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The Sponges of Lake Biwa.

By

Nelson ANNANDALE, *D. Sc.*
Indian Museum, Calcutta,
and
Tamiji KAWAMURA, *Rigakushi,*
Biological Station, Ôtsu.

(*With two Plates.*).

It is evident that conditions are unusually favourable for the growth of the Spongillidae in Lake Biwa, in which the sponges are found mainly in the form of encrustations, often of considerable area, on the pillars of piers and bridges, as smaller ramifying masses attached to water-weeds and stones, as elliptical growths on the shells of molluscs and on pebbles, and even in the form of free spheres lying on a sandy bottom. In collections from the lake made in 1914 and 1915 we are able to distinguish seven species, namely :—

Spongilla (*Euspongilla*) *lacustris* auct.
Spongilla (*Euspongilla*) *semispongilla* (ANNANDALE).
Spongilla (*? Euspongilla*) *asptinosa* POTTS.
Spongilla (*Stratospongilla*) *clementis* ANNANDALE.
Spongilla (*Eunapius*) *fragilis* LEIDY.
Ephydatia mülleri var. *japonica* (HILGENDORF).
Heteromeyenia kawamurae ANNANDALE, sp. nov.

The only other freshwater sponge as yet found in Japan is the typical form of *Ephydatia mülleri* (LIEBK.).

I. Systematic.

Key to the Japanese Spongillidae.

I. Gemmule-spicules, if present, without transverse disks at the extremities. ... ...[Genus *Spongilla*]

A. Free microscleres present in the dermal membrane.
  i. Gemmule-spicules present; gemmules not enclosed in special cages of skeleton-spicules. ...*S. lacustris.*
  ii. No gemmule-spicules; each gemmule enclosed in cage of skeleton-spicules. ... ...*S. aspinosa.*

B. No free microscleres.
  i. Coating of air-cells on gemmule granular in appearance.
    a. Gemmule-spicules abundant, semi-erect, swollen at the extremities, which bear circles of enlarged spines; skeleton-spicules very slender. ... ...*S. semispongilla.*
    b. Gemmules often absent; their spicules scanty, horizontal, tapering at the extremities, without enlarged spines; skeleton-spicules rather stout. ... ...*S. clementis.*
  ii. Coating of air-cells on gemmule resembling a honeycomb; gemmule-spicules cylindrical or subcylindrical, covered with small spines....*S. fragilis.*

II. Gemmule-spicules with transverse disks at the extremities.

A. Gemmule-spicules homogeneous, at least subequal, (the margin of their disks serrated, similar at the two extremities). ... ...[Genus *Ephydatia*].
  i. (Shaft of gemmule-spicule hardly longer than the diameter of a terminal disk); skeleton-spicules smooth or almost so. ...*E. mülleri* var. *japonica.*
  ii. (Shaft of gemmule-spicule similar); middle part of skeleton-spicule spiny or granular.... ... ...*E. mülleri* (typical form).

B. Gemmule-spicules of two distinct kinds, one considerably longer than the other. ...[genus *Heteromeynia*]. (skeleton-spicules smooth or with scattered spines; gemmule-spicules not highly differentiated; foramen of gemmule armed with a simple tube without filamentous processes. ... ...*H. kawamurae.*

Description of the Species.

Genus **Spongilla**, LAMARCK.

Subgenus **Euspongilla**, VEJDOVSKY.

Spongilla lacustris, auct.

Pl. I, Figs. 1—3.

1909, Weltner, Brauer's Süsswasserfauna Deutschlands XIX, p. 181, figs. 301, 304-309.
1909, Annandale, Proc. U. S. Nat. Mus. XXXVI, p. 631.
1915, Annandale, Mem. Ind. Mus. V, p. 26.

This sponge is one of the most widely distributed and the most plastic of the Spongillidae. It is also probably the most primitive in essential characters. Numerous varieties have been described, and it is doubtful whether some of the forms at present recognized as allied species are really distinct specifically. It is very difficult in any case to draw up a diagnosis that will exclude all such forms. The following description will be useful at least in distinguishing the species from the other Japanese Spongillidae.

The sponge is as a rule soft and fragile. It has, when growing in a good light, a bright green colour, which is due to the presence within the cells of its parenchyma of a minute unicellular Alga (*Chlorella*); in a faint light the green colour sometimes disappears, but in this condition the outlines of the capsules of the symbiotic alga can still be detected.

The typical form of the species is that of a thin encrusting layer from which vertical branches, elongate, slender and cylindrical, arise, but it may be massive without branches. The branches may be flattened instead of cylindrical and they may anastomose so as to form a complicated network. On the other hand the sponge may be reduced to a thin film of a small area.

The oscula as a rule are not very conspicuous, but they may grow large and have well-defined borders. In the living sponge they are protected by transparent "collars" of a conical form. The external (*i. e.* subdermal) terminations of the main exhalant canals (which are commonly confused with the dermal pores or ostia) are never very large or conspicuous.

The main element in the skeleton consists of slender but well-defined radiating or vertical fibres composed of spicules connected together by a horny substance. The substance is in continuity with that which forms the delicate membrane at the base of the sponge. The vertical fibres ramify irregularly but not frequently and pursue an irregular upward course. They are joined together to form a loose and irregular network with still more slender and much less well-defined transverse fibres of similar structure.

Free microscleres are present as well as those associated with the gemmules. The macroscleres or skeleton-spicules are smooth, slender, of relatively large size, sharply pointed at both ends (except in abnormal specimens) and as a rule slightly curved. The free microscleres or flesh-spicules, which are as a rule numerous both in the dermal membrane and in the interstices of the skeleton, are similar in form to the skeleton spicules but are much smaller and densely covered with spines.[1] The gemmule-spicules resemble the microscleres but are stouter and as a rule more strongly curved; the spines at their extremities are frequently better developed than on other parts, arranged in one or more circles and retroverted.

The gemmules lie free in the interstices of the skeleton, which does not form special cages or chambers for their protection. They are spherical in form and normally of considerable size, covered with a thick pneumatic coat in which the gemmule-spicules lie tangentially, and with a single micropyle or foramen, which is protected by a cup-like horny structure. As a rule the pneumatic layer is limited externally by a thin horny membrane in which there is a layer of gemmule-spicules lying horizontally. All these accessory structures except the foramen may, however, be absent, and even the gemmule-spicules sometimes disappear. There may be more than one foramen, and the foraminal aperture may take the form of a tube instead of a cup.

The species is probably cosmopolitan and has been found both

1) In the European *Spongilla rhenana* Retzer, which Weltner regards as a form of *S. lacustris*, the free microscleres are smooth.

in the Arctic Regions and the Tropics, but does not appear to have as yet been discovered in Africa or Australia.

In Japan it is known to us from the following localities :–

Lake Noziri, Lake Kizaki and Lake Nakatsuna, Province of Shinano.

Lake Biwa and a small lake at Komatsu, Province of Ōmi.

A small pond at Yodo near Kyoto.

Spongilla semispongilla (ANNANDALE), nob. comb. nov.

Pl. I, Fig. 4.

1909, *Ephydatia semispongilla*, Annandale, Annot. Zool. Jap. V.II, p. 107, Pl. II, fig. 2.

