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Paleolimnological Problems of Lake Biwa-ko

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Introduction

Lake Biwa-ko (35°15′ N., 136°05′ E.), the largest lake in Japan (Fig. 1, Tables 1, 2 and 3), is situated just on the isthmus which seems to be the distorted portion of two arcs building the Honshu Island. This lake has been deeply interested by many Japanese scientists not only by such a physical location of this lake but by the phenomena stated below. However, as the problems require both knowledge and field works of limnology and geology, activities by both limnologists and geologists have been inadequate in contrast with such great concerns. These phenomena are as follows:

(1) A striking negative gravity anomaly of the Lake Biwa basin, amounted to −50 milligal in which isoanomaly lines almost coincide with the outline of Lake Biwa-ko (TSUBOI *et al.*, 1954). It suggests that thick material of low density constitutes the earth's crust of this lake basin.

(2) The most conspicuous earthquake zone, deeply seated in the Japanese Islands, crosses the Honshu Island under the isthmus mentioned above; many great earthquakes have been recorded in our history. This deep-seated earthquake zone starts near the Mariana Islands, running towards north along the edge of the Japan Trench, a famous deep ocean trench in the world, and reaches Siberia through the underground of Lake Biwa basin and the Japan Sea (WADATI, 1940).

(3) Biologically speaking, there occur a great number of endemic species of animals and plants which differ remarkably from the biota of the other parts of Japan. The writer will discuss about this problem in the following paragraph.

(4) There are found a considerable amount of submerged archeologic remains in the northern part of Lake Biwa-ko. Some archeologists interprete this fact as a result of landslide by which they were carried into the lake (OYE, 1950). According to the writer's opinion, however, the interpretation by the downwarping of lake basin seems to be more logical as will be mentioned later.

(5) In addition to these remarkable phenomena, there is one important fact that the Plio-Pleistocene boundary exists in the ancient lake sediments which are preserved as the lacustrine terraces (IKEBE, 1933, 1954). This fact affords us the evidence of an ancient lake of Biwa which appeared at some time during the Tertiary period. The main points of discussion in this paper will be based on this evidence.

The afore-mentioned facts excited the writer's interest for the study of paleolimnology. Although it is not easy to do such investigations, it is the work of great importance in the paleolimnological researches on the sediments of ancient lakes, such as Lakes Baikal, Caspi and Aral, Tanganyika, Ohrid, Prespa, and Titicaca. For the first step of such investigations, the writer began geologic field works in 1959 and has as good as finished recently. The geology of Lake Biwa-ko will be published in detail later. In this paper, the writer will mention the outline of history of Lake Biwa-ko and then will discuss the ecological and biogeographical problems concerning this lake in summarizing the knowledge hitherto obtained. This paper is, of course, very incomplete, but the writer hopes to promote his study in expecting various criticism and advice from many scientists. The writer is now engaged in the sedimentary study of Lake Yogo-ko deposits obtained by a Livingstone borer; this is the second step of his study of Lake Biwa-ko in which he will later begin the research of deep sediment-cores to be taken in its center.

Acknowledgement

The writer expresses his best thanks to Prof. M. UÉNO, Kyoto University, for many valuable suggestion and encouragement in the writer's study. The writer is also indebted to the staff of the Otsu Hydrobiological Station, Drs. K. YAMAMOTO, K. NEGORO and H. YAMAGUTI, for their kind information and discussion about the present study. Prof. M. ICHIKAWA, director of the Station, has kindly arranged a position to the writer for continuing his study; the writer's appreciation is devoted to him. The writer also owes to Prof. E. S. DEEVEY, Yale University, with whom the writer has been able to discuss on the paleolimnological study of Lake Biwa-ko.

The Outline of History of Lake Biwa-ko

As the results of the writer's field works the following facts have become evident.

(1) The base of the Lake Biwa-ko basin is regarded geomorphologically as the Tertiary (Miocene ?) peneplain which dropped by the downwarping accompanied with faulting. From this viewpoint, the former connection between the lake and the sea may be possible since the peneplain was formed in an altitude near sea level. As the writer will discuss later, existence of land-locked fishes

