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Studies on the communication system of Japanese fireflies*

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(With 35 text-figures, 10 tables and 6 plates)

日本産ホタルのコミュニケーションシステムの研究*

大 場 信 義**

Contents

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Abstract

Japanese fireflies are known to range from nocturnal luminescent species to diurnal non-luminescent species. However, their communication system has been little studied except *Hotaria parvula* and *Luciola cruciata*. The present paper records and analyzes the result of the observations and experiments on the behavior of the Japanese fireflies by means of a 16 mm cine-camera, a phototransistor and a photomultiplier. Their communication system was inferred and classified on the basis of the sexual isolation mechanism of the fireflies from the view points of communication system, habitat, geographical distribution, adult seasonal occurrence, morphology, and function of genitalia.

In this study, the following facts have been disclosed.

1. Communication systems of the Japanese fireflies are classified into 6 types as follows. 1) Communication system of *Hotaria parvula* is typical of HP system. In this system, the female responds to the male's flashes after a definite time of delay. This system corresponds to System II of American *Photinus* fireflies. 2) In LL system represented by *Luciola lateralis*, the male is directly attracted by the female's flickering light signals, and copulating behavior is released. Distinctive responding flashes of the female are not recognized in this system. 3) *Luciola cruciata* represents LC system, in which the male emits flashes with various patterns, and displays walking-luminescing, sedentary signaling, chasing, mounting, and copulating. This system corresponds to Complex System of New Guinean firefly, *Luciola obsoleta*. 4) In PR system represented by *Pyrocoelia rufa*, the male is attracted by continuous luminescent signals of the female, and copulating behavior is released by her sex pheromone. This system corresponds to System I of European firefly, *Lampyris noctiluca*. 5) *Cyphonocerus ruficollis* represents CR system. In this system the flying activity of male and female is in the daytime. When the male approaches the female, copulating behavior is released by the female's sex pheromone. The habitat of fireflies having this communication system is narrowly restricted, which favors their mating behavior. Weak luminescent signals may be fulfilling the function of supplementary communication signals. However, the role of the luminescent light is little known. 6) LB system represented by *Lucidina biplagiata* is similar to CR system. However, the luminescent signals have nothing to do with communication between male and female.

2. Communication systems are correlated with morphology, hehavior, and luminescent patterns.

3. Sexual isolation of the fireflies is maintained by the differences in communication system, habitat, geographical distribution, adult seasonal occurrence, morphology, and function of genitalia.

4. The fireflies having PR system and LL system closely resemble in specific morphology and behavior. Copulating behavior between different species can be released artificially. Sexual isolation of these fireflies is maintained by geographical isolation.

Introduction

Most communication systems of fireflies have been studied in nocturnal species, but little is known concerning communication in amphipetal and diurnal species. About 2000 species, including diurnal, amphipetal, and nocturnal species are known throughout the world (McDERMOTT, 1966), possessing various kinds of communication systems. In luminescent species, the role of bioluminescence in sexual communication has been demonstrated (recently reviewed by LLOYD, 1971). However, except for nocturnal species, the communication system of fireflies is generally unknown. Bioluminescence in Japanese fireflies, which include diurnal, amphipetal, and nocturnal species, has been recorded in 39 species (NAKANE and OHBA, 1981). The communication systems of these fireflies have not been clarified except for *Hotaria parvula* where field observations have been carried out (OHBA, 1981d). However, the biology including sexual communication and ecology of the diurnal species is poorly understood. The purpose of this study is to establish a foundation of general knowledge on sexual communication of Japanese fireflies and to elucidate the relationship between morphology and behavior.