This species was originally assigned to the genus *Ephydatia*, but, as its specific name was intended to indicate, actually occupies a position on the border-line between that genus and *Spongilla*. Its status, in fact, is similar to that of *Spongilla* (or *Ephydatia*) *crateriformis* (Potts), which is assigned by some authors to one and by others to the other of the two genera.[1] On the whole it seems best to confine the name *Ephydatia* to the species in which the gemmule-spicules have well-defined transverse disks at the extremities. In *S. semispongilla* the ends of the spicules are irregularly swollen and bear a circle, or more usually several consecutive circles, of enlarged spines, but the specialization of this part of the spicule is only a little more highly developed than it is in some specimens of *S. lacustris*. We, therefore, propose to transfer the species to the genus *Spongilla*, in which it should be placed near the type species.

It is distinguished from *S. lacustris* not only by the peculiarities of its gemmule-spicule but also by the complete absence of free microscleres and by the slenderness of its skeleton-spicules. The last, however, is a character on which, in view of the varieties found in *S. lacustris*, too much weight must not be placed. The foramen of the gemmule is protected by a curved tubule.

The colour in life is bright leaf-green. The external form is either that of a very thin film of limited area when growing on the

1) See Annandale, Faun. Brit. Ind., Freshw. Sponges, Hydroids & Polyzoa, p. 85 (1911).

leaves of water-plants or of an irregular network of considerable relative thicknesss but mainly horizental, though often highly convex, in direction. This form is sometimes lightly attached to weeds with small leaves, but also occurs on stones. In the thin form the upper parts of the gemmules is sometimes devoid of spicules and has the pneumatic layer thin, while the foraminal tubule always lies on the lower surface, by which the gemmule adheres to the leaf. In more robust sponges, however, the coats of the gemmule are developed uniformly, the gemmule lies free in the sponge and the tubule does not always point in the same direction.

The species is only known from the Main Island of Japan. It was described from Kasumi-ga-Ura on the Pacific coast and is not uncommon in L. Biwa, especially in the South Lake. We found a specimen in the small lake at Komatsu also.

Spongilla aspinosa POTTS.

Pl. II, fig. 1.

1887, Potts, Proc. Acad. Nat. Sc. Philadelphia, p. 184, Pl. VIII, fig. vi.

This species is also related to *S. lacustris*, from which it may be at once distinguished, when gemmules are present, by the fact that each gemmule is enclosed in an irregular but dense network or cage of skeleton-spicules. These spicules are sometimes smaller than those that take part in the formation of the skeleton in other regions, but this is not always the case. The gemmules have no special spicules but possess a well-developed coat of "granular" air-spaces and a foramen protected by a horny tubule. The microscleres are confined or practically confined to the dermal membrane. They were described by Potts as being quite smooth, but in the Japanese specimen which we have seen they bear short irregular spines (Pl. II, fig. 1a). Potts's specimens were green, but the one from Lake Biwa was yellowish. Forms of *S. lacustris* are known in which the gemmule-spicules are very few or altogether lacking, but this is exceptional and when it occurs the pneumatic coat is usually degenerate; the gemmules are never enclosed in

definite skeletal cages, and *S. aspinosa*, therefore, appears to be quite a distinct species.

Owing to the absence of gemmule-spicules it is impossible to assign this species definitely to any existing subgenus, but its close relationship to *S. lacustris* leaves little doubt that the two are subgenerically identical. It is related to *S. sinensis* ANN.[1] from Suchau, which may ultimately prove to be identical with it.

S. aspinosa was originally described from the United States of North America and has not as yet (unless *S. sinensis* be identical) been described in any other country but Japan. We have examined a single specimen from L. Biwa near the Biological Station at Ōtsu.

Subgenus **Stratospongilla**, ANNANDALE.

The number of the species as yet attributed to this subgenus is still relatively small and most of these can be readily diagnosed. The one species that occurs in L. Biwa is however, remarkable for its variability.

Spongilla clementis ANNANDALE.

Pl. I, figs 5–8, Pl. II, fig. 2.

1909, *S. clementis*, Annandale, Proc. U. S. Nat. Mus. XXXVI, p. 631.
1910, *S. yunnanensis*, id., Rec. Ind. Mus. V, p. 197.

Three phases of the species may be distinguished, so far as the external characters are concerned, viz.—

Phase I. (Pl. I, fig. 5). In this phase the sponge forms a flat crust of lichenoid outline and as a rule less than 10 mm. thick. The colour may be leaf green, greyish or yellowish. The oscula are numerous and lie scattered on the surface irregularly. Their size is moderate (not more than 1.5 mm. in diameter) and their outline is not very regular; often one horizontal axis is considerably longer than the other at right angles to it. There is sometimes a hollow nodule or cowl at one side of an osculum which has the appearance of protecting it in one direction. Relatively large

1) Proc. U. S. Nat. Mus. XXXVIII, p. 183 (1910).

exhalant canals often run horizontally below the dermal membrane for some distance before opening into the osculum, but such channels never form a regular, star-shaped pattern. Sponges of this and the next phases often cover a considerable area on pillars of bridges and piers and occasionally on the vertical faces of rocks.

Phase II. (Pl. I, fig. 6). This phase, though mainly encrusting, is much more massive than Phase I. It often forms relatively thick ramifying horizontal branches. The external parts of the sponge may be tinged with green, but the colour never extends to the interior. The oscula are large, well-defined and round.

Phase III. (Pl. I, fig. 7). The sponges in this phase are among the most remarkable known in the Spongillidae. They form compact, ovoid, spherical, irregularly massive or pedunculate masses of a greyish or whitish colour with one or several large oscula opening directly from an exhalant canal of the same diameter. This canal, which forms a more or less cylindrical vertical cavity in that part of the sponge which it drains, is frequently separated into two halves a short distance below the osculum by a thin vertical diaphragm. The external surface is often ornamented with low ridges arranged in diverging groups that interdigitate one with another. The sponge is never more than about 8 cm. in diameter. Sponges of this type are either fixed to hard objects of small size or else lie free on the bottom.

We will discuss the significance of the three phases in subsequent pages. Apart from the external variation, the species may be described as follows: —

The sponge varies greatly in consistency and may be either soft or hard, in accordance with the closeness or laxity of the skeletal network. The radiating fibres are always distinct but never massive; they contain very little horny material. The variation in hardness depends largely on the development of the transverse fibres. The oscula are always at least fairly large and the pore-areas distinctly visible with the aid of a hand-lens. The individual dermal pores are relatively large, and the regular dis-

tribution of the areas gives the surface of the sponge a very characteristic appearance.

There are no free microscleres. The skeleton-spicules are short and rather stout, slightly curved, somewhat abruptly and not very sharply pointed. Their axial tubule is often conspicuons. Their external surface is often quite smooth, but sometimes the middle region of the spicule bears a few scattered spines, and specimens occur in which the majority—never all—of the macroscleres are somewhat densely spiny in this region; the extremities are always smooth.

The gemmule-spicules are slender, cylindrical, feebly curved, minutely and not very regularly or closely spined. They are either sharply and gradually or abruptly and bluntly pointed at the extremities.

Gemmules are seldom produced. When they are found they lie at the base of the sponge and adhere to the object to which it is attached. They have not yet been observed in the free or encrusting specimens. They are somewhat flattened in form and have a rather thin granular coat and a short foraminal tubule, which is situated on the upper surface in the natural position.

