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The Freshwater Branchiopoda of Japan. IV*
Genus *Daphnia* of Japan
2. Local Races of Japanese *Daphnia*

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With Plates XI-XIV and 3 Text-figures

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Introduction

The present paper deals with the local races of Japanese species of *Daphnia*, especially those of *D. pulex* and *D. longispina*. In the first chapter is considered the geographical distribution of the genus in Japan in comparison with that in continental Eastern Asia. A comparative study concerning the difference in body shape among various races forms the second chapter, while the third chapter comprises some ecological notes on the habitats with reference to the local variation. The general characteristics of the local races of Japanese *Daphnia* are discussed in the last chapter, in which the difference between Japanese and foreign races of the same species is given.

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Geographical Distribution

As many as 450 plankton samples from 175 different localities were examined. They cover almost all main Japanese lakes and include also about 40 small ponds and periodic pools, ranging from Shimushir of the North Kurile Islands to Formosa and Korea (25°00′–50°50′ n. lat. and 121°50′–156°30′ e. long.). In some samples from Shikoku no species of *Daphnia* was found.

So far as this material is concerned, *Daphnia longispina* seems to be most widely distributed all over Japan. The range of the occurrence of *D. cucullata*, however, seems to be rather local, being restricted chiefly to Hokkaidô (UÉNO 1933a). According to RYLOV (1932), *D. longispina* s. str. is distributed in Russian North Sakhalin; we have at present only one record of this species from the southern half of this island.

On the other hand, the Cladoceran fauna of both Manchuria and the eastern parts of China is very dissimilar to ours. There is found a daphnid quite different from our representatives, namely: *Daphnia carinata* KING (cf. DECKSBACH 1926, 1930). Besides this M-daphnid, we have no species of P-daphnids in Continental Eastern Asia except a record of *D. pulex* from the Yangtsekiang district (UÉNO 1932b).

The distribution of the genus *Daphnia* in Eastern Asia is summarized in the following table.

Table I

Distribution of *Daphnia* in Eastern Asia

Name of species \ Districts		Japanese Is. (Honshu and Kyushu)	Hokkaido	Kurile Is.	Sakhalin	Korea	Manchuria	Mongolia	Eastern China
M-series	*D. magna*	.	.	.	.	.	.	.	+
	D. psittacea	.	.	.	.	+	.	.	.
	D. carinata	.	.	.	.	.	+	+	+
P-series	*D. pulex*	+	.	+	.	.	.	.	+
	D. longispina	+	+	+	+	+	.	.	.
	D. cucullata	.	+	.	.	.	.	.	.

There is seen a rather distinct regional variation of *Daphnia*-fauna in the insular and continental parts of Eastern Asia, only a cosmopolitan eurythermal species, *D. pulex* occurring in both the regions. The *Daphnia*-fauna of the Japanese Islands is composed only of the cosmopolitan elements of northern origin, and the range of cold water forms is chiefly limited to the northern half of the country.

Local Variation

As is well known, the races of *D. longispina* especially of pelagic *hyalina* in Central European lakes show in summer external appearances characteristic to each lake, while in winter these different forms reassume the common round-headed appearance. Therefore, it must be admitted that the differences found among various local races must be attributted partly to seasonal differences. Consequently in the comparative study of many Japanese races, I have made sketches of summer forms as accurate as possible.

A. The series of *Daphnia pulex*

The local variation of this species is very slight, the most remarkable variation being found in the length of the spine. In regard to this character, all the Japanese races of *D. pulex* may be divided into two main types, one having a long spine which is often turned upwards and the other having a considerably short spine or often entirely lacking it. Younger individuals, however, have always a uniform appearance and are always divided with a long spine which is turned slightly upwards. The form with a very short spine is referred to the

Table II

Examples of the sizes of local races of *Daphnia pulex* of Japan (in μ)

Locality	Province	Date	T	A	B	A+B	V	H	S	Number of anal spines	Fig. (Pl. XII)
A pond	Shimushir	18/8/31	3434	190	494	684	2750	2375	760	.	
Madachi-numa	Mutsu	7/8/27	1495	85	220	305	1190	885	200	.	3
Uemura-Oike	Shinano	26/8/29	1372	100	152	252	1120	730	0	.	1
,,	,,	,,	1276	68	68	136	630	400	85	.	
Kojoro-ike	Ômi	22/11/31	1530	136	204	340	1190	900	24	9	2
Hirosawa-ike	Yamashiro	24/ 4 /26	1785	120	220	340	1445	1054	510	10	7
A pool near Kyoto	Yamashiro	-/ 5 /29	1850	—	—	—	—	1150	390	.	
Biwa-ko	Ômi	6/10/26	1530	85	255	340	1190	985	290	.	
,,	,,	23/ 7 /32	1836	204	136	340	1496	1140	300	12	4

series of *obtusa* KURZ. The size of this form varies greatly, T ranging from 1000 to 2300, S being from c. 1/24 of T to zero. The head-profile of the sexual females often shows a strong concavity, as seen in *cavifrons* G. O. SARS of *D. longispina*. The form is probably identical with *middendorfiana* LILLJEBORG.

All the other forms have long spines; T ranges from 1300 to 1900; A+B is always 1/3~1/4 of V, and S is about 1/4~1/5 of T; $\angle\beta$ often attains 10°, and in certain ephippial females it is often −20°.

The pellucidity is remarkable in the races of larger and deeper ponds, and when they appear in brown water ponds of dystrophic nature, they are yellowish or reddish brown in colour. When they occur in shallow and strongly contaminated ponds or pools, they are quite dirty and brownish red. The races living in clear water, such as those of Biwa-ko (*pulex pulex*) or of Uemura-Oike (*pulex obtusa*), are extremely hyaline. The habitats of different races will be dealt with in more detail in a later chapter.

The variation in the number of combs at the base of the terminal claws of the post-abdomen has been noticed by many workers. GRESE (1914) distinguished three types of combs in a population of *D. pulex* in Glubokoje near Moscow: *pulex*-type, *pulex-longispina*-type and pure *longispina*-type. Some great variations in size and in the number of bristles in both distal and proximal combs are also noticed in my material, but such remarkable differences as shown by GRESE are not seen. The number of bristles in both the combs is as follows: 5+6, 8+7, 9+6, 10+5 or 12+6; it varies more in the proximal comb than in the distal. It is also of interest that the series of minute thorns on the concave margin of the claw is more slightly developed in the animals living in large and clear lakes or ponds than in those found in small and contaminated waters, although no distinct differences can be seen in their combs.

Of many races examined, the one living in Biwa-ko (Lake Biwa) is ecologically a very peculiar form which is probably a heritably fixed biotype and represents so far a race endemic in this lake. This is a rather large *Daphnia* with an extremely hyaline broad valve and with well-developed combs on the terminal claws of the post-abdomen. The head is relatively short, about 1/3 of V, but rather broad; $\angle a$ is more than 50°, with rather prominent and bluntly pointed rostrum; in certain older individuals the crest is slightly developed; the profile is slightly concave; the eye is small but with rather large crystal lenses, the pigment spot being very small. The dorsal and ventral outlines of the valve are strongly arched, the ventral free margin being almost bare. H is about 2/3 of T. The spine is straight, being about 1/5 of T, and is nearly parallel with the logitudinal axis of the body; in younger individuals it is turned slightly upwards. The post-abdomen has about 12 marginal long anal spines; the terminal claws are long and curved, and are provided with two combs at the base, of which the distal comb is composed of 6 large thorns and the proximal comb contains

7 smaller thorns; a series of minute spinules is present along the whole concave margin of the claw behind the distal comb; about 6 small denticles are present in the middle of the claw.

B. The series of *Daphnia longispina*

The external appearance in various races of *D. longispina* is greatly different in various localities as compared with that of *D. pulex*.

i). Total length. The size in the summer and autumnal forms varies greatly, T ranging from 750 to 2700 in the egg-producing parthenogenetic females. The typical pelagic *hyalina* is always small, ranging from 1000 to 1500 in total length. Of the numerous races, those of Akagi-Ono in Prov. Kôzuke and Saino-ko in Nikkô are the smallest, T measuring only less than 1100; and in the latter race even a small animal of T=560 produces eggs. Examples of the size in certain representative races are given in Table III.

ii). Head. The ratio of head length to valve length A+B/V is mostly 1/3 or 1/4, rarely 1/5 (e.g. Shirouma-Ôike), only in one exceptional case the ratio being more than 1/2 (Kimon-numa, Iturup). In almost all races living in large lakes, A+B is approximately 1/3 of V, while in some races living in small shallow lakes and ponds it is always 1/4.