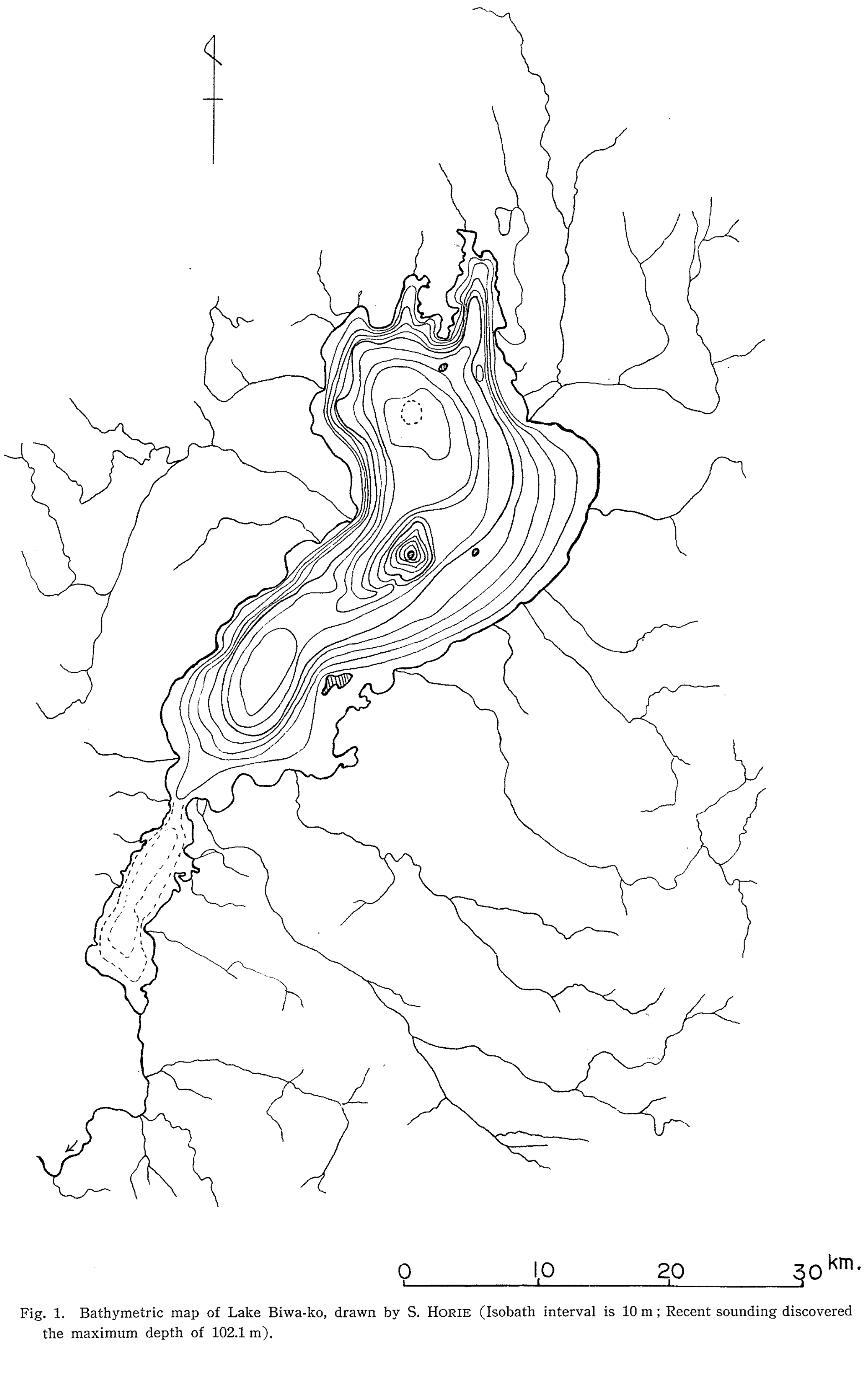

Fig. 1. Bathymetric map of Lake Biwa-ko, drawn by S. HORIE (Isobath interval is 10 m; Recent sounding discovered the maximum depth of 102.1 m).

and molluscs in Lake Biwa-ko also supports the possibility of the existence of such an ancient connection. UÉNO (1943) has stated that in the districts along the Japan Sea coast there are found such land-locked fishes which probably immigrated from north to south along the coast of the Japan Sea. It should be noticed that there is no connection between Lake Biwa-ko and the Japan Sea at present.

(2) There are the six steps of lacustrine terraces around the lake. These terraces occurred by the relative drop of lake level. Among them, the highest, oldest and most extensive terrace is called by the writer "Ancient Lake Biwa Terrace", which consists of Ancient Lake Biwa group. Near the uppermost part of this group, the mammal fossils, *Stegodon orientalis* and *Archidiskodon paramammonteus*, were fonnd. The former is an index fossil of the Plio-Pleistocene time and thereby lower sediments (the base of such ancient lake sediments is not yet observed) probably belong to Pliocene or to earlier epoch than that. There is a remarkable time gap between the first terrace, i.e. the Ancient Lake Biwa Terrace mentioned already and the following five terraces, and after the slow drop of the first lake level which formed the first terrace, five minor drops of lake level happened at the interval of the preceding conspicuous time gap. At our present knowledge, it is unfortunately unable to postulate the cause of each drop of lake level. It is able to list the factors of upwarping of the surrounding area, downwarping of the lake bottom, or both, and the fluctuation of lake level by the climatic changes, as well as gradual lowering of lake level by the discharge of the Seta River. The truth may be, however, the very complicated combination of some factors among them rather than a single cause. The writer is not able to analyse at present, which one was the most important and which one was negligible in each time. So far as the knowledge has been obtained by the writer, the above-mentioned changes of lake level occurred in *relative* sense. But as the writer will state below, it is possible to say that in general the most important one is the (relative) downwarping of the lake basin. The effect of the climatic changes will be deduced after we would succeed to get deep sediment cores by boring in the center of Lake Biwa-ko and to carry out the paleolimnological study on that deposits; until that time the writer will avoid further discussion concerning this matter.

(3) It is apparent that, in Fig. 2, the distribution of the Ancient Lake Biwa Terrace is very poor in the northeastern part of the lake basin; exactly speaking, the area northeastwards from a line connecting between Hikone and Imazu. It should be noticed that Ancient Lake Biwa group has been deformed by the crustal movements, as dip and strike of the group indicate. In general, dip and strike in Fig. 2 show that Ancient Lake Biwa group tilts towards the center of Lake Biwa-ko in the present lake basin, though it tilts towards west in the Iga basin. An indistinct ridge separating the Iga basin from the present Lake Biwa basin is situated near Tsuge; such a separation of the Iga basin, presumably a former sub-lacustrine basin, might occur by the crustal deformation.

(4) Old shoreline altitude of the Ancient Lake Biwa Terrace indicates remarkable difference such as 60–290 m above the present lake level (Fig. 3). Particular high shoreline altitude is observed in the western foot of the Suzuka Mountains. As the writer will discuss in the other paper, that portion shows outcrops of marked faulting which happened in the Ancient Lake Biwa group. Another high shoreline altitude is found in the Shigaraki Plateau. The iso-uplift lines indicate that the mode of crustal deformation resembles the outline of the present shape of Lake Biwa-ko. Such a nature of uplifting might cause the separation of the Iga basin from the present lake basin of Biwa-ko. It is accordingly considered that the Lake Biwa basin is doing basin-making crustal movement, i.e. downwarping deformation of the earth's crust. The most remarkable subsidence is recognized in the northeastern part of the lake and such a phenomenon coincides with the above-mentioned scanty distribution of the Ancient Lake Biwa Terrace, submerged topography of the shoreline, and the existence of the archeological remains on the lake bottom.

(5) Such a basin-making crustal movement having continued, Lake Biwa-ko has its age of over one million years, and it still remains an oligotrophic lake at the present day. Such a limnological condition is considered from the great amount of dissolved oxygen in the hypolimnion during the summer stagnation period as will be shown later. Besides this, there are more facts indicating the lake oligotrophy not only by the morphometry (Tables 1, 2 and 3), but by the poor amount of nitrogen compounds and phosphorus, together with the plankton, benthic fauna and fish. According to NEGORO's recent work (NEGORO, 1957), the chemical nature of Lake Biwa-ko is as shown in Table 4. These data were obtained in the summer stagnation period between July 30 and August 7, 1953, and indicate the oligotrophic nature, though the amount differs in place to place by such local factor as polluted water from the industrial factories. This condition is particularly important as the basis of the following discussion concerning the biogeographical problems of Lake Biwa-ko.

Table 1. Morphometry of Lake Biwa-ko, calculated by S. HORIE—I.

	Altitude	Length	Maximum breadth	Mean breadth	Length of shoreline	Area	Shore development	Maximum depth	Mean depth	Volume
	m	km	km	km	km	km²		m	m	km³
Whole lacustrine basin	85	68.0	22.6	9.9	188.0	674.4	2.04	102.1	41.2	27.8
Main lacustrine basin	85	51.0	22.6	12.1	150.0	617.6	1.70	102.1	44.7	27.6
Sub-lacustrine basin	85	17.0	5.6	3.3	38.0	56.8	1.42	7.5	2.8	0.16

Table 2. Morphometry of Lake Biwa-ko, calculated by S. HORIE—II.