Literature review

The function of flashing as a mating adaptation was established early in the twentieth century largely through the studies of McDERMOTT (e.g. 1910, 1911, 1912). During this period the flash of male of several species and the response flashes of female of a few species were described, and the role of species-specific flash signals in reproductive isolation was demonstrated. BARBER (1951) recognized several cryptic species in the genus *Photuris*. The communicative function of luminescence in *Lampyris noctiluca* was recognized as early as 1957 (HARVEY, 1957). SCHWALB (1960) experimentally analyzed the communicative parameters and found that the male was attracted to a light source and that he recognized a female of his species by the configuration of the female light organ. The mating behavior of most Nearctic *Photinus* has been described by (LLOYD, 1966b) and flash behavior of *Pyractomena* fireflies has been described by WEZEL (1896), McDERMOTT (1911, 1958), and LLOYD (1964, 1966a). Most American *Photinus* and *Pyractomena* fireflies utilize Signal System II in which male flies about broadcasting a species-specific signal to which the female responds with a species-specific signal. LLOYD (1966a) experimentally analyzed the commnnicative parameters of this communication and found that females discriminate pulse length, pulse interval and pulse number, whereas males discriminate response delay time. The female *Phausis reticulata* (SAY) starts glowing when it sees a glowing male by overhead (LLOYD, 1965b). In *Luciola discicollis* LAPORTE

(KAUFMANN, 1965) and *Luciola* sp. (LLOYD, 1973a), the males emit trains of flashes as they fly about and are attracted to the female who emits trains of flashes at a slightly different flash rate. Recently, a third and much more complex mating system has been proposed for *Luciola obsoleta* (E. OLIVIER) (LLOYD, 1972b). This mating protocol includes 5 distinct phases or stages: (1) sedentary signaling, (2) chasing, (3) walking-luminescing, (4) mounting, and (5) copulating. Synchronous flash behavior of Asian fireflies in the genus *Pteroptyx* has been observed by numerous investigators (e.g. REINKING, 1921; BUCK and BUCK, 1966; HANEDA, 1966; BASSOT and POLUNIN, 1967; LLOYD, 1973a), but its role in mating behavior remains uncertain. However, LLOYD (1973b) proposed a model for mating protocol for synchronously flashing fireflies, and BUCK and BUCK (1976) have presented popularized summary of synchronously flashing fireflies. In Europe, in glowworm *Lampyris noctiluca* the larva-like form of the female glows continuously and attracts non-luminous flying males (Signal System I). Another glowworm, *Lamprigera tenebrosus* (WALKER) occuring in India and Sri Lanka, has been studied by PAVIA (1919), BESS (1956) and others. The larva-like form of the female glows to attract the flying male (Signal System I).

In Japan, the two most common fireflies are *Luciola cruciata* MOTSCHULSKY and *L. lateralis* MOTSCHULSKY. The biology and life cycles of these fireflies have been reported by OKADA (1928), KANDA (1935), MINAMI (1961), HARA (1940), HANEDA (1968, 1972) and OHBA (1980b). In both species flashing and flickering behavior leads to copulation (YAJIMA, 1978; KURATA *et al.*, 1979), but the flash communication system is not understood. The timing of the flash in *H. parvula* is the most critical among the Japanese fireflies. OHBA (1980a) has elucidated the flash communication system in *H. parvula* through field observations. Behavior and morphology in other species have also been partially observed by OHBA (1976b, 1978, 1979a, 1979b, 1980a, 1981b, 1981c). Recently, diurnal activities and luminous signals of fireflies of *Luciola cruciata* have been observed (YAJIMA, 1978; OHBA, 1979b, 1981c), and oviposition behavior of this species has been reported by YUMA (1981). In West Africa, *Luciola discollis* LAPORTE is one of most common fireflies, and was studied by KAUFMANN (1965). Both sexs engage in extensive flashing which leads to copulation but the parameter of this flash communication system is not understood.

In *Ellychina corrusca, Lucidota atra* and *Pyropyga nigricans,* the systems are unusual in that the adults have diurnal habits and do not utilize luminescent signals in courtship (WILLIAMS, 1917; HESS, 1920). In these fireflies the female releases a pheromone to attract the male (LLOYD, 1972a).

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Materials and methods

The fireflies studied in this work are listed in Table 1. Of 39 species of Japanese fireflies studied the flash patterns and communication system of 20 species, which included three types of activity, nocturnal, amphipetal, and diurnal, were recorded and analyzed by the following methods described below. These were supplemented by numerous additional observations in the laboratory and field.