The ratio of head length to head basis, A+B/R varies more than in A+B/V, since R varies correlatively with the change of both V and H. Generally speaking, when A+B is 25–35 per cent. of V, it is always more than 50 per cent. of R and is sometimes 60–70 per cent. or more in certain pelagic races. In some races whose head length is approximately 1/5 of V, such as that of Shirouma-Ôike, A+B is only 35 per cent. of R. Another form resembling this with a short head, the race living in Urumobetsu-ko (Iturup), has the head length about 50 per cent. of R.

The profile of the head is generally concave, often showing strong concavity as seen in *cavifrons* SARS. The concavity becomes much more conspicuous in gamogenetic females.

The angle between the ventral outline and the basis of the head ($\angle\alpha$) varies with both A+B/V and A+B/R, being usually more than 65° and often attaining 90°. When A+B is about 30 per cent. of V, $\angle\alpha$ fluctuates 70°–80° or more, and sometimes nearly 90°; when A+B/V is about 25 per cent. of V, $\angle\alpha$ is more or less 60°. In

Table III

Examples of the sizes of local races of *Daphnia longispina* of Japan (in μ)

Locality	Date	T	A	B	A+B	V	H	S	Fig.
Paramushir									
Pond No. 1	5/8/31	1751	85	238	323	1428	900	357	Pl. XII, 12
Pond No. 2	„	2830	152	400	552	2278	1900	380	—
Shimushir									
A pond	18/8/31	2185	133	247	380	1805	1363	700	—
Iturup									
Urumobestu-ko	5/8/32	1411	85	170	255	1156	850	136	Pl. XIII, 14
Kimonma-numa	9/8/32	1208	68	170	238	970	740	50	—
Kimon-numa	1/8/32	1138	238	152	390	748	578	680	Pl. XIII, 13, 13a
„	„	1217	306	136	442	765	530	680	—
A pool at Moyoro	13/8/32	1225	85	170	255	1000	760	425	—
Ugo									
Towada-ko	11/11/30	1225	85	170	255	970	663	595	Pl. XIII, 15
Iwashiro									
Hibara-ko	5/7/31	1105	68	153	221	884	663	442	„ 16
Onogawa-ko	8/7/31	1071	68	153	221	850	408	560	„ 17
Numazawa-numa	17/11/30	1285	85	100	185	1100	884	68	„ 18
„	12/7/31	970	50	120	170	800	630	136	—
Shimotsuke									
Chuzenji-ko	7/6/31	2660	.	.	255	1105	850	560	Pl. XIV, 31
Saino-ko, Nikkô	11/10/30	900	.	.	220	680	483	289	Pl. XIII, 26, 26a
Yuno-ko	22/10/31	1397	.	.	290	1107	833	390	„ 22
Kirigome-ko	24/10/31	1445	.	.	459	986	884	476	„ 21
Maru-numa	12/6/31	1472	85	220	305	1122	850	459	Pl. XIV, 30
Ojiri-numa	1/8/29	1225	.	.	290	935	630	340	—
„	15/6/32	1597	102	255	357	1240	900	680	Pl. XIV, 32
Kozuke									
Akagi-Ono	5/8/29	918	68	152	220	690	544	476	Pl. XIII, 25, 25a
Haruna-ko	–/8/27	1717	119	238	357	1360	1000	340	„ 24
Sagami									
Ashino-ko	8/10/27	1222	100	152	252	970	765	425	„ 23
Shinano									
Nojiri-ko	2/10/27	1072	77	135	212	850	650	630	Pl. XIII, 19
Aoki-ko	21/8/27	1429	120	204	324	1105	782	560	„ 20
Shirokoma-ike	no date	1650	102	188	290	1360	1054	390	—
Togakushi-reservoir	12/9/26	1938	153	255	408	1530	1054	544	Pl. XIV, 33
Kido-ike	6/8/31	2002	152	230	282	1620	1105	410	„ 28
Misuma-ike	7/8/31	1896	152	200	352	1544	1120	400	—
Naga-ike	6/8/31	2176	170	340	510	1666	1160	306	Pl. XIV, 27
Shirouma-Ôike	12/8/29	2200	100	300	400	1800	1600	660	—
„	31/7/32	1955	85	220	305	1650	1275	426	Pl. XII, 10
Happo-ike	13/8/28	730	50	85	135	595	476	34	„ 11
A lake on Mt. Washiba	11/8/31	1716	.	.	306	1410	970	56	„ 9
Hyuga									
Amida-ike	1/6/27	1390	120	170	290	1100	900	300	Pl. XIV, 36
Satsuma									
Sumiyoshi-ike	7/8/29	1502	.	.	306	1196	935	390	„ 35
Chosen									
Fusenko-reservoir	2/10/30	2080	240	240	480	1600	1240	280	Pl. XIV, 34
„	15/6/31	2075	153	272	425	1650	1326	—	—
„	20/10/31	1494	100	170	270	1224	884	340	—

some forms with short heads (A+B about 20 per cent. of V) $\angle\alpha$ is 58°–68°.

A race living in Naga-ike, a small dystrophic lake on Mt. Shiga, differs greatly from the others, the ventral contour of its head being nearly parallel with the longitudinal axis of the body ($\angle\alpha$ more than 90°). In general appearance, particularly in its head contour, this form resembles very much *Daphnia pamirensis* RYLOV (1930) which was recently described from Schor-kul Lake in Pamir, but *D. pamirensis* differs distinctly from the Naga-ike-race by having a comb at the base of the terminal claws.

iii). Height of valve. The height of the valve is generally 3/5 of T, and in some cases it is 2/3. In some pelagic races, such as those of Towada-ko, Onogawa-ko and Aoki-ko, H is hardly 1/2 of T and in that of Kizaki-ko it often exceeds 1/2 of T. Even in the forms with short heads, such as those of Urumobetsu-ko, Numazawa-numa or Shirouma-Ôike, H is more or less 2/3 of T. The dorsal contour of the valve is generally less arched in pelagic forms than in littoral ones.

iv). Spine. The length and direction of the spine vary considerably. The length does not vary correlatively with the total length of animals. For instance, the form of 1370 long living in Urumobetsu-ko has a spine of only 25 long, while a small form (1070 long) of Kizaki-ko has a spine as long as 612. In slender pelagic forms S is nearly as long as 1/2 of T or sometimes 1/3 of T, while in most forms it is as long as 1/3, 1/4, 1/5, 2/5 or 3/4 of T. However, in some forms with short heads, such as those of Urumobetsu-ko or Numazawa-numa, S fluctuates from 1/7 to 1/8 or sometimes 1/15 or 1/17 of T and in a few cases the spine is entirely obliterated, as will be seen in Table IV.