As will be gathered from the above description, *S. clementis* is of extreme variability not only in respect to the external form and colouration but also as regards the structure of the skeleton and the form of the spicule. Until we had examined a very large series of specimens, in which forms intermediate in all respects were found, we separated the specimens provisionally into four or five distinct species or varieties. The comparatively stout skeleton-spicules are a distinctive character so far as the Spongillidae known from Japan are concerned, but in most specimens some spicules can be discovered that are much more slender than the others. When the majority of the spicules are spiny it is usually the smooth ones that are the slenderest. It appears to be safe to say that at least some of the skeleton-spicules are always at least $\frac{1}{20}$ time as broad as long.

The difficulty of preparing an exact diagnosis of the species is increased by the fact that gemmules are very seldom produced.

In a series of many hundred specimens only two were found that contained these bodies and both of these were taken in a single haul of the net.

If only Phase III were to be considered, there can be no doubt that *S. clementis* would have to be regarded as a very distinct species closely allied to the species belonging to the genera *Pachydictyum* Weltner from Celebes and *Cortispongilla* Annandale from Palestine, both of which it resembles in its compact form, large and conspicuous oscula and unusually spacious and well-developed exhalant system. We have not, indeed, seen any specimen in which the central cavity connected with this system is so large or so regular as it appears to be in the only known species of *Pachydictyum*, while the skeletal cortex characteristic of *Cortispongilla* is either altogether absent or else represented by mere rudiments possibly not at all homologous. These rudiments consist of the interdigitating ridges to which a reference has been made above. Their skeletal support is consolidated in a manner strongly suggestive of the external consolidation of the skeleton that takes place in the Palestinian genus, and their frequent absence may be due in part to erosion of the surface of the sponge—a phenomenon also manifested in *Cortispongilla*. The peculiarities of this phase of *S. clementis* are, moreover, correlated with the fact that the sponge lives in comparatively deep water, attached to hard objects of small size (if it is attached at all), and on a bottom composed of sand or fine gravel, the particles of which are liable to be carried into its interior and can only be voided with great difficulty. The conditions also enter into the environment in which *Cortispongilla* is found, and probably occur in that of the habitat of *Pachydictyum*, of which nothing very precise is known. Notwithstanding, however, the apparent strong differentiation of the Phase III of *S. clementis* we have found some specimens in fairly deep water that are exactly intermediate between it and Phase II, and we can not correlate any differences in the structure of the skeleton or the form of the spicules with the differences usually so conspicuous in the external characters.

Phase II roughly corresponds with the specimens on which

the diagnosis of *S. clementis* was based, while Phase III is not far removed from those that formed the type of *S. yunnanensis*—so far as external characters are concerned,—but the supposed differences in the skeleton and the spicules are, as will be clear from what we have already said, by no means diagnostic of any one phase or variety.

S. clementis was described from Luzon in the Philippine Islands, while the type of *S. yunnanensis* were from Lake Tali-Hu in Yunnan, China. Otherwise the species is only known from Lake Biwa, in which it is abundant in situations not exposed to dessication, and from the settling-tanks of the Kyoto water-works, which are supplied from the lake.

Subgenus **Eunapius**, Gray.

The air-spaces on the gemmules of this subgenus have a very regular form and arrangement. They are relatively large, polygonal in cross-section and arranged in numerous concentric layers. The gemmule-spicules are as a rule more or less horizontal. The only species of this subgenus found in Japan is almost cosmopolitan.

Spongilla fragilis Leidy.

Pl. I, fig. 9.

1909, Annandale Annot. Zool. Japon. VII, P. 106, Pl. II, fig. 1.

The external appearance of this species is usually characteristic, for it forms flat layers or crusts without branches or conspicuous protuberances and has numerous small oscula, each of which is surrounded by a star-like figure produced by the main exhalant canals running superficially in a horizontal direction to the orifice. The colour is usually brown.

The skeleton is more compact than in *S. lacustris*. The skeleton-spicules are smooth, fairly slender and sharply pointed. There are no free microscleres. The gemmule-spicules are somewhat variable in form and may be either cylindrical or spindle-shaped in outline. They are always slender and relatively long and covered with short irregular spines.

The gemmules are either fastened together in groups that lie free in the substance of the sponge or else adhere in a single layer at the base. Each has a curved foraminal tubule that projects outwards or upwards through the pneumatic coat.

The following are the Japanese localities of the species:

Lake Noziri, Lake Aoki, Lake Nakatsuna, Lake Kizaki and Lake Suwa, Province of Shinano.

Tokyo.

Lake Biwa.

Lake Ogura near Kyoto.

Genus **Ephydatia** Lamouroux.

This genus is distinguished from all others by the following characters: —

1. There are as a rule no true flesh-spicules (free microscleres), but immature gemmule-spicules often lie loose in the parenchyma. Microscleres with more than one main axis are always absent.

2. The gemmule-spicules consist of a cylindrical shaft that bears a well-defined disk or rotule at each extremity. The two disks of each extremity are equal or at any rate similar; their margins are indented, denticulated or serrated.

Only one Japanese species, with two varieties, can be assigned to this genus, namely *Ephydatia mülleri* (Liebk.), an almost cosmopolitan sponge.

Ephydatia mülleri (Liebk.).

1909, Weltner, Brauer's Süsswasserfauna Deutschlands XIX, p. 186, figs. 318-320.

The sponge forms more or less flat growths that are often thickened and irregularly nodular in the central region.

It is never very massive and never produces slender branches. The skeleton is compact but fragile. Vesicular cells ("bubble-cells") are always abundant in the parenchyma.

In the typical form the skeleton-spicules, which are always

at least moderately slender and sharply pointed, are densely spiny in the middle region but smooth at the extremities. There are no free microscleres. The gemmule-spicules are short and bear large terminal rotules, which are deeply and irregularly indented round the edge. The shafts are very little, if at all, longer than the diametre of a single rotule; they are usually quite smooth. The rotules are flat.

The typical form of the species, though it is known to occur in Japan (Tokyo and neighbourhood), has not been found in Lake Biwa, in which the following variety is found abundantly.

var. ***japonica*** (HILGENDORF), nob. comb. nov.

1909. *Ephydatia japonica*, Annandale, Annot. Zool. Japon, VII, p. 119, pl. II, fig. 3.

This variety only differs from the typical *E. mülleri* in having skeleton-spicules that are as a rule quite smooth and bear at most a few minute and scattered spines on the central region. Sometimes the birotulate spicules are arranged on the gemmule in several tiers, and not infrequently they have one rotule distinctly larger than the other.

From *E. fluviatilis* auct. the variety only differs in the presence of bubble-cells in the parenchyma and in the shortness of gemmule-spicules, while from *E. meyeni* (CARTER) only the latter character serves to distinguish it.

There has been much confusion between *E. fluviatilis* and *E. mülleri*, and the races of *E. fluviatilis* called *syriaca* and *himalayensis* described by Topsent and Annandale respectively seem to render the recognition of the two species more difficult and more uncertain.

E. mülleri is widely distributed in Europe and N. America and is represented in Lake Baikal in northern Asia by a form that seems to be more than an aberrant phase or variety. The variety *japonica* has been found in the Potomac River on the Atlantic side of N. America. In Japan it has been reported from Tokyo and Lake Aoki, Province of Shinano. In Lake Biwa it is abundant, and we have also seen specimens from following localities :—

Yanaidzu, Province of Rikuzen.

Lake Nakatsuna, L. Kizaki and L. Suwa, Province of Shinano.

A small pond at Yodo, and Osawa Pond near Kyoto.

At Okayama (Province of Bizen) and Hiroshima (Province of Aki) it has been found in the leading pipe of the city water-works.[1)]

Genus **Heteromeyenia**, Potts.