	Isobath m	Area within isobath km^2	Ratio %	Length of shoreline and isobath km	Development
Whole lacustrine basin	0	674.4	100	188.0	2.04
Main lacustrine basin	0	617.6	91.6	150.0	1.70
	10	523.3	77.6	136.0	1.68
	20	450.0	66.7	124.8	1.66
	30	392.9	58.3	112.0	1.59
	40	351.0	52.0	105.6	1.59
	50	292.8	43.4	97.6	1.61
	60	230.2	34.1	88.0	1.63
	70	155.3	23.0	78.4	1.76
	80	87.1	12.9	51.2	1.55
	90	30.3	4.5	24.0	1.23
Sub-lacustrine basin	0	56.8	8.4	38.0	1.42
	3	34.7	5.1	33.6	1.60
	5	13.7	2.0	28.8	2.19

Table 3. Morphometry of Lake Biwa-ko, calculated by S. HORIE—III.

	Interval of isobath m	Volume between two isobaths km^3	Ratio %
Whole lacustrine basin	0 –102.1	27.8	100
Main lacustrine basin	0 –102.1	27.6	99.3
	0 – 10	5.2	18.7
	10 – 20	4.9	17.6
	20 – 30	4.2	15.1
	30 – 40	3.7	13.3
	40 – 50	3.2	11.5
	50 – 60	2.6	9.4
	60 – 70	1.9	6.8
	70 – 80	1.2	4.3
	80 – 90	0.6	2.2
	90 –102.1	0.07	0.25
Sub-lacustrine basin	0 – 7.5	0.16	0.58
	0 – 3	0.09	0.32
	3 – 5	0.05	0.18
	5 – 7.5	0.02	0.072

Table 4. Physico-chemical nature of Lake Biwa-ko (NEGORO, 1957).

	Epilimnion, 0 m	Hypolimnion, 40–90 m
Temp. °C	26.4 –29.7	7.28– 9.19
pH	7.4 – 7.6	6.8 – 7.0
SiO_2 mg/l	1.5 – 2.1	1.2 – 5.0*
Cl mg/l	5.5 – 7.4	2.1 – 7.4
Fe mg/l	0.00– 0.05**	0.00– 0.04
Ca mg/l	10.4 –12.0	10.8 –16.8
NO_3-N mg/l	0.00– 0.40	0.01– 0.55
NH_4-N mg/l	0.00– 0.50	0.00– 0.90
PO_4-P mg/l	0.01– 0.04	0.00– 0.02
$KMnO_4$ consumption	3.4 – 7.3	3.9 –29.6

* One station shows the exceptional amount of SiO_2 8.0.
** One station shows the exceptional amount of Fe 0.15.

Limnological and Biogeographical Implication to the History of Lake Biwa-ko

As DEEVEY (1955a) stated, paleolimnology is nothing but Pleistocene stratigraphy applied to lakes, that is, it is lacustrine biogeography with a stratigraphic time scale. Therefore, in the problems of such ancient lake as Biwa-ko, we have to discuss the discontinuous distribution of biota, for instance, about relics, in the light of the stratigraphic viewpoint of lake sediments. Without such a stratigraphic study, we may fall in the wrong interpretation or at least in insufficient inference. Accordingly, detailed discussion on the biogeographical questions of Lake Biwa-ko should be carried forward to the time of our deep core sampling of this lake. At present, the writer states an outline of limnological and biogeographical implication to the lake history, constructed by the geologic work by the writer.

It is well known that Lake Biwa-ko has a great number of endemic species of animals and plants. UÉNO (1937, 1960) has discussed that the fishes such as *Acheilognathus rhombea*, *A. cyanostigma*, *Gnathopogon elongatus caerulescens*, *G. gracilis*, *G. japonicus*, *G. biwae*, *Ischikauia steenackeri*, *Chaenogobius isaza*, *Opsariichthys uncirostris* were endemic as same as *Difflugia biwae*, *Ancylobdella biwae*, *Eodiaptomus japonicus* and *Daphnia biwaensis*. KURODA (1948) has pointed out that the following molluscs were characteritic of the fauna of Lake Biwa-ko. They are: *Heterogen longispira*, *Semisulcospira decipiens*, *S. niponica*, *Radix onychia*, *Gyraulus biwaensis*, *G. amplificatus*, *Lanceollaria oxyrhyncha*, *L. biwae*, *Inversidens reiniana*, *I. hirasei* var., *I. brandti*, *Hyriopsis schlegeli*, *Anodonta lauta tumens*, *A. calipygos*, *Corbicula sandai*, *Pisidium kawamurai*, *Sphaerium japonicum biwaense*. KURODA also stressed that they resembled the continental ones. NEGORO (1956, 1959) who studied the algae in Lake Biwa-ko indicated that there occurred such endemic species as *Pediastrum Biwae*, *Staurastrum Biwaensis*, *S. dorsidentiferum*