The first method employed was the same as that used in a previous study (OHBA, 1980a). This method consisted of recording with a 16 mm cine-camera (Method A). The second method employed a photomultiplier connected to a pen recorder (Method B). The photomultiplier is able to detect very weak luminescence and this method which is the same as the one used in a previous study (OHBA, 1979d), was employed only in the laboratory. In the third method a photocell transducer was employed (Method C). The transducer was connected to a portable stereo-tape recorder. This method was used in field and laborotory observations. In the fourth method, intervals between male flashes were measured by timing 5 or 6 flashes with a stopwatch in the field and dividing by the number of intervals involved, or flashes were recorded with a tape recorder and the intervals were measured later with a stopwatch (Method D). Females to be recorded were placed in a plastic cage (2.0×2.5×20.0 cm) with a movable partition

Table 1. Materials used in this firefly study.

SPECIES	LOCALITY AND DATE OF COLLECTION AND OBSERVATIONS
CYPHONOCERINAE	
Cyphonocerus ruficollis Kiesenwetter, 1879	Juniso, Kamakura City, 13-15 Jun., 1975; 13 Jun.,1976; Mt. Hirugatake(alt. 1600 m), Kanagawa, 14 Jul., 1979
OTOTRETINAE	
Drilaster axillalis Kiesenwetter, 1879	Juniso, Kamakura City, Kanagawa, 15 Jun., 1977; Mabori, Yokosuka City, Kanagawa, 5 Jun., 1978; Hatano City, Kanagawa, 14 Jul., 1979
Drilaster ohbayashii M. Sato, 1968	Mt. Banna, Ishigaki Is., Okinawa, 5 May, 1977; 30 Oct. 1979
Drilaster fuscicollis Nakane, 1977	Nago City, Okinawa Is., 6 May, 1978; 5 Nov., 1979
LUCIOLINAE	
Luciola cruciata Motschulsky, 1854	Toyoda, Yamaguchi, 28 May, 1976; Juniso, Kamakura City Kanagawa, 6 Jun.,1977; Nobi, Yokosuka City, Kanagawa, 20 Jun., 1981; Yoshii, Yokosuka City, Kanagawa, 29,Jun. 1981
Luciola lateralis Motschulsky, 1874	Juniso, Kamakura City, Kanagawa, 21 Jun., 1977; Yoshii Yokosuka City, Kanagawa, 29 Jun., 1981
Luciola kuroiwae Matsumura, 1918	Nago City, Okinawa Is., 6 May, 1979; Hyakuna, Okinawa Is., 7 May, 1979; 6 May, 1980
Luciola yayeyamana Matsumura, 1918	Mt. Banna, Ishigaki Is., Okinawa, 5 May, 1977; 4 May, 1979
Hotaria parvula Kiesenwetter, 1874	Ohtsubashi, Nagoya City, 30 May, 1976 ---30 May, 1981; Mt. Hakone, Kanagawa, 30 Jun., 1979; Mt. Hirugatake, Kanagawa(alt. 1600 m), 14 Jul., 1979; 13 Jul., 1980; Mt. Adatara, Fukushima, 27 Jul., 1975
Curtos costipennis Gorham, 1880	Mt. Banna, Ishigaki Is., Okinawa, 5 May, 1977; 4 May, 1979; Ohhara, Iriomote Is., Okinawa, 29 Apr., 1979; 2 May, 1979
Curtos okinawana Matsumura, 1918	Nago City, Okinawa Is., 11 May, 1980; Hyakuna, Okinawa Is., 6 May, 1979
LAMPYRINAE	
Pyrocoelia rufa Olivier, 1886	Izuhara, Tsushima Is., Nagasaki, 15 Oct., 1979; Sasuna, Tsushima Is., Nagasaki, 17 Oct., 1979; Kyozuka, Tsushima Is., Nagasaki, 7-9 Oct., 1979
Pyrocoelia miyako Nakane, 1981	Kurimajima, Miyako Isls., Okinawa,5 Nov., 1979
Pyrocoelia atripennis Lewis, 1896	Ohhara, Iriomote Is., Okinawa, 1 Nov., 1979; Kabira, Ishigaki Is., Okinawa, 30 Nov., 1981
Pyrocoelia fumosa Gorham, 1883	Mt. Adatara, Fukushima, 23 Jul., 1975; Juniso, Kamakura City, Kanagawa, 20 Jun., 1977
Pyrocoelia matsumurai Nakane, 1961	Nago City, Okinawa Is., 6 May, 1979
Pyrocoelia abdominalis Nakane, 1977	Mt. Omoto, Ishigaki Is., Okinawa, 30 Apr., 1977; Yonehara, Ishigaki Is., Okinawa, 30 Oct., 1978
Lucidina biplagiata Motschulsky, 1866	Juniso, Kamakura City Kanagawa, 14 Jun., 1976; 6 Jun., 1977; Mt. Tanzawa, Kanagawa(alt. 1000 m), 9 Jul., 1978; Mt. Ohgusu, Yokosuka City, Kanagawa(alt. 100 m), 4 Jul., 1980
Lucidina accensa Gorham, 1883	Mt. Tanzawa, Kanagawa, 9 Jul., 1978
Pristolycus sagulatus Gorham, 1883	Sengokuhara, Mts.Hakone, Kanagawa(alt. 1000 m), 21 Jul., 1979