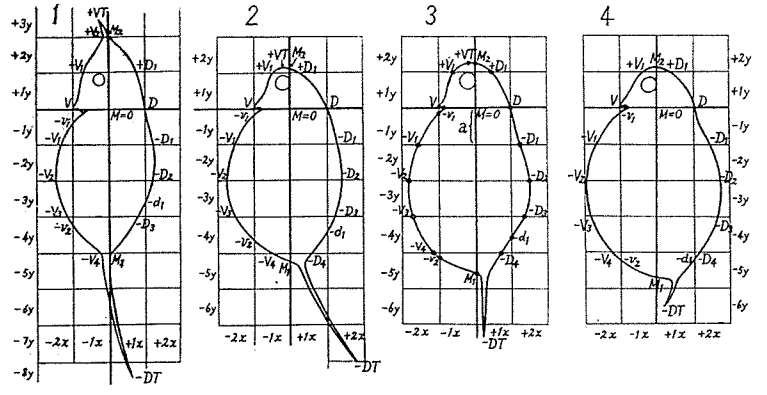
The spine is in most cases prolonged in a direction parallel to the longitudinal axis of the body, but in many pelagic forms it is slightly or rather strongly turned upwards. The angle between the axis of the spine and the longitudinal axis of the body ($\angle\beta$) is very variable, ranging from 0° to 50° and mostly less than 10°. There are, however, certain froms whose spines are not turned upwards but curved downwards. Such a case is commonly met

Table IV

Daphnia longispina (*primitiva*-type) of Urumobetsu-ko (in μ)

T	S	Remarks
1370	25	With one egg
1326	187	—
1290	68	—
1190	136	With one egg
1020	238	Primipara
952	153	„
595	220	Neonata

with in some ephippial females, but in some races even parthenogenetic females have $\angle\beta$ ranging from -2° to -5°. Among such races, that of Urumobetsu-ko is most peculiar, its $\angle\beta$ being often from -20° to as large as -25°. On the contrary, some pelagic forms, such as those of Towada-ko, Aoki-ko or Shirouma-Ôike have $\angle\beta$ as large as 30°–50°. These relations will be more clearly seen, if they are compared by the coordinate system (fig. 1), as applied by WOLTERECK (1924).



Ventral			Dorsal		
	x	y		x	y
+VT	-0.3a	+2.5a			
+V2	-0.1a	+2 a	M2	0	+2 a
+V1	-0.7a	+1 a	+D1	+0.7a	+1 a
V	-1 a	0	D	+1 a	0
-V1	-1 a	-0.3a			
-V1	-1.3a	-1 a	-D1	+1.2a	-1 a
-V2	-1.5a	-2 a	-D2	+1.2a	-2 a
			-d1	+1 a	-2.6a
-V3	-1.1a	-3 a	-D3	+0.8a	-3 a
-V2	-1 a	-3.2a			
-V4	-0.2a	-4 a	M1	0	-4 a
			-DT	+0.6a	-7.5a

Ventral			Dorsal		
	x	y		x	y
+VT	-0.2a	+1.1a			
			M2	0	+1.1a
+V1	-0.5a	+1 a	+D1	+0.3a	+1 a
V	-1 a	0	D	+1 a	0
-V1	-1 a	-0.1 a			
-V1	-1.5a	-1 a	-D1	+1.3a	-1 a
-V2	-1.8a	-2 a	-D2	+1.4a	-2 a
-V3	-1.5a	-3 a	-D3	+1.2a	-3 a
			-d1	+1 a	-3.4a
-V2	-1 a	-3.6a			
-V4	-0.5a	-4 a	-D4	+0.6a	-4 a
M1	0	-4.2a			
			-DT	+1.8a	-7 a

Ventral			Dorsal		
	x	y		x	y
+VT	-0.2a	+0.3a			
			M2	0	+1.2a
+V1	-0.6a	+1 a	+D1	+0.5a	+1 a
V	-1 a	0	D	+1 a	0
-V1	-1.0a	-0.1a			
-V1	-1.4a	-1 a	-D1	+1.2a	-1 a
-V2	-1.8a	-2 a	-D2	+1.5a	-2 a
-V3	-1.7a	-3 a	-D3	+1.3a	-3 a
			-d1	0	-3.6a
-V4	-1.1a	-4 a	-D4	+0.6a	-4 a
-V2	-1 a	-4.1a			
M1	0	-4.6a			
			-DT	+0.2a	-6.4a

Ventral			Dorsal		
	x	y		x	y
			M2	0	+1.1a
+V1	-0.4a	+1 a	+D1	+0.4a	+1 a
V	-1 a	0	D	+1 a	0
-V1	-1 a	-0.1a			
-V1	-1.7a	-1 a	-D1	+1.4a	-1 a
-V2	-1.7a	-2 a	-D2	+1.7a	-2 a
-V3	-1.8a	-3 a	-D3	+1.6a	-3 a
-V4	-1.2a	-4 a	-D4	+1.1a	-4 a
-V2	-1 a	-4.2a	-d1	+1 a	-4.2a
M1	0	-4.7a			
			-DT	+0.2a	-5.5a

Fig. 1. Four different races of *Daphnia longispina* compared by the coordinate system.

1. Race (*galeata*) of Kimon-numa, Iturup. 2. Race of Towada-ko. 3. Race of Haruna-ko. 4. Race of the *primitiva*-type of Urumobetsu-ko, Iturup. Unit of size.....a; unit of section.....½ VD.

The length of the spine and $\angle\beta$ in neonatæ are always greater than in the mature animals. For example, in the race of Urumobetsu-ko $\angle\beta$ of its neonatæ exceeds $+20^\circ$, though it is often -25° in its mature females. Neonatæ are always in an uniform appearance in various local races (fig. 2).

Several examples of relative size in some local races with different body contour are summarized in the following table:

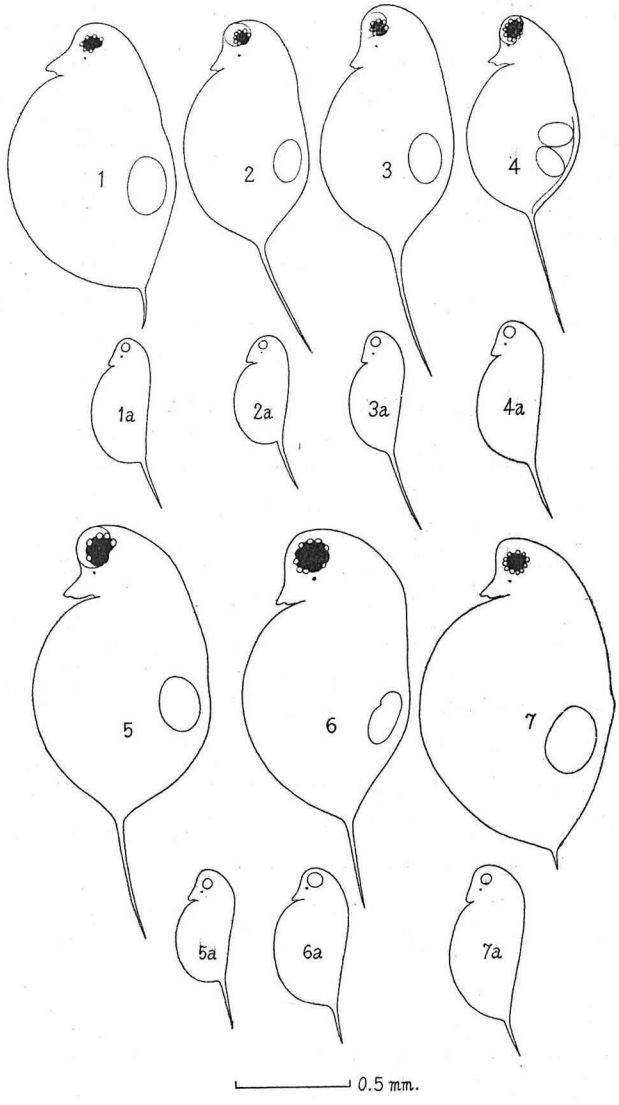


Fig. 2. Seven examples of different races of *Daphnia longispina* compared with their neonatæ. Summer form.

1, 1a: Urumobetsu-ko. 2, 2a: Towada-ko. 3, 3a: Aoki-ko. 4, 4a: Akagi-Ono. 5, 5a: Maru-numa, Nikkô. 6, 6a: Ichi-numa, Shinano. 7, 7a: An alpine lake at Takamagahara on "North Japanese Alps", Shinano.