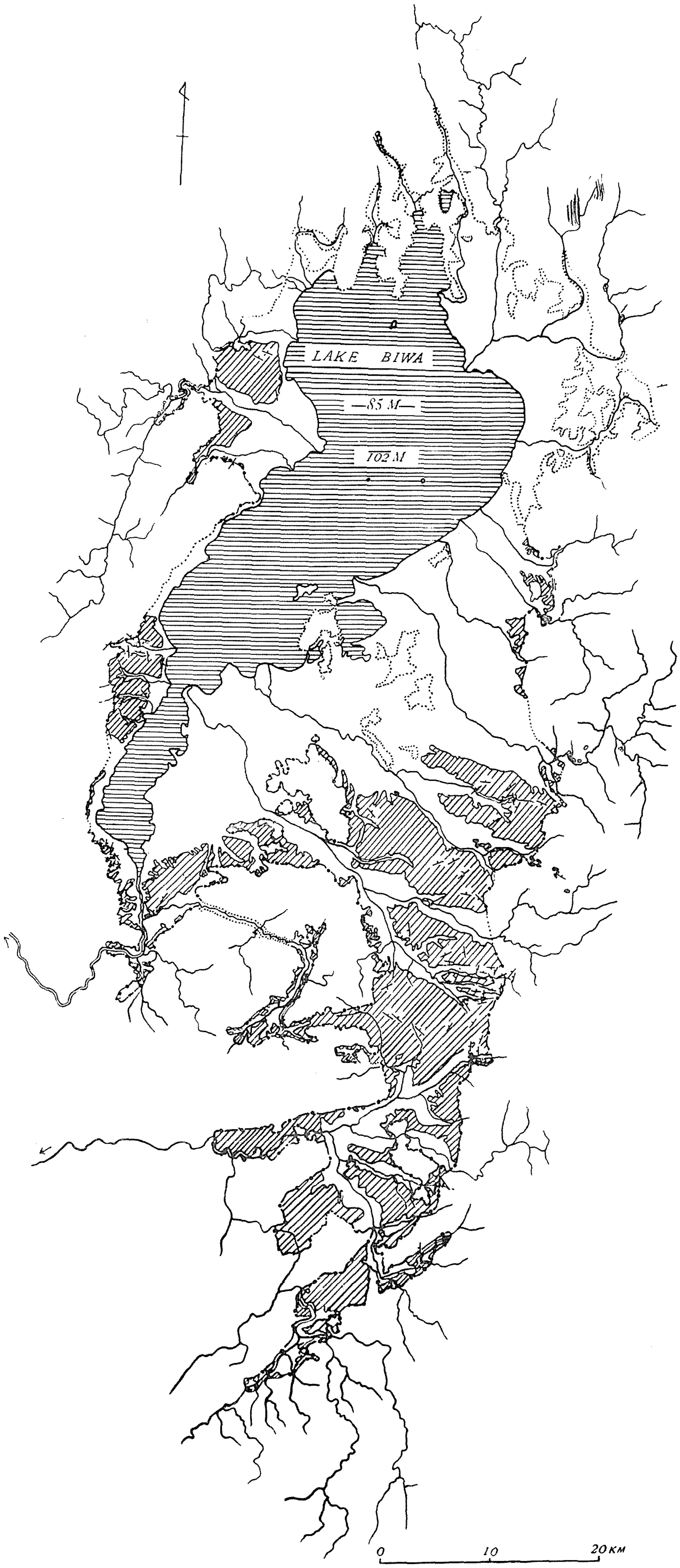

Fig. 2. Map showing the distribution of the Ancient Lake Biwa Terrace (oblique line), drawn by S. HORIE (In this figure, chain line indicates ancient shoreline and dotted line indicates deduced ancient shoreline).

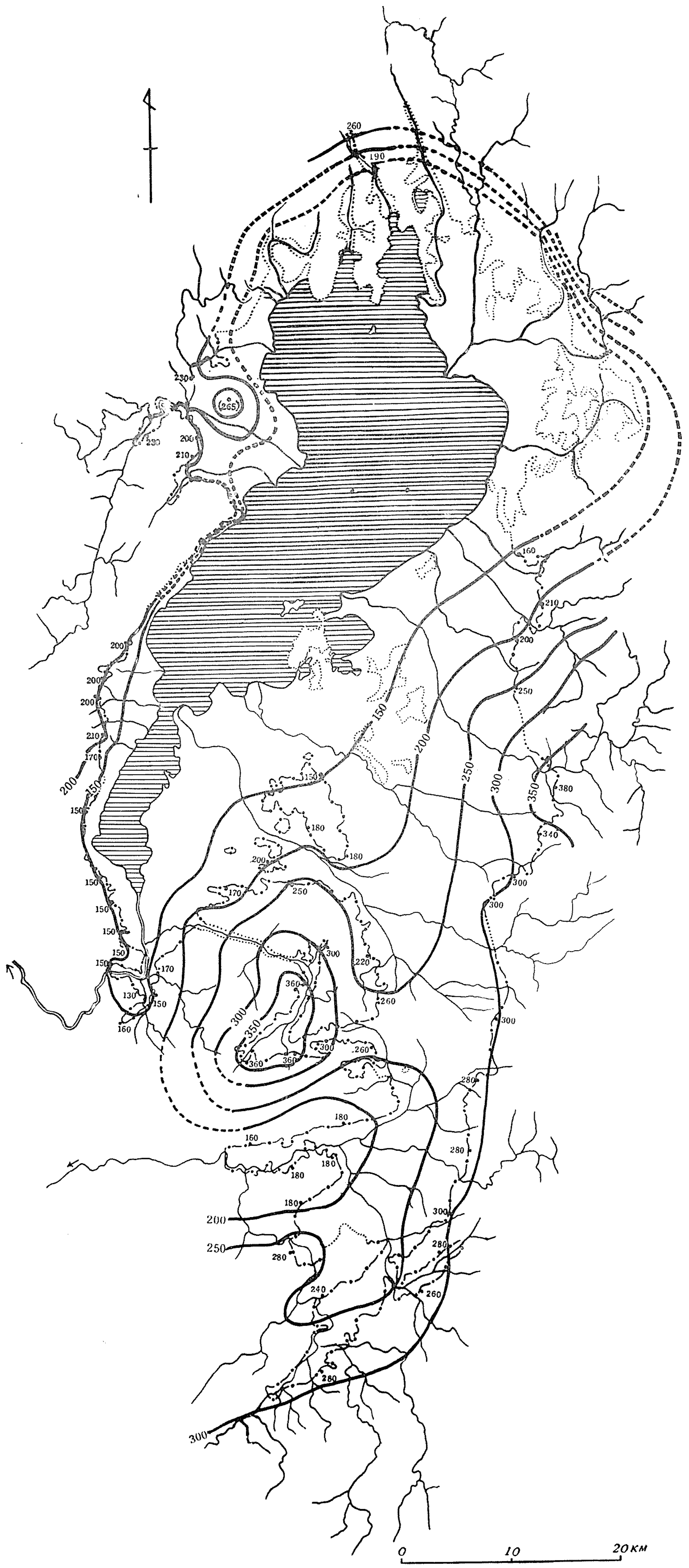

Fig. 3. Iso-uplift line of the lake basin since the time of ancient Lake Biwa-ko, drawn by S. HORIE (In this figure, altitude of each spot of the ancient shoreline is shown in numeral).

var. *ornatum*, *S. limneticum* var. *Burmense*, *Oedogonium* sp., *Melosira solida*, *Stephanodiscus carconensis* and a peculiar race of *Ceratium hirundinella*. In connection with the present question, Mr. H. YAMAGUTI informed the writer that a vascular plant named *Vallisneria biwaensis* also belonged to an endemic species. Such phenomena might be produced by this lake not only in its large area and the appropriate depth but also in its exceptionally long history since its birth. Lake Biwa-ko has probably kept its isolated environment and stable ecological conditions for extremely long years.

As mentioned above, the Tertiary peneplain had downwarped together with faulting. Since that occurrence, the lake basin has continuously occupied the environment isolated by the surrounding barrier for more than one million years without any serious geologic disturbance, except the first remarkable drop of lake level. Such an abrupt change of lake level which formed the Ancient Lake Biwa Terrace, probably in the Plio-Pleistocene time, might affect the living world of ancient Lake Biwa-ko. The writer is, however, not able to discuss its paleoecological and biogeographical significance at present. The isolated environment as a lake might progressively has prevented the invasion of aquatic species abroad as well as the escape of species already living in the lake. "Progressively" means the transformation of the value of barrier. In the writer's present opinion, Lake Biwa-ko had been established when the peneplain occupied a wide area of the Japanese Islands. After such flat earth's surface was formed, the warping and faulting of the earth's crust might raise the barrier around Lake Biwa-ko step by step. Hence, both invasion and escape of fauna and flora were easier in older time when the barrier was generally low, whereas younger the age, the ability of invasion and escape might be restricted.

