotris fusca*.

‡ *Awaous crassilabris*.

cease to be such when the facts necessary to understand them are at our hand.

DISTRIBUTING MARINE FISHES.

The distribution of marine fishes must be indicated in a different way from that of the fresh-water forms. The barriers which limit their range furnish also their means of dispersion. In some cases proximity overbalances the influence of temperature; with other forms, questions of temperature are all-important.

PELAGIC FISHES.

Before consideration of the coast lines, we may glance at the differences in vertical distribution. Many species, especially those in groups allied to the mackerel family, are pelagic—that is, inhabiting the open sea, and ranging widely within limits of temperature. In this series, some species are practically cosmopolitan. In other cases the genera are so. Each school or group of individuals has its breeding place, and from the isolation of breeding districts new species may be conceived to arise. The pelagic types have reached a species of equilibrium in distribution. Each type may be found where suitable conditions exist, and the distribution of species throws little light on questions of distribution of shore fishes. Yet, among these species are all degrees of localization. The pelagic fishes shade into the shore fishes on the one hand and into the deep-sea fishes on the other.

BASSALIAN FISHES.

The vast group of bassalian or deep-sea fishes includes those forms which live below the line of adequate light. These, too, are localized in their distribution, and to a much greater extent than was formerly supposed. Yet, as they dwell below the influence of the sun's rays, zones and surface temperatures are nearly alike to them, and the same forms may be found in the arctic or under the equator. Their differences in distribution are largely vertical, some liv-

ing at greater depths than others, and they shade off by degrees from bathybial into semi-bathybial, and finally into ordinary pelagic and ordinary shore types.

The fishes of the great depths are soft in substance, some of them blind, some of them with very large eyes, all black in color, and very many are provided with luminous spots or areas. A large body of species of fishes are semi-bathybial, inhabiting depths of 200 or 300 fathoms, showing many of the characters of shore fishes, but far more widely distributed. Many of the remarkable cases of wide distribution of type belong to this class. At such depths, red colors are almost universal, corresponding to the zone of red algæ, and the colors in both cases are perhaps determined from the fact that the red rays of light are the least refrangible.

A certain number of species are both marine and fresh water, inhabiting estuaries and brackish waters, while some more strictly marine ascend the rivers to spawn. In none of these cases can any hard and fast line be drawn, and some groups which are shore fishes of one region will be represented by semi-bathybial or fluviatile forms in another.*

LITTORAL FISHES.

The shore fishes are in general the most highly specialized in their respective groups, because exposed to the greatest variety of selecting conditions and of competition. Their distribution in space is more definite than that of the pelagic and bassalian types, and they may be more definitely assigned to geographical areas.

* The dragonets, *Callionymus*, are shore fishes of the shallowest waters in Europe and Asia, but inhabit considerable depths in tropical America. The sea-robins (*Prionotus*) are shore fishes in Massachusetts, semi-bathybial fishes at Panama. Often, arctic shore fishes become semi-bathybial in the temperate zone, living in water of a given temperature. A long period of cold weather will sometimes bring such to the surface.

DISTRIBUTION OF LITTORAL FISHES BY COAST-LINES.

Their distribution is best indicated, not by realms or areas, but as forming four parallel series, corresponding to the four great north and south continental outlines. Each of these series may be represented as beginning at the north in the Arctic fauna, practically identical in each of the four series, actually identical in the two Pacific series. Passing southward, forms are arranged according to temperature. One by one in each series, the Arctic types disappear; sub-arctic, temperate and semi-tropical types take their places, giving way in turn to south-temperate and Antarctic forms. The distribution of these is modified by barriers and by currents, yet though genera and species may be different, each isotherm is represented in each series by certain general types of fishes.

Passing southward, the two American series, the East Atlantic and the East Pacific, pass on gradually through temperate to antarctic types. These are analogous to those of the arctic, and in a few cases they are generically identical. The West Pacific* (East Asian) series is very much broken

* The minor faunal areas of shore fishes may be grouped as follows:

EAST ATLANTIC.	EAST PACIFIC.	WEST PACIFIC.
Icelandic,	Arctic,	Arctic,
British,	Aleutian,	Aleutian,
Mediterranean,	Sitkan,	Kurile,
Guinean,	Californian,	Hokkaido,
Cape.	San Diegan,	Nippon,
	Sinaloan,	Chinese,
WEST ATLANTIC.	Panaman,	East-Indian,
Greenlandic,	Peruvian,	Polynesian,
New England,	Revillagigedan,	Hawaiian,
Virginian,	Galapagan,	Indian,
Austroriparian,	Chilian,	Arabian,
Floridian,	Patagonian.	Madagascarian,
Antillean,		Cape,
Caribbean,		North Australian,
Brazilian,		Tasmanian,
Argentinian,		New Zealand,
Patagonian.		Antarctic.