Table V

Examples of different local races of *Daphnia longispina* of Japan

(A) Adult female

No.	Lake	Ratio, $\frac{A+B}{V}$ per cent.	Ratio, $\frac{A+B}{R}$ per cent.	Ratio, $\frac{H}{T}$ per cent.	Ratio, $\frac{S}{T}$ per cent.	∠α	∠β
1.	Kimon-numa	60	110	44	56	55°	12°
2.	Aoki-ko	35	68	55	56	78°	18°
3.	Ichi-numa	34	57	57	30	80°	15°
4.	Maru-numa	33	60	71	42	78°	15°
5.	Nojiri-ko	31	65	55	51	80°	10°—24°
6.	Akagi-Ono	31	65	57	62	70°	17°
7.	Towada-ko	30	61	56	52	70°	28°
8.	Urumobetsu-ko	24	52	62	15	55°	0° or <0°
9.	A pool on Mt. Washiba	21	50	62	7	75°	12°

(B) Neonata

No.* of lake	Ratio, $\frac{A+B}{V}$ per cent.	Ratio, $\frac{A+B}{R}$ per cent.	∠α	∠β
1	52	c. 100	80°	12°
2	32	56	80°	25°
3	35	67	80°	20°
4	41	69	78°	20°
5	34	69	80°	25°
6	30	56	70°	22°
7	33	67	75°	28°
8	30	67	70°	20°
9	32	56	80°	25°

*Compare the adult females (Table V, A).

Some Ecological Notes

A. Ecological Classification of the Habitats with reference to the Local Variation

As far as my investigations go, the habitats of the Japanese races of daphnids may be shown as follows (cf. WOLTERECK 1930):

1. *Daphnia pulex* (brachycephala).
   - a. Small shallow and contaminated pools, rice-fields and ponds .....*D. pulex pulex* and *D. pulex obtusa*.
   - b. Small and shallow ponds of brown water of peaty nature..... .....*D. pulex obtusa*.
   - c. Large and deep eutrophic ponds and small lakes..... .....*D. pulex pulex*.
   - d. Large and deep oligotrophic lake (Biwa-ko, 95 m) ....*D. pulex pulex*.

2. *Daphnia longispina* (brachycephara and very rarely mesocephala).
   a. Small and shallow contaminated pond; a large and clumsy form (*leydigii* HELLICH) .....Example: a pool at Kujirawan in Paramushir.
   b. Oligotrophic or dystrophic small and shallow lakes and ponds .....Examples: Naga-ike and Kido-ike.
   c. Large and deep ponds as well as some lakes of medium area and of medium depth and of eutrophic water; subsp. *longispina* s. str. (*typica*, *litoralis*, *crassiseta*, etc.).....Examples: Haruna-ko, Sumiyoshi-ike.
   d. Lakes of medium to great depth and of mostly oligotrophic type; typical *hyalina* (*lacustris*, *galeata*, etc.).....Example: Towada-ko.
   e. Small and shallow lakes of cool water in the alpine regions in middle Honshû and several large and deep lakes in Northern Japan; the habitats of *primitiva* with a short head and short spine.....Example: Numazawa-numa.
3. *Daphnia longispina* (dolichocephala).....A shallow oligotrophic lake in the Kurile Is. (Kimon-numa in Iturup).
5. *Daphnia cucullata* (brachycephala).....A deep oligotrophic lake in Hokkaidô (Shikaribetsu-ko, 99 m).
4. *Daphnia cucullata* (dolichocephala).....A shallow lake (c. 4 m) of strongly eutrophic-dystrophic type (so-called para-mixotrophic type); Tôro-ko in Hokkaidô.

Besides a typical pelagic race living in Biwa-ko, there are certain hyaline pelagic races of *D. pulex pulex* living in some large ponds, such as Ariga-ike and Ko-ike in Kyoto. In these races which are without any alteration of the body contour, the spine is always well-developed and turned slightly upwards as in certain pelagic races of *D. longispina*.

Typical pelagic races of *D. longispina hyalina* (*lacustris*, *galeata*, etc.) occur chiefly in large and deep oligotrophic lakes, such as Towada-ko, Nojiri-ko or Aoki-ko, while some races with heavier bodies (*longispina* s. str., *typica*, *litoralis*, etc.) appear mostly in small lakes of eutrophic water, such as Sumiyoshi-ike in southern Kyûshû. It is also noticed that among the true pelagic *hyalia* there are recognized two main types, one having a fragile and relatively small body with a thin valve and the other of a large and stronger body with a thick valve. The former is found in large lakes with great depths and with oligotrophic water, while the latter is found in lakes with rather great depths and areas but with eutrophic waters.

One type of *D. longispina* without any elongation of head and with a rather short or sometimes considerably short spine is commonly found in large oligotrophic lakes of cold water. The other type of *D. longispina* is seen in a group of some shallow dystrophic lakes in the province of Shinano (e.g. Naga-ike).

But in spite of the fact that many lakes have similar origin and physical and chemical, as well as nutritive, conditions, the same daphnid species may be found in some of the lakes and not in others. This fact is difficult to understand at present.

B. Relation between the Nature of Milieu and the Local Variation

i). Water temperature. In a country like Japan where there is a great geographical difference not only horizontally but also altitudinally, the climatic difference in various provinces may play an important rôle in the distribution of aquatic organisms. The distribution of various local races of *Daphnia* in different lakes seems also to be limited primarily to the climatic conditions, i. e. the water temperature. For instance, the lakes supporting the races with short and round heads (*primitiva*-type) are found only in Hokkaidô, South Kurile Is. (UÉNO 1933) and Northern Honshû as well as some alpine lakes in middle Honshû. In the habitat of this form, the surface temperature is usually about 15°C, though it may attain as high as 20°C or more in mid-summer, and the surface may be covered with thick ice in winter. *D. cucullata* is also distributed only in the coldest districts of Hokkaidô (UÉNO 1933a). However, it must be remembered that, as far as local variation is concerned, the ecological difference of the habitats (e.g. large lakes, ponds, pools, bogs, etc.) is as important as the geographical difference or it may be more important.

ii). Chemical factors. There are only a few data relating to the physical and chemical nature of the habitats of *Daphnia*. WAGLER (1923) was unable to find in *D. cucullata* any clear relation between the nature of the milieu on the one hand and the distribution and the shape of the body on the other, but he found that the temperature alone was the most important factor within the range of its distribution. On the contrary, HUTCHINSON, PICKFORD and SCHUURMAN (1932) found that in Transvaal "the genus *Daphnia* among the Cladocera provides the most clear-cut cases of chemical limitation". They also state that "a form referred to *D. longispina* occurs in Potchefstroom Dam and is also found in Florida lake but was found in no other

localities." The water of the former Dam is very low in chloride and sulphate, but Florida lake contains, though similarly very low in chloride, a large amount of sulphate (30–60 mg per litre).

My examinations of the chemical nature of the water of many Japanese lakes either holding or lacking *Daphnia*-population have failed to demonstrate any clear correlation between certain chemical components in solution and the occurrence of *Daphnia*. Except for a few peculiar cases, almost all races occur similarly in different waters that contain different amounts of chemical components, such as total residue, chloride, sulphate, silicate, calcium or magnesium, and so forth, and, at the same time, there is found no clear correlation between the amounts of these electrolytes and the difference in the shape of bodies. However, it has been noted that both the pH and peculiar nutritive conditions of water appear to affect the different forms of the daphnid found in various localities. A short comment relating to the races living in the lakes of Hokkaidô has been published (UÉNO 1933a).

The pH of the water of about 30 lakes and ponds in which *Daphnia* occurs ranges from 4.4 to 8.5. When this range of pH is divided into five groups, the frequency of the occurrence of *D. longispina* in each group is about as follows:

	pH 4.4–5.0	5.1–6.0	6.1–7.0	7.1–8.0	8.1–8.5
D. longispina.....	13.3	16.7	46.6	20.0	3.4 per cent.

The species is most frequently found in weakly acid and weakly alkaline waters (pH 6.0–8.0), whereas *D. cucullata* is found in both of the lakes, one weakly, and the other strongly, alkaline.

A great majority of large and deep Japanese lakes are of volcanic origin and of oligotrophic nature, their water being usually either neutral or weakly acid. Typical pelagic hyaline forms of *D. longispina* chiefly abound in such lakes, while large forms with thicker valves (*longispina* s. str.) occur principally in eutrophic waters, the pH of which is more or less alkaline. The *primitiva*-type of *D. longispina* is limited to the waters of oligotrophic type, the pH ranging round 6.0. In a group of dystrophic small lakes in Shinano where the water is rather acid (pH below 5.0), we have met with some peculiar races with large extremely hyaline valves and large broad heads.