It should be debatable whether the lake has had any connection with the sea. The writer has no adequate data at present concerning that question, but such a connection seems to be possible when we consider the peneplain discussed above, and the examples of land-locked animals such as a bivalve *Corbicula sandai*, which might originate in either sea or brackish waters. According to BROOKS' elaborate work (BROOKS, 1950), "thalassoid" appearance of snail shells of Speke and Böhms, the discovery of a trachyline medusa *Limnochnida tanganicae*, and also Arachnoidea, *Schizopera* and *Victorella*, suggest the former connection of Lake Tanganyika with the sea. Similar situation was pointed out by VEREŠČAGIN (1940) regarding most species of the Baikal fauna, while BERG (1935) recognized that the Baikal fauna was derived from an ancient fresh water fauna. Referring to such previous studies of ancient lakes, the need of more data is keenly felt for detailed argument regarding the former connection between Lake Biwa-ko and the sea.

In the discussion on the endemic species, we cannot neglect the Pleistocene climatic changes. In contrast with the limited area of the dimension of tectonic accident, climatic accident occurs in by far the wider region, at least in the hemispheric, possibly in the global scale. The physico-chemical and biological state of a lake is so greatly controlled by climate that we have to pay special attention to this accident. Even though a lake is protected from other accidents in its isolated portion and continuously keep ecological conditions, it cannot be saved from the influence of the change of climate. The writer will briefly discuss regarding this problem.

YOSHIMURA (1937) stated shortly about the existence of the glacial relics in Lake Biwa-ko, though not in detail. UÉNO (1937, 1943, 1960) pointed out the occurrence of many animal species of northern origin living in Lake Biwa-ko. They are: *Oncorhynchus rhodurus*, *Anisogammarus* (*Eogammarus*) *annandalei*, *Gasterosteus aculeatus microcephalus*, *Chaenogobius isaza*, *Bdellocephala annandalei*, and also *Valvata* which inhabits only the profundal zone of Lake Biwa-ko in the Honshu Island. *Pisidium* of Lake Biwa-ko is also the northern species (KURODA, 1947). It is possible to say that such animals had spread into this lake basin during the glacial age and that, when cold climate had improved, they found their shelters in the profundal zone of the lake, such animals had also migrated to the high mountains as well as into the subterranean waters. The writer will discuss such phenomena in more detail in the following limnological and geological consideration.

The accompanied two figures based on the writer's field observations show that the center of downwarping of the Lake Biwa basin almost coincides to the center of gravity anomaly (TSUBOI *et al.*, 1954). There is an argument among geophysicists whether such a peculiar anomaly of gravity is caused by mainly the special structure of the earth's crust or by mainly the thick lacustrine sediments. If the former is true, we cannot anticipate the presence of lacustrine sediments so thick, but if the latter is true, we can expect the existence of extremely thick one. We cannot estimate at present the exact total thickness of Lake Biwa sediments; at any rate, such an amount of sediments which have been accumulated since sometime in Tertiary should be huge. Similar striking anomaly of gravity was also found in Lake Tanganyika (KRENKEL, 1939; HORSFIELD and BULLARD, 1937). From such considerations, it will be possible to interprete that the center of downwarping indicates a great amount of continuous sinking in the lake basin. In other words, owing to the supply of both allogenic and autogenic materials, such a load may cause the sinking of the earth's crust forming this lake basin, roughly in proportion to the amount of load. Such a situation is similar to the geosyncline in the pre-orogenic movements. In the other examples, it is said that the delta deposits of the Mississippi River or the Nile River are thick; the delta is continuing to subside in accordance with the supply of load. Of course, such a sinking does not appear only by load, and peculiar structure of the earth's crust is first. However, when we refer to the evidence of isostatic uplift of both the Scandinavian Peninsula and the northeastern part of the North American continent after the recession of ice sheet, we are not able to neglect the effect of load in question. Accordingly, peculiar negative (thick material of SiAl) gravity anomaly of the

Lake Biwa basin is suggestive to the presence of a considerable amount of lake sediments. From these thinking, it may be correct to regard that almost the same maximum depth has been continuously kept since the birth of tectonic lake basin.

Since the morphometry of a lake is important for judging its limnological nature, such a geologic situation which has kept almost the same morphometric features of a lake seems to be significant. As to the heat budget of lake, it is a function of both "size of lake and depth of lake". Generally speaking, "First-class lake" of the HUTCHINSON's definition (HUTCHINSON, 1957) or "Lake of first order" of the WHIPPLE's classification (WHIPPLE, 1898) transits towards the Second-class (Second order), and finally towards the Third-class (Third order) lake as the result of deformation of the lake basin by the sedimentation. Such a deformation of lake basin morphology must affect the physico-chemical and biological nature in that lake. According to DEEVEY (1955b) who discussed on the obliteration of hypolimnion, warmer climate must supply apparently more organic materials into lake, advancing the filling up of lake basin rapidly. Even if we neglect such a change of climate, the burial should progress continuously. As the result, more amount of dissolved oxygen in the hypolimnion will be consumed by the oxidation for such materials and the flat area of the lake bottom will increase. According to MORTIMER (1941, 1942), redox potential (Eh) at the mud-water interface in an oligotrophic or an eutrophic lake during the circulation period is found at E_7, 0.6 volt. The consumption of dissolved oxygen, however, causes the geochemical change at the mud-water interface which is especially important for the trophic degrees of lakes. The decrease of dissolved oxygen in the hypolimnion produces the drop in redox potential and then at $E_7=0.2$ volt oxidation layer covering bottom ooze begins to disappear; thereafter a considerable amount of Fe^{++}, Mn^{++}, NH_4^+, and P being dissolved out and diffused into the bottom layer of hypolimnion. The disappearance of the oxidation layer is accordingly important for lake metabolism. Therefore, much more consumption of dissolved oxygen in the hypolimnion due to the above-mentioned burial of the lake basin causes the drop in redox potential, and the eutrophication, both morphometric and edaphic, progresses.

However, tectonic lake may be exception. As discussed above, sedimentation has a tendency to cause the subsidence of the earth's crust by the compensation in tectonic lake, keeping almost the same maximum depth. Hence, both morphometric and edaphic eutrophy do not appear in such a tectonic lake so far as the subsidence of lake basin continues. In other words, the profundal part of tectonic lake is constantly occupied by inorganic sediments. Even though the compensation level might be shifted by the Pleistocene fluctuation of cloudiness which was caused by the oscillation of atmospheric moisture, the amount of dissolved oxygen in the hypolimnion of a tectonic lake was thus kept in sufficient quantity and the drop in redox potential did not occur.