so that the cage could be divided into two compartments. This arrangement allowed the female to climb the plastic cage and expose its light organ in position easily accessible to the transducer. The artificial flasher (AF) was placed slightly above the female at a distance of 5–10 cm away. Females were tested for pulse interval, and duration. Tests were made with photo-cell transducer, a tape recorder, and a 16 mm cine-camera. The recorded tapes were analyzed latter with an multi-auto pen recorder. The following operational description was provided with the equipment. The artificial flasher was little more than a flash light bulb and electric switch. Its purpose is to emit a flash of light of predeter-

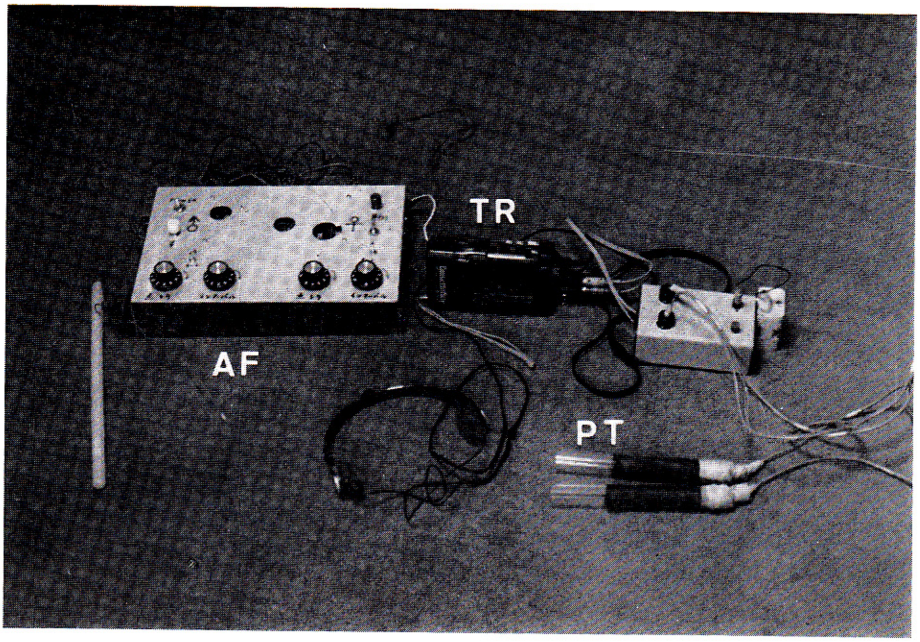


Fig. 1. Phototransistor system for recording luminescent signals and AF flasher. PT=phototransistor, AF=artificial flasher, TR=tape recorder.