In Algeria and Tunisia in North Africa, GAUTHIER (1928) has made a similar observation on the range of the pH of the habitats of *Daphnia*; i. e. *D. longispina* is found in the waters of the pH 6.6–7.6, while *D. pulex* occurs in the waters of the pH 6.4–7.6. POULSEN

(1928), on the contrary, arrived at a different result in Denmark, where *D. longispina* was most frequent in the waters weakly alkaline (pH 7.1–7.9) and *D. cucullata* occurred most abundantly in strongly alkaline waters as seen from the following data:

	pH 3.8–6.0	6.1–7.0	7.1–7.9	8.0–8.8
D. longispina.....	11.4	10.7	22.7	17.0 per cent.
D. cucullata	0	10.7	31.1	56.6 per cent.

Results obtained in Japan and Denmark must not be arranged on the same line, since the strongly alkaline waters in Japanese lakes are often caused by pronounced assimilation of phytoplankton in the epilimnion, while in Denmark the high alkalinities are always due to geological characters of the drainage areas (chiefly due to lime).

iii). Peculiar nutritive conditions. In regard to the nutritive conditions of the lakes, there are found some interesting facts relating to the shape of *Daphnia*. For instance, most of the races living in oligotrophic lakes have a relatively long spine which is strongly turned upwards. In some other races (*primitiva*-type) living in the lakes of the same nature, such as Numazawa-numa or Shirouma-Oike, the spine is remarkably turned upwards, even though it is rather short. On the contrary, many races of various lakes and ponds of eutrophic nature have spines not turned upwards but prolonged behind parallel with the longitudinal axis of the body. In some dystrophic lakes in North Shinano, the water of which is of oligotrophic nature in nutritive conditions, several forms of *D. longispina* always have upturned spines.

WOLTERECK (1909) also observed such a phenomenon in the two races of the lakes at Lunz, Austry. According to him (l. c, p. 140), one race living in Untersee that contains poor nutriment in the water has a large $\angle\beta$, while the other race living in Obersee where the nutriment is richer than in the former lake, has $\angle\beta=0°$. He called these two races "Mastform" (of Obersee) and "Hungerform" (of Untersee) respectively, and suggested that they are distinct races heritably fixed to their respective lake with different conditions.

A strange case observed in the race of Urumobetsu-ko, in which the spine is curved downwards, is difficult to understand at present.

C. Stratification and Associations

The stratification or "*biozones*" (WOLTERECK 1930, cf. also 1928) of pelagic daphnids in Japan have been thoroughly studied by KIKUCHI (1927, 1930) in four races, of which three are *longispina hyalina* and

the fourth *pulex pulex*. According to him, *D. longispina hyalina* found in three deep lakes, Aoki-ko, Kizaki-ko and Nojiri-ko always live below the thermocline. On the other hand, some races of pelagic daphnids living in several lakes in Hokkaidô are confined even to the epilimnion (UÉNO 1933a). An allied phenomenon is seen in an alpine lake Shirouma-Oike (max. depth 13.5 m) in middle Honshû. On the 1st of August 1932, I found in this lake that *D. longispina* (*primitiva*-type) occur most abundantly in deep cold water; the number of individuals occupying a layer below 10 m deep were twice as numerous as that in an upper layer (0–2 m or 2–5 m).

The stratification of a pelagic race of *D. pulex* in Biwa-ko was, according to KIKUCHI (1930, 1930a)[1], found below the thermocline both in September and October[2], as seen in *D. longispina* mentioned above. I obtained, however, a somewhat different result of the stratification in the same lake on the 23rd of July 1932, at 13h. The population on this day was not confined to the hypolimnion but found also in the upper layer of the thermocline, i. e. a small number of individuals were seen even in the epilimnion (thermocline 6–10 m, 26°–19.8°C) and the individuals living in a layer below 10 m deep were three times as numerous as those in the upper layer of 10 m Below 30 m (temp.: 30 m 11.8°C, 48 m 8.9°C) it decreased again in number.

The associations of pelagic daphnids in Japanese lakes are quite simple. If a lake has any species of *Daphnia*, this always belongs to only one race, either *D. longispina* or *D. cucullata*, or rarely *D. pulex*. A single exceptional case that has two pelagic differentiates of *Daphnia* in one lake is met with in Shikaribetsu-ko (99 m) in Hokkaidô (UÉNO 1933a). Even in small and shallow lakes or ponds, only one race is found in a single body of water. Japanese lakes that are deeper than 50 m and have any race of *Daphnia* are given below (*l–longispina*; *l–p–longispina primitiva*; *p–pulex*; *c–cucullata*):

Lakes deeper than 100 m

Shikotsu-ko (363 m) .....*l.*
Towada-ko (378 m) .....*l.*
Mashû-ko (211.5 m).....*l–p.*
Tôya-ko (183 m).....*l.*
Chûzenji-ko (167 m).....*l.*
Kutcharo-ko (125 m).....*l–p.*

Lakes deeper than 50 m

Shikaribetsu-ko (99 m)...*l–p* & *c.*
Biwa-ko (95 m).....*p.*
Numazawa-numa (92 m) .....*l–p.*
Aoki-ko (62 m) .....*l.*

1. KIKUCHI (l.c. 1930) treated this race as *D. longispina*.
2. Thermocline: October 6, 1926, 12-20 m; September 1927, 12-20 m.

Characteristics of the Local Races of Japanese *Daphnia*

Numerous subspecies, varieties or forms of *Daphnia* have been described in both Europe and the United States of America for many years. It is however difficult to apply any of these names to individual forms living in various waters, because it is very difficult to distinguish cleary many different forms from one another. Moreover, from the ecological point of view, it is desirable not to use too many names for avoiding confusion as much as possible. Therefore, it is better to apply WOLTERECK's classification (1930) which is based upon genetical and ecological standpoints. According to him, many races of *Daphnia*, particularly pelagic ones, can be divided into three main types according to the maximum cyclomorphosis in mid-summer, namely, dolichocephala, mesocephala and brachycephala.

The Japanese races of *D. longispina* are all brachycephala in his nomenclature and are very rarely mesocephala-*galeata* or dolichocephala-*galeata*. The development of the helmet in summer never occurs in the lakes south of Hokkaidô, the extreme race with an elongated head (A+B more than 50 per cent. of V) being found only in the South Kurile Islands (UÉNO 1933). This is one of the most important characteristics of the local races of *D. longispina* found in Japan.

More important is the fact that the number of pelagic differentiates of *D. longispina* is fewer in Japanese races than in either European or North-American (United States and Canada) races. In Japanese lakes there are seen no such predominant forms as those which live in either European or American lakes. For instance, a form with a procurved helmet (*procurva*-type) or that with a convex profile (*pellucida*-type) or that having a retrocurved helmet and elongated rostrum (*nastua*-type) are all entirely absent in our lakes. The common pelagic differentiate of *D. longispina* found in Japan are *hyalina* of the commonest type, viz. *longispina lacustris*, or very rarely *galeata*. There are also some forms of a strange shape with a very large broad head and very short spine living in shallow dystrophic lakes on Shiga mountain group.

There is another peculiar daphnid which has a very short head and a very short spine probably belonging to the *primitiva*-type of *D. longispina*. The races belonging to this type are found always in lakes with cold water that are located chiefly in the northern part of Honshû and Hokkaidô as well as in the south Kurile Is. (Iturup). There are, however, some peculiarities among the races of the *primi-*

tiwa-type. The small races with a very short spine live in rather deep lakes with cold water, such as Numazawa-numa (92 m) and Urumobetsu-ko (48 m). The other large races with a rather long spine which is turned upward, occur in some large lakes in Hokkaidô and in the alpine lake Shirouma-Ôike in middle Honshû. Nearly allied races are living also in some small and very shallow alpine lakes of cold water.

It is also an important fact that the difference in shape between Japanese and European races of *D. longispina* is much smaller than that between Japanese and American races of the same species, i. e. it can be said that the difference between the American and Eurasian differentiation of *D. longispina* is rather large and sharp.