Heteromeyenia kawamurae Annandale, sp. nov.

Pl. II, figs. 3.

This sponge is known to me only from two somewhat degenerate specimens taken on a single occasion. It is impossible, therefore, to give a detailed description of its external form that would likely be of permanent value. All that can be said is that the type-specimen appears to have consisted of a thin film giving rise to short anastomosing branches and that the colour in life was bright green.

The skeleton is very fragile. Its fibres are well-defined but slender and lacking in horny matter. They form a loose, irregular network.

The skeleton-spicules are small, relatively slender, sharply and gradually pointed, smooth or with a few minute scattered spines.

The free microscleres are minute, relatively very slender, irregularly spined and often bearing a few relatively long spines near the middle. These spicules are very scanty. The gemmule-spicules are not so strongly differentiated into two types as in some species of the genus. Indeed, there is little difference except in point of actual length. The shafts of the shorter spicules are, however, as a rule slightly stouter relatively than those of the larger ones. In both cases the shafts are straight, rather slender and either smooth or armed with but a few scattered spines of relatively large size. In the shorter spicules the shaft is about 3 to 5 times as long as the diameter of one rotule, while in the longer ones it may be as much as 10 times, though sometimes not

1) cf. Parker: Proc. Zool. Soc. London, 1913, Part IV, p. 973–976.

more than 7 times, as long as the rotule. It barely projects beyond it. The rotules are flat or nearly so in both cases. Their margins are deeply and irregularly serrated but the individual serrations are angular and rarely curved.

The gemmules are small, somewhat flattened and as a rule elliptical as seen from above. They are scattered in the interstices of the skeleton. The pneumatic layer is moderately thin. The foramen is protected by a stout curved tubule which expands somewhat at the distal extremity but is totally devoid of process.

Length of skeleton-spicule (average) .....0.296 mm.
Transverse diameter of skeleton-spicule (average)...0.011 mm.
Length of shaft of shorter gemmule-spicule (average)0.042 mm.
Length of shaft of longer gemmule-spicule (average) 0.062 mm.
Greatest diameter of gemmule ..... 0.86 mm.

Type. In the Biological Station at Ôtsu; a schizotype in the Indian Museum, Calcutta.

Locality. Ôtsu, L. Biwa (coll. T. KAWAMURA): Oct. 7, 1914.

I have much pleasure in naming this interesting species after T. Kawamura, my collaborator in other parts of the present paper, who discovered the only known specimens. *H. kawamuraé* is closely allied, in my opinion, to *Heteromeyenia* (''*Carterius*'') *latitenta* (POTTS) from North America. The most striking difference lies in the structure of the foraminal tubule of the gemmule—a feature which is, however, regarded by many others as of generic importance.

II. Geographical.

The distribution of the different species of Spongillidae in Lake Biwa itself will be discussed in the third section of this paper, as it is essentially a bionomical rather than a geographical question. Precise data are not yet available for a discussion of the distribution of the Spongillidae in the Japanese Archipelago.

Of the seven species known from Lake Biwa two are as yet known only from the Main Island of Japan, namely *Spongilla semispongilla* (ANNANDALE) and *Heteromeyenia kawamurae* ANNANDALE.

Both of these species have close Holarctic affinities, but the *Heteromeyenia* is perhaps more closely related to American than European forms; no species of the genus is yet known from Continental Asia.

It is possibly no more than fortuitous that while *H. kawamurae* is only reported as yet from Lake Biwa, *S. semispongilla* has been found also in Kasumi-ga-Ura on the Pacific coast of the Island, for the *Spongilla* is abundant wherever it occurs, whereas the *Heteroeyenia* is apparently rare.

One species (*Spongilla aspinosa*) has been found only in Lake Biwa and in a single locality in North America, if it be not identical with *S. sinensis* from Su-chau in Eastern China, with which it is at least closely allied. The species is evidently a rare one, or rather a very "local" form, and it is probable that it will be found in other countries also.

Three species are cosmopolitan, or at any rate have practically universal distribution in the Holarctic Zone, if not beyond its borders. They are *Spongilla lacustris*, *S. fragilis* and *Ephydatia müller*i. Varieties of the first of these are known from India, Malaysia and possibly South America, as well as from many parts of Europe, N. America and northern Continental Asia; *S. fragilis* occurs in Australia as well as in the Holarctic Zone and is represented in Tropical Asia and South Africa by closely related forms, while *E. müller*i is common in N. America and Europe and is replaced in India and Malaysia by *E. meyeni* (CARTER), which is perhaps no more than a subspecies. The variety *japonica* has hitherto been found only in Japan and in N. America, whence it has been recorded from a single locality, namely the Potomac River. Its distribution is therefore apparently somewhat similar to that of *S. aspinosa*. The seventh species (*Spongilla clementis*) has been found also in the Island of Luzon in the Philippine Archiperago and in south-western China.

The distribution of the seven species, therefore, casts, so far as it is known, but little light on the origin of the fauna to which they belong. All that we can say is, that the species are mainly Holarctic, exhibiting perhaps close affinities with North American

than with European[1]: that there is apparently an endemic Japanese element among them ; and that one form is probably of eastern tropical origin.

A consideration of the genera and subgenera does not lead to any definite conclusion. *Spongilla* and *Ephydatia*[2] are cosmopolitan, while *Heteromeyenia* is mainly Nearctic. Two of the three subgenera into which *Spongilla* may be conveniently divided (viz. *Euspongilla* and *Eunapius*) are co-extensive in range with the genus, but *Stratospongilla*, the third subgenus, is mainly Ethiopian and Oriental and to a large extent tropical. Single species occurs, however, in Fiji and in South America.

On the whole, therefore, the genera and subgenera of Spongillidae represented in L. Biwa would merely suggest that the fauna of which they form a part is of somewhat mixed origin, mainly Holarctic, with perhaps Nearctic affinities, and with a certain endemic element, but also containing an element derived from the south and possibly of Oriental origin.

III. Bionomical.

Lake Biwa is partially separated into two regions by a pair of opposed promontories. These regions differ greatly in size and in the nature of the environment they offer to animal life. The smaller of the two is known locally as the South Lake, the larger as the North Lake. These names may be used conveniently if it be understood that there is a comparatively broad passage between the two "lakes." The South Lake is nowhere more than 30 Japanese feet (about 9 meters) in depth; the bottom is for the most part muddy, and there is a very profuse growth of waterweeds. The North Lake, which is far larger than the other, has, on the other hand, a depth of from 200 to 320 Japanese feet (60 to 97 meters) over the greater part of its area. The deepest depressions have a bottom of fine mud, and sponges are apparently

1) The sponges of the greater part of northern Continental Asia are still very imperfectly known.

2) Further study does not bear out the view that *Ephydatia* is unusually predominant in Japan (see Annandale, Annot. Zool. Japon., VII., p. 105).

absent from them, but a great part of the marginal region, to a depth of at least 150 feet in places, has a bottom of very fine gravel and coarse white sand, which does not support more than a scanty growth of weed. In both "lakes" there are places where the margin is stony.

The sponge-fauna of the two "lakes" differs considerably, though there is probably no species confined to either. Generally speaking, that of the South Lake is much the richer, *Spongilla lacustris*, *S. semispongilla* and *Ephydatia mülleri* var. *japonica* being the most abundant forms. *S. clementis*, on the other hand, is characteristic of the North Lake; it is only found in very pure water and avoids positions liable to complete or partial dessication.