As the writer will discuss in the other paper, Pleistocene climatic fluctuations might cause the change of the circulation pattern of lake water. Nowaday, Lake Biwa-ko circulates once a year, when its surface water temperature in autumn reaches approximately 7°C, and does not stagnate during the whole winter. During the low temperature age, however, the temperature of water of Lake Biwa-ko was probably several degrees in centigrade lower than that at present, such as during the classical Wisconsin maximum (FLINT, 1957), and probably circulated twice a year. It seems to be reasonable speculation when we notice a close relationship between the nowaday circulation pattern and isotherm around any lake. Although Lake Biwa-ko, which is classed as tropical (FOREL, 1892, 1895), subtropical (YOSHIMURA, 1936), warm monomictic (HUTCHINSON, 1957) at the present day, might stagnate during the winter under such colder climate of the past, having the amount of dissolved oxygen which might be not much consumed during that season. This is suggested from the dissolved oxygen concentration of Lake Biwa-ko during the summer stagnation period at present (Fig. 4). Hence, under the colder climate during the glacial ages water temperature in the hypolimnion of this lake had probably been kept at 4°C.

From these consideration, the writer suspects that Lake Biwa-ko has been keeping almost the first class lake type for long years, though the hypolimnion temperature might fluctuate between 4° and 9°C due to the climatic changes in the hemispheric or global scale. Accordingly, it seems to the writer that the heat budget of a tectonic lake is controlled mostly by the fluctuations of the Pleistocene solar radiation. So far as the profundal zone of Lake Biwa-ko is concerned, water temperature might be only 1°–2°C higher than today during the Hypsithermal Interval (DEEVEY and FLINT, 1957). Such a low temperature in the hypolimnion of Lake Biwa-ko during the whole Pleistocene epoch should be appropriate as refuge of glacial relics. According to KIKUCHI (1927, 1930), among the zooplanktonts both of the eurythermal forms as well as of stenothermal cold water forms which live in the layer deeper than the metalimnion during the summer occur in whole year, while the stenothermal warm water forms are found only in summer. This fact indicates that the hypolimnion of Lake Biwa-ko affords a favorable environment to such northern species as *Oncorhynchus rhodurus*, *Anisogammarus* (*Eogammarus*) *annandalei*, *Chaenogobius isaza*, *Bdellocephala annandalei*, *Valvata*, and *Pisidium*, all of which belong to the glacial relics. However, the problems seem to the writer not to be so simple. The first question is the frequency of the glacial ages and their amplitudes. EMILIANI (1955) has verified that deep sea sediments clearly indicated this matter. It is apparent that the amplitude of the Pleistocene temperature changes were about 6°C in every occurrence and that the frequency of the glacial ages was more than the previous terrestrial evidence which was recorded four times. It is also evident that the temperature today is close to the maximum of that in the interglacial climate. On the other hand, UÉNO (1937) has indicated that the fauna of Lake Biwa-ko is conspicuous in mixing of both the northern and southern species; there is nearly at the limit of the distribution of southern species, while the northern species extend to much further south. ÔSHIMA (1923, 1930, 1934, 1936) has discussed the discovery of *Oncorhynchus masou* in a cold water of mountain stream in Formosa. He has interpreted that the inhabitance of this trout might be the result of immigration during the glacial age after the end of which it became land-locked. Such a discussion by ÔSHIMA bolsters UÉNO's opinion.

The writer considers from these studies that the invasion of northern species to Lake Biwa-ko was performed in many times if the topography of barrier was permissible to them, in accordance with the coming of every glacial age. At every improvement of climate after the glacial age, they might find the shelter in the cold hypolimnion of such an oligotrophic lake kept by the down-warping of the earth's crust, as well as in the subterranean waters. Such marine fishes of cold water as *Oncorhynchus rhodurus*, *Gasterosteus aculeatus microcephalus*, *Chaenogobius isaza*, and *Plecoglossus altivelis* might find their refuge in deep bottom or the upper reaches of inflowing rivers, where they might become land-locked thereafter. Concerning the geologic evidence, however, the lake basin of Biwa-ko seems to be more inaccessible to invadors of newer age as discussed already. In contrast with such northern species, southern species has had no shelter except small springs when the climate deteriorated. Lake Biwa-ko has been more favorable for the endemic species of northern origin; such a special condition was caused by an exceptional structure of the earth's crust which has kept the lake in oligotrophy.

MIYADI (1933) classified Lake Biwa-ko as an exception of the THIENEMANN's classification, as follows:
"Some Exceptional Lakes......The largest Japanese lake, Biwa-ko, is also interesting not only for the presence of many endemic species, but also for the absence of typical chironomid forms characteristic of it. Its deep water is rich in oxygen and the bottom is occupied by steno-oxybionts, such as *Gammarus*, *Valvata* and *Pisidium*. It seems to correspond to ALM's Amphipoda type and is in many respects similar to oligotrophic *Tanytarsus* lakes."
It is presumably interpreted by the writer's discussion given above. Since the dissolved oxygen amount has been kept enough to oxidize the organic materials and as the redox potential in the mud-water interface has not dropped below 0.2 volt, both morphometric (Tables 1, 2 and 3) and edaphic eutrophy might not advance and *Tanytarsus* might not inhabit such a silty bottom of almost inorganic sediments. *Tanytarsus* is very scanty in the profundal zone of Lake Biwa-ko even at present.

At this point of view, let the writer consider for a while the conditions of other two lakes abroad. Lake Baikal contains sufficient amount of dissolved oxygen in the whole mass of lake water throughout year, but *Tanytarsus* fauna may not be found even though its lake bottom ought to have been buried for much longer time than Lake Biwa-ko. The sufficient amount of dissolved oxygen suggests that oxidation is active in Lake Baikal and the profundal sediment consists of inorganic materials. High endemicity of the fauna in Lake Tanganyika is also peculiar. HUTCHINSON (1930) has pointed out that one important factor for this phenomenon may owe to an exceptional amount of dissolved radioactive material in this lake. Lake Tanganyika, however, probably lacks benthic fauna, because of its oligomictic thermal condition under the tropical climate.