The local differentiation of *D. pulex* is much smaller than in *D. longispina*. The Japanese races of this species are all brachycephalic and may be divided into the two following series:

1. *Daphnia pulex pulex*
   - a. Races living in small ponds and pools.....Examples: Madachi-numa; a pool at Ninnaji near Kyoto, etc.
   - b. Race living in large and deep ponds.....Example: Arigaike, etc.
   - c. A race living in a large and deep lake; a true pelagic form .....Biwa-ko.
2. *Daphnia pulex obtusa*.....Examples: Uemura-Ôike, Kojorô-ike, etc.

The development of a pelagic differentiate of *D. pulex* in Japan is most noticeable. As far as known to us, such pelagic differentiation of *D. pulex* with a distinct alteration of the post-abdomen implies the four following species:

1. *Daphnia clathrata* FORBES.....Grobe Lake, Yellowstone Park.
2. *D. arcuata* FORBES.....Heart Lake, Yellowstone Park.
3. *D. pulicaria* FORBES.....Lakes in Yellowstone Park.
4. *D. pulicarioides* BURCKHARDT.....Lake Lugano, Switzerland.

Besides these, JUDAY (1915) described a pelagic race of *D. pulex* from a large lake Atitlan in the republic Guatemala, Central tropical America, though he gave no taxonomic detail on his material. Therefore, the pelagic differentiations of *D. pulex* seem to occur in some lakes in the United States and tropical America as well as in Central Europe (cf. WOLTERECK 1932). The race of Biwa-ko resembles very much *pulicarioides* BURCKHARDT, but differs from it in having fewer number of spines on the post-abdomen.

The zones of habitation of Japanese *Daphnia* seem to be rather

different from lake to lake throughout Japan, some populations occupying from the layer above the thermocline to the hypolimnion and some being most abundant either in the thermocline or in the hypolimnion, and some others having the maximum number in the hypolimnion. The populations living in the hypolimnion were first described by JUDAY (1915) from two great deep lakes, Atitlan and Amatitlan, in Central America. Though some great regional differences are found between these tropical and Japanese lakes, the races of *Daphnia* living in these lakes of two different regions show close resemblance in general shape of the body. Judging from WOLTERECK's drawings (1932, Pl. 16, figs. 22–23) the race of Atitlan is *primitiva*-type without any crest or helmet, while that of Amatitlan is a typical *apicata*-type with a pointed head.

The populations living in the hypolimnion in three Japanese lakes (KIKUCHI 1930) are also typical brachycephalic *hyalina* with a round head (Aoki-ko and Nojiri-ko) or in one case (Kizaki-ko) with pointed head in summer.

The stratification of pelagic races of *D. pulex* have been little studied; we have hitherto only JUDAY's work (1915) in tropical Central America. He found that in a large lake Atitlan (38 km long, depth 322 m) on the 11th of Feb. (1910) *D. pulex* was present in the layer below 100 m. deep and reached its maximum number in the layer of 150–200 m. This lake is homothermal and has no distinct O_2-stratification (0 m 19.6°, 315 m 19.2°C; O_2 68.7 to 60.4 per cent. of saturation). Therefore, this lake differs entirely from Biwa-ko as a habitat of pelagic *D. pulex*. In Biwa-ko a distinct temperature stratification is seen in summer, but no remarkable diminution of O_2 in deep water is found owing to its oligotrophic nature.

In regard to the associations, most European lakes of the post-glacial character have one or two differentiates of pelagic daphnids, such as either *longispina* or *cucullata*, or both of them. In American lakes of the same character, however, the common associations of pelagic daphnids are greatly different from those in European lakes. According to WOLTERECK (1932), in American lakes especially in those in Wisconsin, there are found from three to five races of *Daphnia* in the associations of the same lake. For instance, Crawling Stone Lake which has a maximum depth of 28 m contains four different races, one *pulex*, two different *parapulex* (*breviceps* and *retrocurva*), one *longispina apicata* (*galeata*) and one *longiremis*.

The associations of pelagic daphnids in Japanese lakes are, as mentioned already, quite different from either those in Europe or America. If a lake has any population of *Daphnia*, we are certain that it belongs to one of the races of *D. longispina* or rarely to either *D. cucullata* or *D. pulex*. The lake with two pelagic differentiates of *Daphnia* is met with in only one case. This is the most important point in the associations of *Daphnia* in Japanese lakes.

Summary

1 All Japanese local races of *Daphnia* have undoubtedly been derived from the two species, *D. pulex* and *D. longispina*.

a. Local variation of *D. pulex* is rather slight. All Japanese races of this species may be one of the two series: *D. pulex pulex* and *D. pulex obtusa*. A typical pelagic differentiate of *D. pulex pulex* is also found in Japan.

b. Local variation of *D. longispina* is rather great as compared with that of the other species, their external appearance differing much from lake to lake. Almost all Japanese forms have either weakly or strongly concave head-profile which is more conspicuous in ephippial females.

2. It is a most important fact that all Japanese races of *D. longispina* are brachycephalic, the development of the helmet in summer having been seen in a single lake north of Hokkaidô. The races of *primitiva*-type of *D. longispina* are also found in some bodies of cold waters in the northern parts of the country. The number of pelagic differentiates of *D. longispina* is rather smaller in Japan than in either Europe or America.

3. No Japanese lake has any association of pelagic *Daphnia*, holding invariably a single race of *D. longispina*, very rarely *D. pulex*, or *D. cucullata* in the same lake. A single exception to this rule was found in a lake of Hokkaidô, where two species, *D. longispina* (*primitiva*) and *D. cucullata* (mesocephala) lived in association.

4. The zones of habitation of pelagic *Daphnia* seem to be rather different from lake to lake, some living only in the hypolimnion while some others occupy the whole strata.

5. There is no clear correlation between any chemical factor in waters and the distribution as well as local variation of Japaness *Daphnia*. The variation of the pH alone seems to be responsible for the limitation of the ditribution of various local races. One thing that can

be safely concluded in regard to the peculier nutritive conditions of lakes is that in the races living in oligotrophic waters the spine is turned upwards, while in those living in eutrophic waters it is shifted towards the opposite side.

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Explanation of Plates

Plate XI

Five examples of pelagic races of Japanese *Daphnia*.

Fig. 1. A pelagic race of *D. pulex pulex* of Biwa-ko. July. Fig. 1a: terminal claw.
Fig. 2. *D. longispina* (*galeata*) of Kizaki-ko. August. Fig. 2a: terminal claw.
Fig. 3. *D. longispina* of Maru-numa, an eutrophic mountain lake, Nikkô. June.
Fig. 4. A race of the *primitiva*-type of *D. longispina*. Urumobetsu-ko, an oligotrophic crater lake in the Island of Iturup, S. Kuriles. August.
Fig. 5. Another example of the *primitiva*-type of *D. longispina*. Numazawa-numa, a deep oligotrophic lake in Northern Honshû. October. 5a: terminal claw.

Plate XII

Racial series of *Daphnia pulex* of Japan. (Figs. 1-8).

Fig. 1. Uémura-Oike, a small oligotrophic mountain pond in Shinano.
Fig. 2. Kojorô-ike on Mt. Hira, Prov. Omi. Ephippial female, 22. XI. 1931.
Fig. 3. Madachi-numa on Mt. Hakkôda, Northern Honshu.
Fig. 4. Biwa-ko, Omi.
Fig. 5. An *obtusa*-race found in a pond west of the city of Nara.
Fig. 6. Uzuratori-iké, a small dystrophic pond in Shinano.
Fig. 7. Hirosawa-iké, a large eutrophic pond west of Kyoto.
Fig. 8. A *pulex*-race collected in a pond at Taihoku, Formosa.

Racial series of *Daphnia longispina* of Japan. 1. (Figs. 9-12).

Fig. 9. A *primitiva*-race of a small alpine lake on Mt. Washiba, Shinano.
Fig. 10. A large race of the *primitiva*-type found in Shirouma-Ôike, a panoligotrophic alpine lake in Shinano.
Fig. 11. Happo-iké, an alpine lake, Shinano. Younger animal.
Fig. 12. A contaminated pool at Kujira-wan in the Island of Paramushir, one of the North Kuriles.