It is probable that all the species in the fauna except *S. clementis* can live in water from 2 feet to at least 20 feet deep, but they are most abundant, in the cases in which they are abundant at all, in less than 10 feet of water. *S. clementis* usually lives at depth of from about 6 to about 150 feet, but has been found on Seta railway bridge and in the Kyoto water-works near the surface.

S. fragilis is most usually found attached to sticks and twigs that have fallen into the water or to the stem of reeds, but it also occurs on stones. In a small lake communicating with the main body of water at Komatsu on the western side, it is particularly common on reeds, often growing together with *S. lacustris*. The latter sponge is, however, perhaps most often found on stones near the edge and on the piers of landing-stages, particularly at the south end of L. Biwa. *S. semispongilla* grows both on stones and lightly attached to weeds that sway freely in the water, such as *Nitella*, *Myriophyllum*, etc. *E. mülleri* var. *japonica* occurs on stones, on dead bamboos and on other bodies that afford a smooth surface of some area. *S. clementis* spreads itself on the piers of landing-stages and the pillars of bridges, whether they be of wood or stone, and in its massive form is attached to the shells of molluscs and to small pebbles.

In some cases a definite correlation can be established between the nature of the object to which the sponge is attached and its external form, though in most species the general appearance of

the sponge is characteristic. No two species growing side by-side in the same environment are liable to be confused, but often the same species may assume a very different appearance in different environments, sometimes even in an environment that seems, at any rate on a superficial examination, to be homogeneous. In this respect *S. clementis* is the most interesting sponge found in L. Biwa, but it may be conveniently considered from the point of view after others in which the environmental variation is less strongly marked.

S. semispongilla, as has already been pointed out, occurs in two very distinct phases, one of which is a mere film of very limited area, while the other forms a compact, shrub-like growth. The dwarf phase has been found only on the flat transverse leaves of water plants, but the bushy phase grows either on stones or on water-weeds with small leaves. A very profuse growth occurred in October and November, 1915, on stones near the edge of the lake close to the Ôtsu station. The sponge had much the appearance of the compact tufts produced by many rock-loving plants. *S. lacustris* produces when encrusting reed-stems much more delicate branches than it usually does when growing on stones and posts. The growth of *S. fragilis* on stones is always feebler than on cylindrical bodies. In the former position it is often found on the lower or protected surface and is thus the only sponge in the lake-fauna that shows any tendency to conceal itself either as a protection against sunlight, against mud, or against enemies. In some lakes (*e.g.* the Lake of Tiberias in Palestine) this tendency is well marked in the case of most sponges, so that a superficial examination would seem to indicate an almost complete absence of sponge-fauna, but in L. Biwa such species as *S. semispongilla*, *S. lacustris*, *S. clementis* and less commonly *E. mülleri* var. *japonica* are very conspicuous objects in calm weather. The absence of suspended silt in the water is probably responsible to a very considerable extent for this striking feature.

It is probable that the three phases of *S. clementis* are correlated, or may be correlated, in all cases with environment, but Phase I and Phase II are sometimes found growing together, and indeed

passing from the one to the other, on the same pillar. Phase I may, therefore, be no more than a young form of Phase II, but in places where a strong current passes the point of attachment it is probable that the thinner phase persists.

A remarkable variation in colour, correlated to some extent at any rate with environment, occurs in these two phases. On the stone pillars of Seta railway-bridge, which is largely built of iron, the sponge has invariably a yellowish tinge, while on the wooden pillars of a landing-stage only a few hundred yards away it is dark grey or almost black. The colour in the latter case is due to minute blackish particles in the cells of the parenchyma, but their nature has not been investigated. On the wooden piers of Katata landing-stage, on the other hand, the sponge varies from almost white to bright green in colour and is sometimes greyish and sometimes brownish. The green colour is due to symbiotic algae and may be brought about by infection from *S. lacustris* or *S. semispongilla*. It is noteworthy that the algae are confined in the more massive specimen of *S. clementis* to the superficial parts of the sponge, whereas in thin encrusting examples they permeate the whole organism except the dermal layer.

The correlation between external form and environment is much more definite in Phase III. of *S. clementis*. Here the small but massive growths are produced only on bodies too small to admit of a spreading out of the sponge, and for the most part capable of movement in comparatively deep water. In most cases these bodies are the shells of living molluscs, but sponges of the same type are also found on small stones. We will discuss the precise nature of the relation between the sponge and the molluscs later. Here we may point out again (see page 10) that the strong development of the exhalant system and the large calibre of the oscula and the main exhalant canals is correlated with the comparatively large size of the particles of silt or gravel by which the sponge is liable to be overwhelmed, and is exactly comparable to the same phenomenon in the Palestine species *Cortispongilla barroisi* (Topsent).[1] This species lives in a lake (the Lake of Tiberias) the

1) Journ. As. Soc. Bengal, (n.s.) IX, p. 67, Pl. II, Fig. 1, Pl. IV, Fig. 4 (1913).

greater part of which has a muddy bottom, but is found only in one part of the lake, where the mud is washed away by the currents of the R. Gordam passing through the lake, and sweeping clean a bed of fine gravel not unlike that on which Phase III of *S. clementis* is commonly found in L. Biwa. In both the species minute stones are found imbedded in the sponge and covered with a horny laydr, evidently secreted to protect the soft parts from contact with them. This proves not only that the sponge engulfs and has difficulty in expelling such particles, but also that their presence is undesirable.

Although Phase III of *S. clementis* is abundant on the Corbicula-beds of the North Lake, we did not find it in its full development on them in the South Lake. On the beds in the latter, small thin encrusting specimens were, however, occasionally seen on Corbicula-shells. The fact is noteworthy, because some of the richest of the beds in L. Biwa lie close to Seta bridge, on which the less massive phases of the same sponge grow luxuriantly. The absence of the massive phase in this region may be correlated with the greater impurity of the water in the neibourhood of very luxuriant aquatic vegetation. It is not wholly due to the more muddy character of the bottom, for the sponge is very common off Hikone and in the channel between the Island of Okinoshima and the main land, in both of which places the bottom is of a somewhat mixed character composed both of larger and finer particles.

The colour of the third phase of *S. clementis* varies somewhat on different kinds of bottom. When the bottom consists of coarse sand or fine gravel it is almost white, while a mixture of sand or gravel with fine mud produces a greyish tinge. If grey sponges are kept, however, for a few days in a vessel of clean water they become quite white, thus showing that the grey tint is due to the absorption of microscopic particles of mineral matter.

Seasonal variation is a marked feature of several of the sponges of L. Biwa. Only its grosser manifestations have as yet been investigated, but the cytological changes promise a rich field for inquiry, which we hope will not be neglected in the future.[1)]

1) cf. Weltner: Arch. Naturg. Berlin, LXIII, P. 273 (1907).

In summer the phase of *S. clementis* that occurs on stones in the lake is a somewhat peculiar one, more massive than is usual in the species and having large round oscula, the main exhalant canals connected with which are usually of small calibre and somewhat deeply buried. The surface is often somewhat nodular, but there are no branches. Towards the end of summer or in early autumn the sponge begins to increase its superficial area by spreading out in a thin layer. At the same time slender, elongate branches begin to grow out from the surface, while the oscula formed in the peripheral, younger parts are smaller, and the canals opening into them more superficial than in the more massive central region.