In conclusion of this brief discussion, the writer repeats the importance of ecological and biogeographical studies of Lake Biwa-ko. The analyses on the endemic species in Lake Biwa-ko are not formulated at present. Some of them may be due to the former vast distribution but others may be due to autochthonous intra-lacustrine evolution as well as to immigration (BERG, 1925, 1935, 1949; BROOKS, 1950; STANKOVIĆ, 1960). Effect of the Pleistocene climatic changes such as fluctuation of lake level, the change of chemical nature of lake water, water temperature oscillation, shift of the compensation level might be somewhat effective to the fauna and flora of Lake Biwa-ko. The writer will discuss these problems in near future, only emphasizing at present the necessity to keep these in mind on their influence to the endemic species. In addition, investigations on geographical transition around Lake Biwa basin is also required. As the writer will discuss in the other paper, there are many evidence of the existence of former ancient lakes around the lake basin of Biwa. They were much more extensive than ancient Lake Biwa, which were situated in the present Seto-naikai (Inland Sea), the Ôsaka Bay, the Kyoto basin, the Nara basin, and in the Nagoya-Ise district. Mammal fossils found in the lacustrine sediments in these regions indicate us interesting limnic history of Central and Western Japan during both Tertiary and Quaternary periods. Researches on the endemic species must be carried on with close contact to such paleogeographical works. The problems concerning the former connection between these ancient lakes and the sea should be dealt with from this point of view.

Limnological Aspects of the Ancient Lakes in the World other than Lake Biwa-ko

In the writer's opinion, we have to take into account carefully of other ancient lakes in the world, since Lake Biwa-ko must be studied as an exceptional case among the other Japanese lakes. Some descriptions of the other ancient lakes of the world were stated in the preceding paragraph, but it seems to be not unnecessary to glance at the physico-chemical characters of them. So far as we have known, there are seven ancient lakes except Lake Biwa-ko. The writer, however, has only inadequate data of them to discuss in full, but he intends to collect data as much as possible he can. In this paragraph, the writer will discuss only Lakes Baikal, Tanganyika and Ohrid in connection with the problems of Lake Biwa-ko.

Lake Baikal, the deepest and probably the oldest lake in the world is a typical tectonic lake. According to the previous studies, its transparency is 40.5 m, which will indicate its oligotrophic nature, and is the greatest value among the lakes of the world. It stratifies during the summer between July and November, showing direct thermal stratification with the surface water temperature of 20°C in early August (DOROGOSTAISKY, 1922). The temperature of surface water is below 4°C between early December and late June, being frozen between mid-January and early May. Hence, circulation occurs twice a year, one in late June and the other in early December. The water below 250 m deep, however, keeps the constant temperature throughout the year. Even at 1700 m deep, water temperature was 3.2°C in 1934, and the deeper part of the hypolimnion presumably stagnates the whole year without any circulation. According to VEREŠČAGIN (1927), the quantities of both carbon dioxide and silica dissolved in lake water seem to increase slightly in the deeper part of the hypolimnion, while dissolved oxygen amount tends to decrease in that level. However, even at 1600 m deep the water contains dissolved oxygen 6.77 c.c./1 or 70% saturation (VEREŠČAGIN, 1927, 1936). It is surprising that such amount of dissolved oxygen might be supplied by partial circulation from the shallower level of several hundred metres. Lake Baikal apparently belongs to the oligotrophic lake type, and it is likely that such a condition in this exceptionally old lake is interpreted as the result of downwarping of the lake basin, as the same mechanism in Lake Biwa-ko discussed already. There remain, however, so many unsolved problems even when only the physico-chemical nature is concerned.

Lake Tanganyika which lies in the graben of the Great Rift Valley in East Africa is also a model tectonic lake in the world. It is well known by geologists that the most striking fault line in the world runs between Middle East and Mozambique Channel through the eastern side of the continent of Africa. It is accompanied with world-shaking earthquake zone (WILLIS, 1936) and active vulcanism. As the result, there are many lakes in this region. It is also evident that there exists in this tectonic lake zone striking negative gravity anomaly (KRENKEL, 1939; HORSFIELD and BULLARD, 1937), a close resemblance to Lake Biwa-ko. This is the important basic data for Lake Tanganyika study. Its physico-chemical nature is peculiar among the other ancient lakes, since it lies under the tropical climate and its surface is elevated not so high (Fig. 4). There is seen no circulation in East African lakes (WORTHINGTON, 1932; BEAUCHAMP, 1939). They are mostly meromictic, having the bottom sediments reducing in nature and anaerobic. Lake Tanganyika is not an exception among them, the anaerobic condition being indicated by the presence of hydrogen sulfide in water. Lake Tanganyika therefore differs in this regard from Lakes Baikal, Ohrid and Biwa-ko, and is certainly oligomictic lake *sensu* HUTCHINSON (1957). The writer has no data at present relating to the complete circulation in Tanganyika, though HUTCHINSON (1957) has stated the evidence for nocturnal mixing down to at least 80 m in depth and for seasonal variation in the top 200–250 m. Even if the temperature of water dropped during the glacial ages

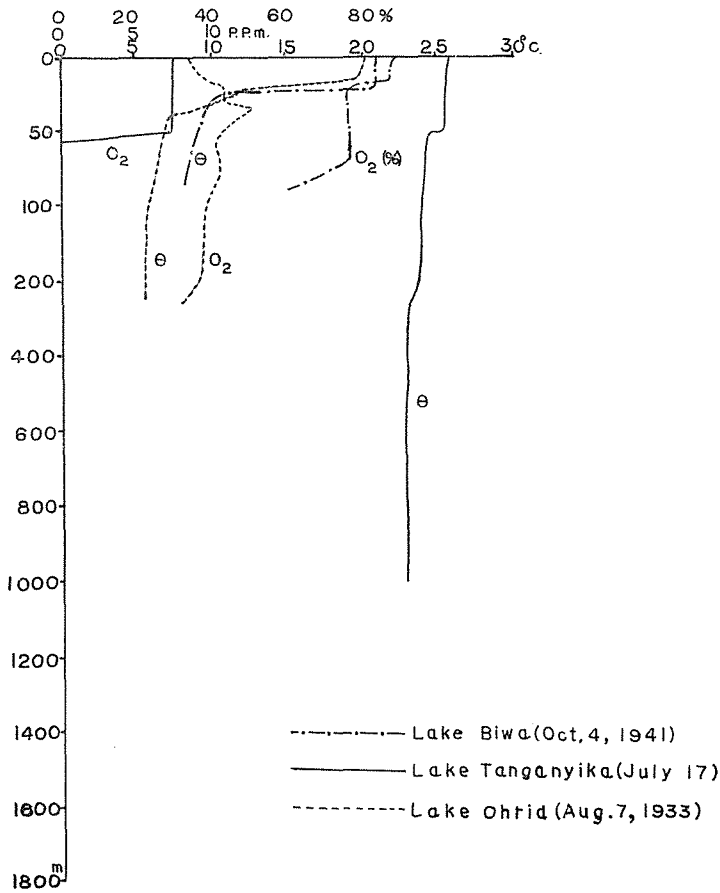

Fig. 4. The vertical distribution of water temperature and dissolved oxygen in three ancient lakes (compiled by S. HORIE from various sources).

of Pleistocene and the destruction of thermal stratification was possible, such an opinion might be mere speculative. In such a deep lake as Tanganyika (Table 5, the second deepest lake in the world), crenogenic meromixis *sensu* HUTCHINSON (1957) may exist. In any rate, it is unable to the writer's present purpose to compare the trophic condition of Lake Tanganyika with other ancient lakes. But the extremely great depth 1470 m of Lake Tanganyika in contrast with the oldness of its age and the existence of remarkable negative anomaly of gravity strongly suggest the downwarping of lake basin. Such phenomena will supply valuable data for the solution of the problems concerning Baikal, Ohrid, Biwa-ko and other ancient lakes in the world.