mined duration and interval. The circuit consists basically of a pair of transistors and condensers. The transducer assembly consists of a pair of phototransistor on short cables connected to a small aluminium box (Fig. 1). The microphone is connected to a tape recorder, allowing complete records to be made of the transduced data, supplemented with variable notes. The two pairs of phototransistor are connected by circuits to each other. The input circuit is operated in the following way: Two small phototransistor cells are used and when the cell is dark, very little current flows; when sound is transduced, the flow of current increases. The amplified signal is fed into a portable stereo-tape recorder. The signal is loud enough to be heard so that a continuous check can be made on the performance of the equipment. The tape recorder used in conjunction with the phototransducer was an Aiwa stereo cassette tape recorder Model HS-F1. Tape recordings were analyzed with a multi-auto pen recorder. The calibrated base of the pen recorder permitted time readings to be made directly from the chart record and could be read to 1/100 of a second. In diurnal species of fireflies, luminescent signals are not used in courtship. In these fireflies the female releases pheromone to attract the male. Therefore communication between a male and a female was observed and recorded by camera and by additional experimental observation such as influence of a dead female to a male.

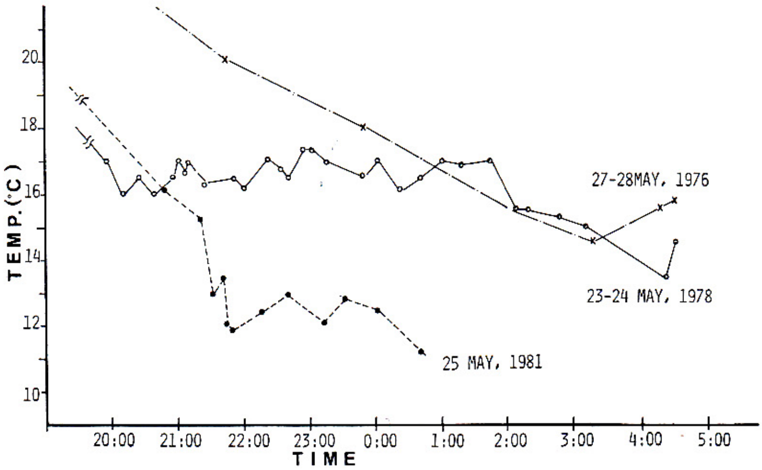


Fig. 2. Air temperature of habitat of *Hotaria parvula*. Recorded at Ohtsubashi, Nagoya City, central Japan.

Observations and experiments

Communication signals and associated behavior

Hotaria parvula KIESENWETTER

Field observations

Most of the research presented here was conducted on a large population of *H. parvula* inhabiting the marsh area of the moat of the Nagoya Castle, Nagoya City. Observations were made in late May at this site. Air temperature of this site is shown in Figure 2. Observations were also made at the top of Hirugatake of Tanzawa Mts., Kanagawa Prefecture (Pl. 1. 3), in the middle of July. The ground level of this area is approximately 1640 m. The habitat is covered with grass and is located at the edge of a forest. In Hirugatake, the season of adult activity was mid to late July. The following observations were made at Nagoya. The population studied numbered thousands of individuals. During peak activity flashing males could be seen along either bank of the moat of the Nagoya Castle for 1000 m and extending 50 m in width. The usual season of adult activity was from late May to early June. In 1981, males began to flash after sunset. At 21:00, males flew 0.5–1.0 m above the ground, but did not fly for very long. At 21:30, standing or walking males emitted flashes on the leaves of grass. The flashes were 2.19–3.92 (average 2.97) seconds in interval at 23°C. Then males flew and emitted flashes 0.73–1.03 seconds, and an averaging of 0.88 second, in interval at 23°C. During a period of 381 seconds, a male flew 1–2 m above the ground and moved 80 m distance as if in search of a female (Fig. 3). Then the average flight rate was 21 cm/sec. If a male could not find a female, the male flew and flashed until daybreak. Flash patterns of *H. parvula* are summarized