Changes of a similar nature, but much less pronounced, occur in all the commoner, shallow-water species so far as the external appearance of the sponge is concerned, and it is possible that the dwarfed phase of *S. semispongilla* is no more than an arrested summer form.

It is in *S. clementis*, however, that the most remarkable seasonal change has been observed. In this species it is the structure of the skeleton rather than the external form that is affected, the winter growth having a much more diffuse and open network than that produced in summer and autumn. In many sponges of this species the change seems to be gradual and specimens are to be found, especially in the latter part of autumn, that have the laxer skeletal structure throughout their substance. Specimens also occur, however, in which the change is quite abrupt and the sponge can be seen even by the naked eye to consist in vertical section of two quite distinct layers, the uppermost of which has the skeleton-fibre much more widely separated than the lower layer (Pl. I, Fig. 8). Such sponges have only been found in winter. As sexual reproduction takes place freely in this species from about the middle of September to the middle of October, it seems probable that the majority of the parent sponges die and disintegrate after breeding, that the young sponges which grow up from larvae in autumn do so with considerable rapidity and have a delicate skeleton consisting of comparatively few spines, and that the sponges which do not

breed or which survive breeding continue their growths on similar lines to their or their neighbours' autumnal offspring.

It is not possible to lay down any definite rules as to the dates on which these seasonal changes occur. It is probable, indeed, that they are influenced not only by actual temperature, which of course varies from year to year, but also by other factors in the environment and possibly by individual idiosyncrasy on the part of the sponge. Generally speaking, however, it is clear that, just as the seasons are somewhat later in Japan than they are in northern and central Europe, so the fresh-water sponges are somewhat later in attaining their full development, which rarely occurs in L. Biwa before September or the latter part of August.

This lateness of growth is illustrated in particular by the production of gemmules, if a general statement is permissible—for here again other questions but those of temperature and season intrude themselves. All the species, moreover, do not produce gemmules simultaneously. Speaking quite generally, it is safe to say that *S. lacustris* is as a rule the latest to do so, and *S. semispongilla* perhaps the earliest. We noticed in the autumn of 1915 that gemmules were already being produced commonly in the latter species as early as the beginning of October, whereas as late as the beginning of November there was as yet no rudiment of them visible with the aid of a hand-lens in *S. lacustris*. Another specific difference of the same kind was demonstrated in a remarkably clear manner in the small lake at Komatsu on the west side of L. Biwa at the latter date. In this lake, which is connected with the main body of water by a narrow channel, we obtained numerous specimens in which either *S. lacustris* or *S. fragilis*, or the two species together, coated the stems of reeds (Pl. I, Fig. 10). While in *S. lacustris* there were no gemmules and vegetative growth was evidently still active, *S. fragilis* invariably contained a large number of these reproductive bodies and in some cases was already completely degenerate, the sponge-substance in extreme examples having almost completely disappeared, leaving a pavement-layer of gemmules with remains of the bare skeleton clinging to the reed-stem.

In *S. clementis*, remarkable in this respect as in so many others, the production of gemmules does not appear to be a seasonal event, but to be brought about by the physiological changes, as to the nature and cause of which we have as yet no precise information. All that we can say is, that out of many hundreds of specimens of this species, only two which were taken in a single haul of the net in the first week of October contained gemmules; that both were attached to living shells of *Corbicula*, and that in both of them the sponge was completely degenerate.

As to sexual reproduction in the Spongillidae of L. Biwa we have little precise information, except that larvae are produced in great abundance by *S. clementis* in the latter part of September and the first half of October, and more sparingly at the beginning of November. It is probable that this is the case also in other species as there appears to be a somewhat luxuriant new growth, in particular of *S. semispongilla*, at this time of year.

The bionomical relations between fresh-water sponges and other organisms are still for the most part imperfectly understood. In L. Biwa a small Oligochaet worm of the genus *Chaetogaster* is not uncommon in the canals of *S. semispongilla* growing on weeds in the South Lake. Apparently it avoids *S. fragilis* in close proximity and, unlike *Ch. spongillae* ANNANDALE[1] (which lives only in dead or dying sponges), is found in specimens in full vegetative vigour, even before the appearance of gemmules. S. Matsumura has described an interesting Heteropteron (*Aphelocheirus kawamurae* MATSUM.)[2] as yet found only in a cavity on the surface of the semi-massive phase of *S. clementis* collected at Seta, while we noticed a suctorial Protozoon (*Sphaerophrya sp.*) abundant on the dermal membrane and a small Gammarid in the canals of the massive form of the same species gathered off Komatsu in November, 1915. This phase of the species, although it sometimes grows on small stones, is so frequently attached to the shells of molluscs of the genera *Corbicula*, *Nodularia*, *Melania* and *Vivipara* that it is known to the fisherman at several places as *Kai-no-kuso*, or molluscs' excreta.

1) Journ. As. Soc. Bengal. (n.s.) II, p. 189 (1906).
2) Entomol. Mag. Japan, Vol. I, No. 3, p. 104 (1915).

The relations between the sponge and the molluscs to which it attaches itself are clearly those of parasite and host. The Lamellibranchs on which we observed the phenomenon most commonly were *Corbicula sandai* and *Nodularia reiniana*. Both these species live with the blunter anterior end of the shell buried in the sand and the more pointed posterior extremity protruding therefrom. It is naturally to the latter extremity that the sponge attaches itself. Its growth is always at first restricted to a single valve and as long as the mollusc can prevent it, by the currents of water it ejects from time to time, from spreading to the other shell, it is unable to injure the animal greatly, except in so far as it may impede its movements. As the sponge is often several times as large as the shell, it may possibly, however, cause inconvenience in this respect. Sometimes, especially when the host is a relatively large *Nodularia*, a cavity is formed near the base of the sponge where it arches over the siphonal orifice of the mollusc, and we have observed specimens in which this had occurred and in which larvae, doubtless produced by the same sponge, had settled down and undergone their metamorphosis on the other valve of the shell. Sooner or later, at any rate in the case of *Corbicula*, the sponge manages to bridge over the space between the two valves, and then the fate of the mollusc is sealed. We have, however, observed an individual of *C. sandai* in which the siphonal orifice was completely covered by the growth of a sponge about three times as large as the shell, but which yet remained not only alive but capable of movement. Doubtless its inhalation aud exhalation of water took place through the sponge's canal system. This condition of affairs could not persist for long, as the sponge secretes a very thick horny membrane at its base if irritated.

The two other molluscs on which *S. clementis* most commonly grows are *Vivipara sclateri* and *Melania multigranosa*. In the case of the former, in which the natural position of attachment is the upper surface of the largest whorl ; but in the *Melania*, which as a rule holds its shell transversely, the position is near the middle of the upper surface. In both cases the sponge spreads first over the upper surface of the shell and then gradually round its sides, and

finally over its lower surface, thus at last completely enclosing it. We have noticed many specimens of *Melania* which still remained alive and able to progress with some speed, although their shell were completely covered and the living parts of the animal could only be extended through a small aperture in the sponge. Molluscs in this position moved with a curious jerky action, bearing a sponge-mass several times as large as themselves. As in the case of the Lamellibranchs, however, the mollusc is finally overwhelmed. In both cases, the sponge, as the body of its host decays, spreads out over the inner surface of the shell, doubtless absorbing the decaying body as it does so. *S. lacustris* in L. Biwa sometimes attaches itself to living individuals of *Vivipara* and *Melania* and grows round them in the same way (Pl. I, Fig. 3), and a similar phenomenon has been observed in the case of both of Spongillidae and of Suberitidae in India[1] and elsewhere.