by the presence of Australia, the East-Indies and Polynesia. The irregularities of these regions make a number of sub-series, which break up the simplicity expressed in the idea of four parallel series. Yet the fauna of Polynesia is strictly East-Indian, modified by the omission or alteration of species, and that of Australia is Indian at the north, and changes to the southward much as that of Africa does. In its marine fishes, it does not constitute a distinct 'realm.' The East Atlantic (Europe-African) series follows the same general lines of change as that of the West Atlantic. It extends, however, only to the South Temperate Zone, developing no Antarctic elements. The relative shortness of Africa explains in large degree, as already shown, the similarity between the tropical elements in the two Old World series, as the similarity in tropical elements in the two American series must be due to a former depression of the connecting Isthmus. The practical unity of the Arctic marine fauna needs no explanation in view of the present shore lines of the Arctic Ocean.

EQUATORIAL FISHES MOST SPECIALIZED.

In general, the different types are most highly specialized in equatorial waters. The processes of specific change, through natural selection or other causes, if other causes exist, take place most rapidly there and produce most far-reaching modification. As I have elsewhere stated, the coral reefs of the tropics are the centers of fish-life, the cities in fish-economy. The fresh waters, the arctic waters, the deep sea and the open sea, represent forms of ichthyic backwoods, regions where change goes on more slowly, and in them we find survivals of archaic or generalized types. For this reason, the study in detail of the distribution of marine fishes of equatorial regions is in the highest degree instructive.

The study of the origin of the fish groups of Japan affords a fascinating index to its multifarious problems.

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*THE LABORATORY TEACHING OF PHYSIOLOGY.**

THE student of physiology should perform the classical experiments upon which the science rests. The writer of these papers has for several years endeavored to place the laboratory teaching of physiology within the reach of every school. To accomplish this it is necessary that apparatus of precision be designed upon lines permitting its manufacture in large quantities at a small cost. The apparatus described below is believed to show progress in this direction.

the box admits the rays from a lantern or other source of light. This circular window may be closed by a clear glass plate or by any of the several diaphragms described below. Two pins, one at the side and one below the opening, are so placed that when the diaphragm rests against them its aperture will lie in the axis of the optical system. The lenses and mirrors employed with the box are mounted in square wooden blocks, to protect them from injury. When the side of the wooden block is placed against the 'rabbit strip' shown at the lower inside angle of the box the center of the lens or mirror mounted in the block will lie in the optical axis. The rays of light entering the box are made visible by the fumes of Japanese incense, a small stick of which is lighted and placed in a hole in a cork upon which fits a tin cylinder shown in Fig. 1.

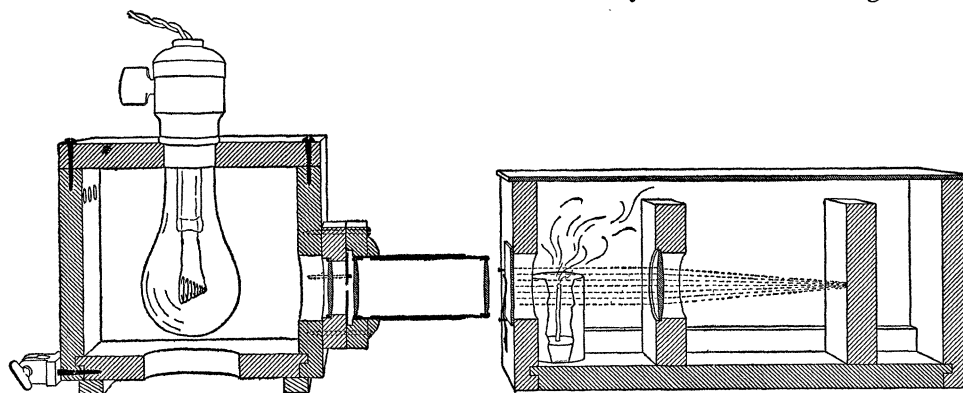


FIG. 1. The optical lantern and artificial eye.

I. THE ARTIFICIAL EYE.

The artificial eye (shown in section in Fig. 1, one fourth the actual size) consists of a wooden box the top of which is closed by laying upon it a piece of clear plate-glass. A circular opening in the front of

The optical lantern consists of a sixteen-candle-power electric lamp, with small spiral filament, mounted in a wooden box pierced with holes which permit thorough ventilation but do not allow the escape of light to disturb the observer. The lantern box is provided with a condensing lens and two focusing lenses mounted in draw tubes which may be easily removed. The slot for the diaphragms is furnished with a stop so placed that when the diaphragm is shoved against it the aperture of the

* Porter, W. T.: *Boston Medical and Surgical Journal*, Dec. 29, 1898. *Philadelphia Medical Journal*, Sept. 1, 1900. 'An Introduction to Physiology,' Cambridge, 1900 and 1901. 'Experiments for Students in the Harvard Medical School,' Second Series, Cambridge, Jan., 1901. Third Series, Cambridge, May 1901.