Plate XIII

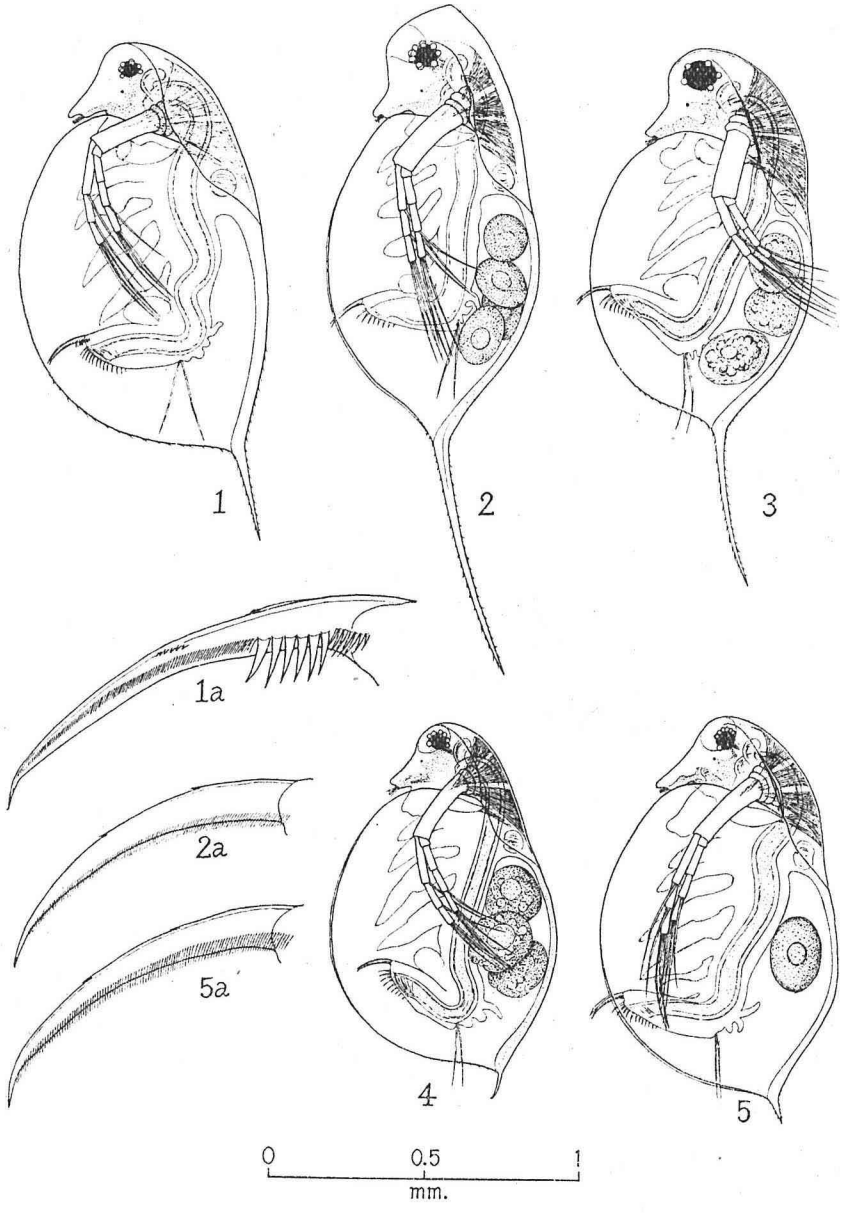
Racial series of *Daphnia longispina* of Japan. 2.

Figs. 13-13a. A *galeata* race living in Kimon-numa, Iturup, S. Kurile Is.
Fig. 14. A race of the *primitiva*-type living in Urumobetsu-ko, Iturup.
Fig. 15. Towada-ko, a large oligotrophic lake in northern Honshu.
Fig. 16. Hibara-ko, an oligotrophic lava-dammed lake on Volcano Bandai.
Fig. 17. Onogawa-ko, another lava-dammed oligotrophic lake on Volcano Bandai.
Fig. 18. A race of the *primitiva*-type found in Numazawa-numa, a deep oligotrophic lake.
Fig. 19. Nojiri-ko, an oligotrophic lake in N. Shinano.
Fig. 20. Aoki-ko, another deep oligotrophic lake in Shinano.
Fig. 21. Kirigome-ko, an oligotrophic lake at Nikkô.
Fig. 22. Yuno-ko, a small eutrophic lake at Nikkô, where appears "water-bloom" of diatoms during summer months.
Fig. 23. Ashino-ko, an oligotrophic lake at Hakone, Sagami.
Fig. 24. Haruna-ko in Prov. Kozuké. 1927. The population entirely disappeared from this lake in 1931, owing to the rapid eutrophication.
Fig. 25-25a. Akagi-Ono in Prov. Kozuké.
Fig. 26-26a. Saino-ko in Nikkô. The smallest race of *D. l.* in Japan.

Plate XIV

Racial series of *Daphnia longispina* of Japan. 3.

Fig. 27. A race of a large head living in Naga-ike, a dystrophic lake in North Shinano.
Fig. 28. Kido-ike, another dystrophic lake in N. Shinano.
Fig. 29. Hyotan-ike, a dystrophic lake lying near Kido-ike.
Fig. 30. Maru-numa at Nikkô.
Fig. 31. Chuzenji-ko at Nikkô.
Fig. 32. Ojiri-numa, an eutrophic lake lying close to Maru-numa.
Fig. 33. Togakushi-reservoir of the Nagano Water-Work, N. Shinano.
Fig. 34 Fusenko reservoir, northern Chosen (Korea).
Fig. 35. Sumiyoshi-ike, an eutrophic lake (maar) in Prov. Satsuma, southern Kyushu.
Fig. 36. Amida-ike near Nobeoka, Kyushu.
Fig. 37. A dwarf race of *longispina* living in a bog-pool at Ozehara, near Nikkô.



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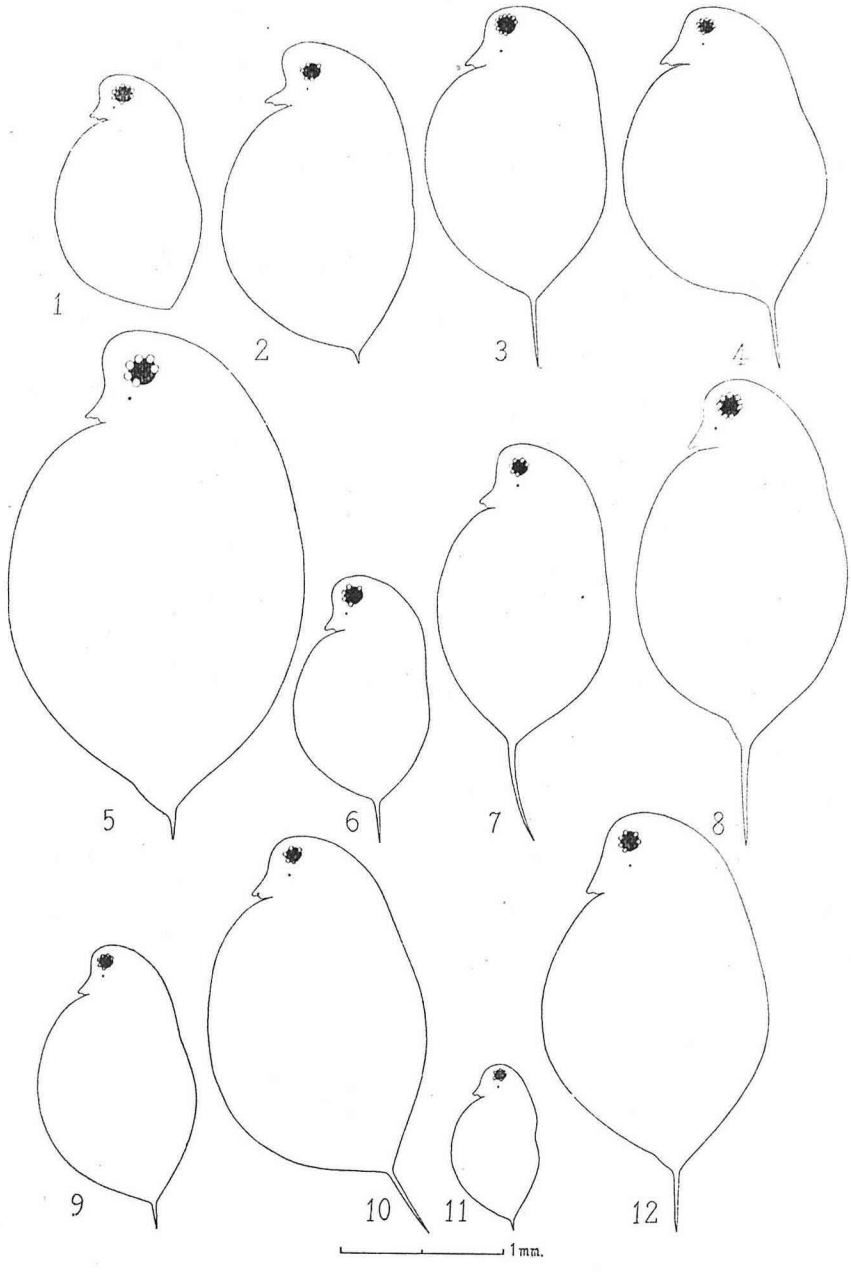