The free spherical specimens of *S. clementis* may originate in one of the two ways: either they may have broken loose from pebbles or shells, or they may have completely covered the hard bodies to which they were originally attached. In the former case the original point of attachment is indicated by a closer reticulation of the superficial skeleton. We have found a perfectly free spherical specimen, however, that was less than 1 cm. in diameter, had no hard extraneous core and no such differentiation of the skeleton, and it seems possible that the sponge may have been free from a very early stage of growth.

The largest specimen of *S. clementis* that we found attached to molluscs were some that we took off Komatsu in November, 1915, on the comparatively large shells of *Anodonta calipygos*. They were intermediate in form between Phase II and III of the species. With them we found similar specimens spreading irregularly over a bottom of small stones. We have already noted that at Seta the sponge occasionally attaches itself to *Corbicula*-shells without being able to form more than a fine crust of small dimensions.

1) Annandale, Mem. Ind. Mus. V, p. 41 (1915).

Summary.

I. We have examined specimens of seven species of Spongillidae from L. Biwa, of which one (*Heteromeyenia kawamurae*) is described above as new.

II. The majority of the species are widely distributed Holarctic forms, but one (*Spongilla clementis*) is probably of Oriental origin.

III. The distribution of the species in L. Biwa is correlated with definite differences in environment, and several forms, more particularly *S. clementis*, differ considerably in different surroundings.

IV. The sponges of L. Biwa attain their full growth as a rule somewhat later in season than those of Europe. The production of gemmules is also somewhat retarded, but the exact season differs slightly in different species. No form, so far as we are aware, produces gemmules at the beginning of the hot weather.

V. *S. clementis* gives shelter on its surface or in its canals to several incolae of different groups, but its precise relation with them are still obscure. It often grows on the shells of several Gastropods and Lamellibranchs and finally overwhelms and probably absorbs the body of the molluscs, the relationship in this case being that of parasite and host.

Ōtsu, December 1915.

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N. ANNANDALE AND T. KAWAMURA

THE SPONGES OF LAKE BIWA.

PLATE I.

Explanation of Pl. I.

Fig 1. *Spongilla lacustris* encrusting stone. L. Biwa, July 1915. ×$\frac{2}{3}$

Fig. 2. „ with vertical branches. L. Biwa July 1915. ×$\frac{1}{2}$.

Fig. 3. „ catching living *Vivipara sclateri*. L. Biwa, July 1915. ×$\frac{2}{3}$

Fig. 4. *Spongilla semispongilla* growing on stones. L. Biwa, Sept. 1915. ×$\frac{2}{3}$

Fig. 5. *Spongilla clementis*. Phase I, a thin film on a wooden pillar. L. Biwa, Oct. 1915. ×$\frac{2}{3}$

Fig. 6. *Same*. Phase II, a more massive growth on the same. L. Biwa, Oct. 1915. ×$\frac{2}{3}$

Fig. 7. *Same*. Phase III, a spherical growth on the shell of living *Nodularia reiniana*. L. Biwa, Oct. 1915. ×$\frac{2}{3}$

Fig. 8. *Same*. A vertical section showing abrupt change in skeletal structure. Dec. 1914. ×1

Fig. 9. *Spongilla fragilis* covering an old bamboo stick. Oct. 1914. ×$\frac{3}{4}$

Fig. 10. *S. lacustris* and *S. fragilis* growing together on the stem of reeds. Small lake at Komatsu, Nov. 1915. ×$\frac{3}{4}$

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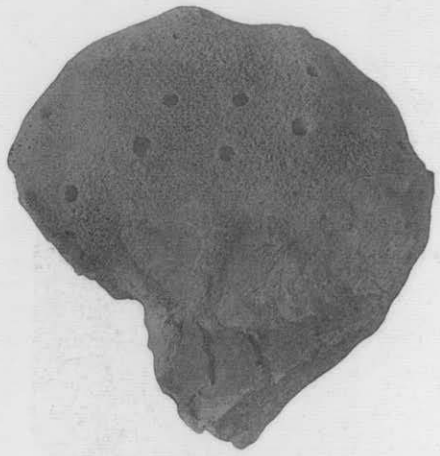

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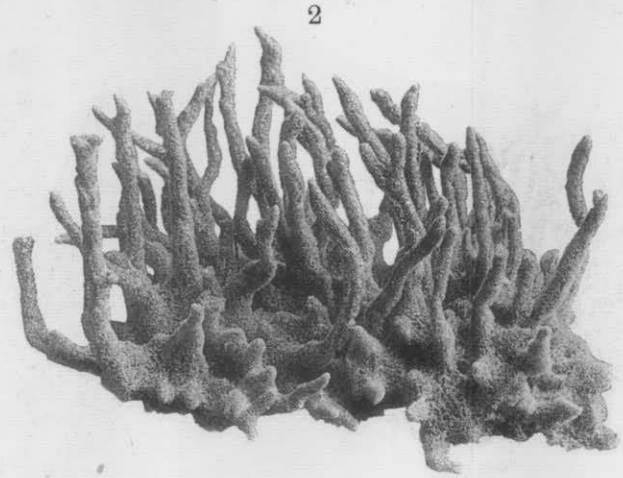

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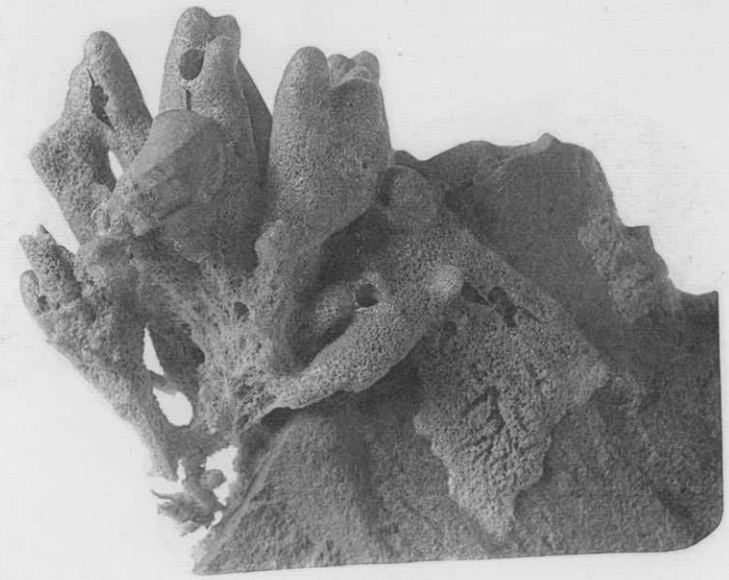

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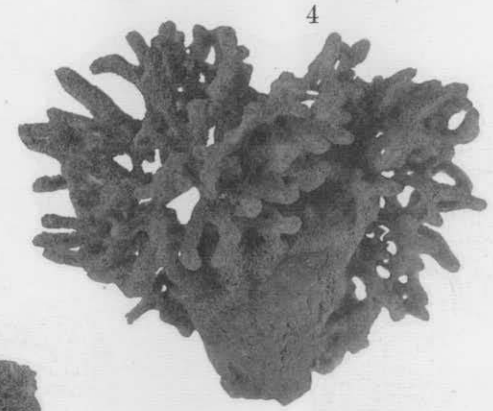