Another ancient lake whose history has been comprehensively studied is

Ohrid in the Balkan Peninsula. According to STANKOVIĆ, who recently made up a book entitled "The Balkan Lake Ohrid and its Living World" (1960) based on his many years researches, this tectonic lake is evidently doing crustal deformation. STANKOVIĆ has called such a crustal movement in the lake basin of Ohrid "rejuvenation", which is a common term in geomorphology. This term is defined as the mechanism which causes discontinuous inclination in river profile by uplift and subsidence of the earth's crust or by the climatic change or by the vulcanism. Such a term expressing the "cycle of erosion" is appropriate to be applicable to the downwarping of lake basin mentioned above. Lake Ohrid has apparently kept oligotrophic nature (Fig. 4), which is likewise in Lake Biwa-ko.

From the above discussion, it may be permissible to say that the ancient lakes of the world have probably special structure of the earth's crust. The writer is anxious to emphasize that these lakes have been able to continue their existence as lakes for long years and that oligotrophy in the present lake is an evident proof of the continuation of active crustal deformation. When such a deformation comes to its end, the lake basin is buried rapidly and finally disappears. Without such geologic and geophysical consideration of tectonic lake in question, we are unable to construct its exact limnic history and to discuss ecological and biogeographical problems in such ancient lakes of tectonic origin.

Conclusion

In the preceding discussion, the writer has tried to show the significance of ecological and biogeographical investigations of the tectonic Lake Biwa-ko on the basis of his field works about the terrestrial proof.

In addition, the writer will state some problems about this study. Immediately after the return to Japan from the United States, the writer began his glacial-geologic field works on the Japanese high mountains. The result of this study will be discussed in another paper, but he hopes to point out the significance of the glacial-geologic study to the paleolimnological researches. As discussed already, paleoecological and biogeographical studies are unable to formulate without the knowledge and data of the Pleistocene climatic changes, on which the expansion and recession of the glacier is the most sensitive indicator. In other words, if the reconstruction of glacial fluctuations is completed by moraines and other evidence, it will certainly make rapid progress in ecological and biogeographical discussion and such a progress must also contribute to the discussion of glacial geology. Beside this, in the writer's opinion, the fluctuation of temperatures and precipitation seems to affect lake trophication as an external influence. In this connection, it is to be noted that the glacial expansion is not caused only by the drop of temperature and the increase of precipitation. On the contrast, much precipitation accompanied with high temperature also produces the glacial advance. The evidence of the youngest

(VI) and the second youngest (V) moraines in the central Japanese mountains supports that there occurred two recent glacial expansions in high temperature and much precipitation, comparing with the glacial-geologic evidence in the Hidaka Mountains, Hokkaido. Such phenomena have been already verified by the paleolimnological and glacial-geologic studies in both Europe and North America (DEEVEY and FLINT, 1957). Glacial-geologic discussion on the Japanese Islands is beside the purpose of this paper; the results will be printed in detail in other publications.

In the contrast with the effect of the climatic change upon Lake Biwa-ko, this lake has special significance to the study of the earlier climatic changes in Japan. According to the writer's glacial-geologic field works, there happened in Japan probably six expansions of the glacier during the Würm (Wisconsin) glacial stage, those fluctuations being closely similar to the oscillation of the ice sheets in both the continents of Europe and North America. Such evidence in Japan therefore suggests that similar climatic fluctuations to the other two continents occurred along the eastern margin of the Eurasiatic continent, and that Late Pleistocene climatic changes were probably synchronous throughout the Northern Hemisphere. In Japan, however, there is no such evidence as drift sheet or moraine derived from the former glacial fluctuations before the Würm glacial stage. It owes partly to the atmospheric circulation pattern in the Northern Hemisphere. Thereby, proof of such earlier changes of climate in Japan is only obtainable in the subsurface data. The most useful method is the study of bottom sediments in any ancient lake which has continued its existence throughout the whole Pleistocene. Lake Biwa-ko is properly the case. The exact thickness of bottom deposits in the center of Lake Biwa-ko is not known yet, but it seems to be considerably thick when the striking negative gravity anomaly there is noticed. A paleolimnological study of deep core-samples will indicate not only the developmental history of Lake Biwa-ko but the whole Pleistocene climatic history of the East Asiatic continent.

Table 5. Ancient lakes in the world (compiled by S. HORIE from various sources).

Name	Altitude m	Area km^2	Maximum depth m	Originated age	Location
Lake Baikal	453	31,500	1,741	Late Cretaceous∼Paleocene	Siberia
Caspian Sea	−26	436,400	946	Paleogene	West Asia
Sea of Aral	50	62,000	68		
Lake Biwa-ko	85	674	102	Miocene∼Pliocene	Japan
Lake Tanganyika	782	34,000	1,470	Pliocene	East Africa
Lake Ohrid	695	348	286	Pliocene	Balkan
Lake Prespa	906	298	54	Plio-Pleistocene	Balkan
Lake Titicaca	3,804	7,700	281	Plio-Pleistocene	Andes

As an initial step to the sedimentary study of Lake Biwa-ko, the writer began his research on the sediments obtained by Livingstone borer in Lake Yogo-ko, which lies north of Lake Biwa-ko (Fig. 2). Since it had been a part of Lake Biwa-ko for the considerable length of time, Lake Yogo-ko had the same limnic history that Lake Biwa-ko had at least during the same period. Having been completed the sediment investigation of Lake Yogo-ko, the writer will begin studies of Lake Biwa-ko for his ultimate purpose. As the writer postulates (Table 5), at our present knowledge Lake Biwa-ko is the third oldest lake in the world next to Lake Baikal, the Caspian and Aral Seas. It precedes the other Tertiary lakes such as Lakes Tanganyika, Ohrid, Prespa, and Titicaca. The paleolimnological studies do not yet begin in these ancient lakes; thereby, such researches in Laka Biwa-ko is extremely important in this fine field of study.

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