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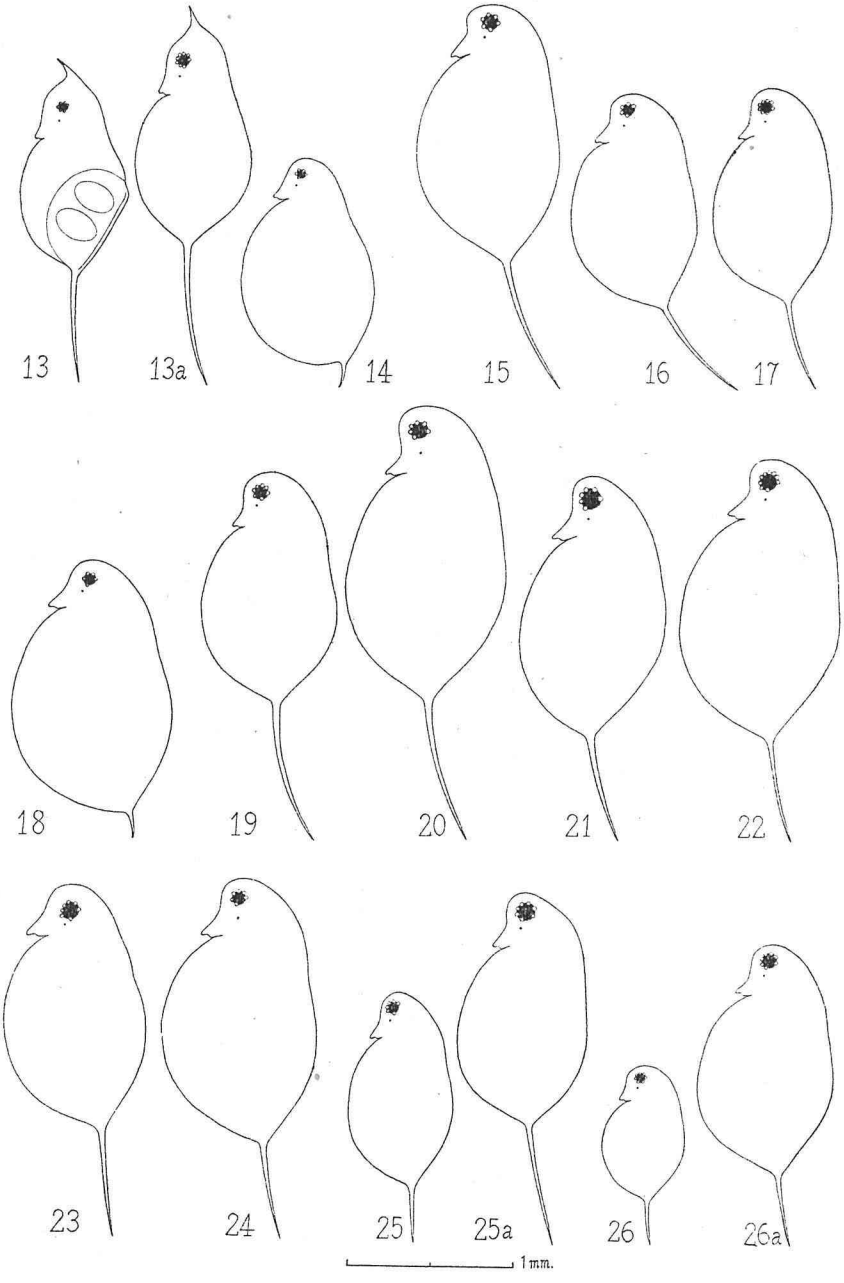

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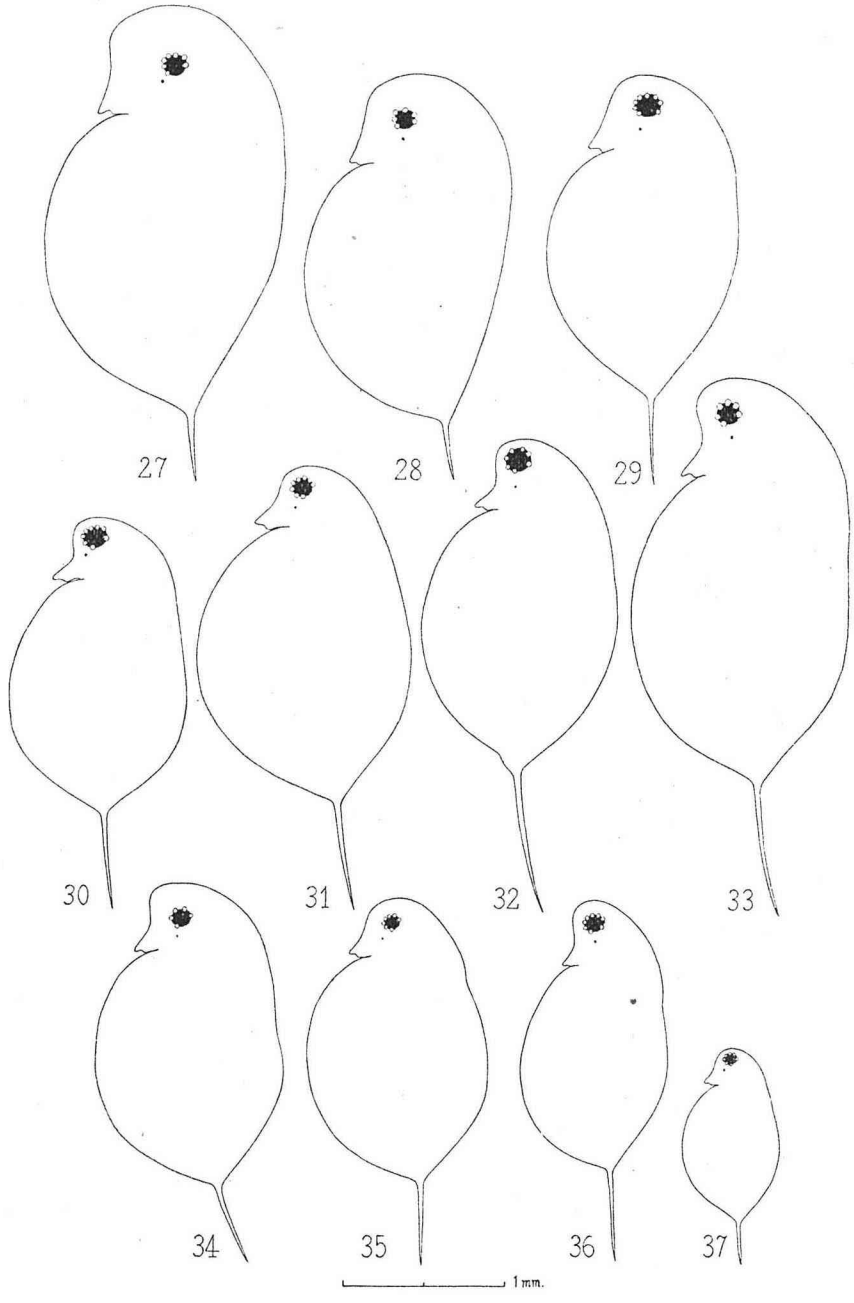

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