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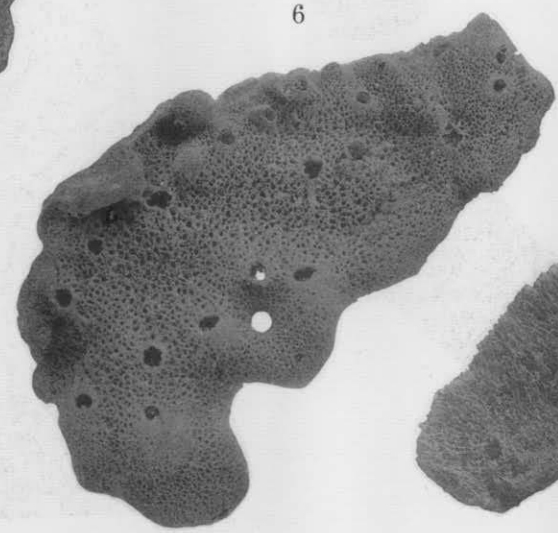

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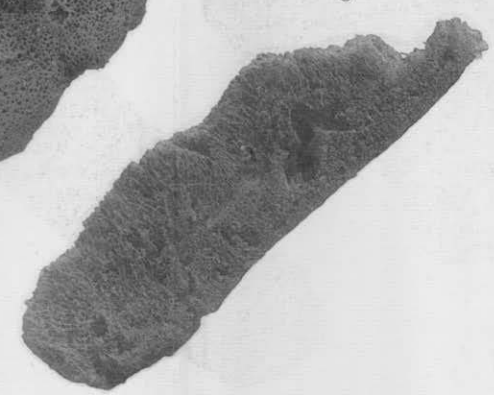

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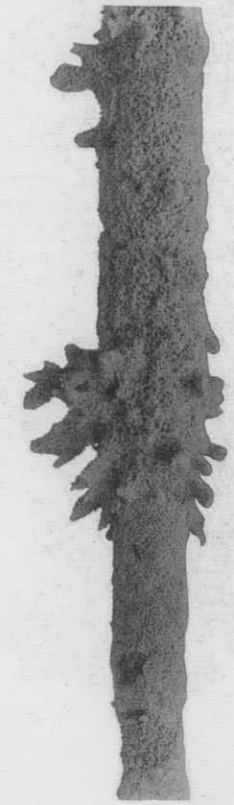


Nelson Annandale and Tamiji Kawamura: The Sponges of Lake Biwa.

PLATE II.

Explanation of Pl. II.

Figs. 1, 1a. *Spongilla aspinosa.*

Fig. 1. Skeleton-spicules. ×300.

Fig 1a. Microscleres. ×300.

Figs. 2, 2a, 2b. *Spongilla clementis.*

Fig. 2. Gemmules and skeleton-spicules. ×50.

Fig. 2a. Skeleton-spicules. ×300.

Fig. 2b. Gemmule-spicules. ×300.

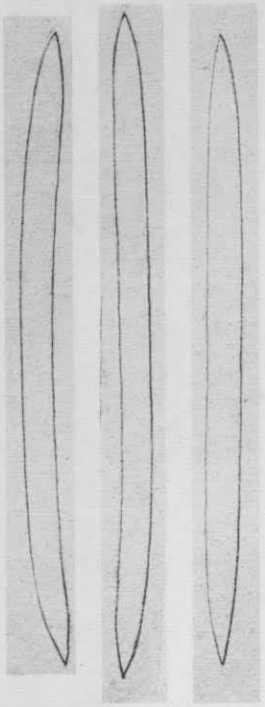
Figs. 3, 3a, 3b, 3c. *Heteromeyenia kawamurae.*

Fig. 3. Gemmule. × 70.

Fig 3a. Skeleton-spicules. ×300.

Fig. 3b. Free microscleres. ×300.

Fig. 3c. Gemmule-spicules. ×300.



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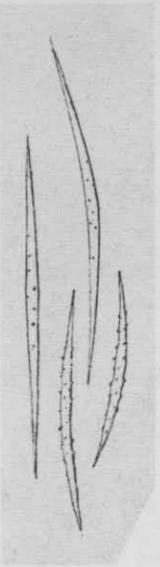

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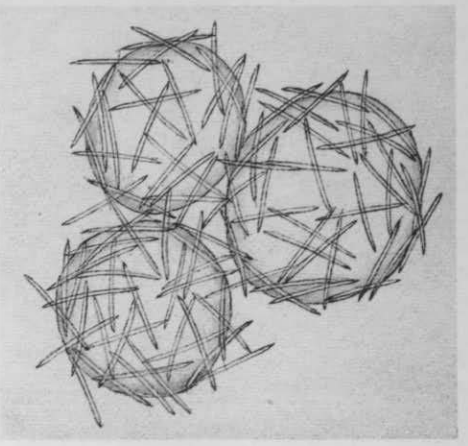

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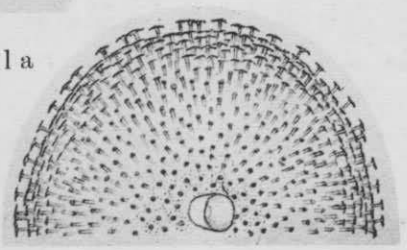

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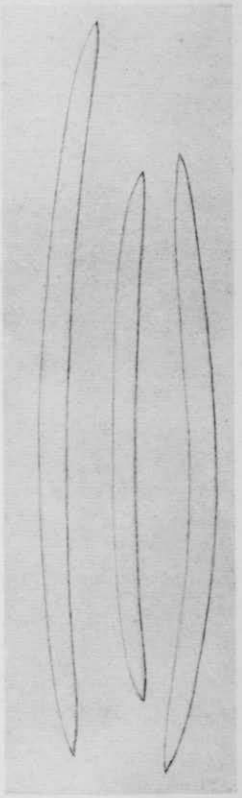

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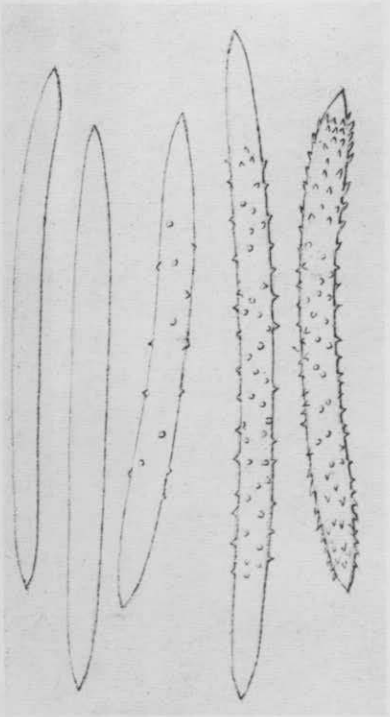

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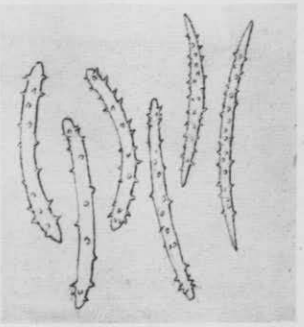

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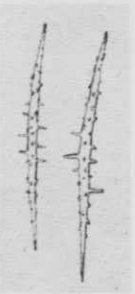

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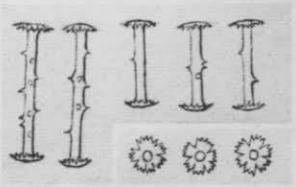

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