Table 2. Flash interval and duration of *Hotoria parvula*.
M=male, F=female, SD=standard deviation

DATE	TIME	TEMP.(°C)	SEX	N	MEAN(SEC.)	RANGE(SEC.)	SD	NOTE
26 MAY, 1979	0:30	18.0	M	3	0.94	0.15	0.07	FLYING
27 MAY, 1979	23:04	14.0	M	7	0.85	0.41	0.13	FLYING
	23:19	14.0	M	1	0.82	----	----	FLYING
25 MAY, 1981	21:42	13.0	M	4	1.02	0.11	0.04	FLYING
24 MAY, 1981	21:30	13.0	M	3	0.88	0.11	0.12	FLYING
	21:50	12.0	M	4	0.96	0.19	0.19	FLYING
	21:10	12.0	M	3	0.97	0.04	0.03	FLYING
	21:43	12.0	M	2	0.75	0.07	----	WALKING
27 MAY, 1979	23:56	15.0	M	2	0.79	0.23	----	WALKING
27 MAY, 1980	1:13	16.0	M	2	0.95	0.12	----	WALKING
	1:25	16.0	M	3	0.82	0.16	0.05	WALKING
	1:57	16.0	M	20	0.80	0.17	0.09	WALKING
24 MAY, 1981	21:30	13.0	M	3	2.97	1.73	0.72	WALKING
	22:23	13.5	M	1	3.00	----	----	WALKING
	21:22	13.0	M	7	2.54	3.69	1.11	WALKING
26 MAY, 1979	0:30	18.0	M		0.94	0.16	0.07	WALKING
28 MAY, 1979	0:00	14.5	M	1	0.67	----	----	WALKING
	22:40	12.0	M	2	0.59	0.54	----	WALKING
27 MAY, 1979	0:00	14.5	F	2	2.30	1.22	----	
26 MAY, 1979	0:30	18.0	F	4	2.34	1.92	0.69	
			F	2	2.85	1.61	----	
28 MAY, 1979	0:00	14.5	F	2	2.30	1.20	----	

Fig. 3. Luminescence of flying *Hotaria parvula*. Exposure was 30 seconds on recording film, developed at ASA 400.

in Table 2. Females remained stationary or sedentary and emitted species-specific signal to which the males were attracted. The female of this species has no hindwings and its luminous organ is species-specific form (Pl. 6. 1). If a female was emitting species-specific flashes and a make flew near the female, the male would be attracted by the flashes of the female within a distance 5–30 cm

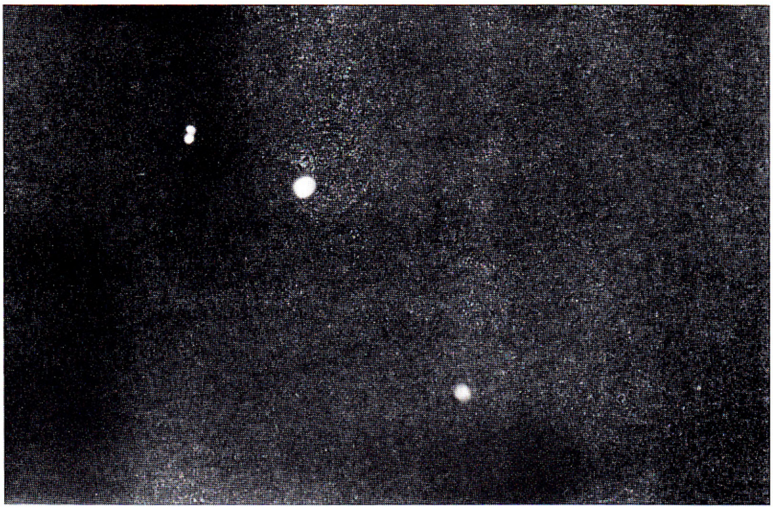


Fig. 4. Sexual flash communication during male-female interaction in *Hotaria parvula*. Showing a male attracted by a female. upper: female flashes, middle and under: male flashes.

Fig. 5. Male and female *Hotaria parvula* in copulation.

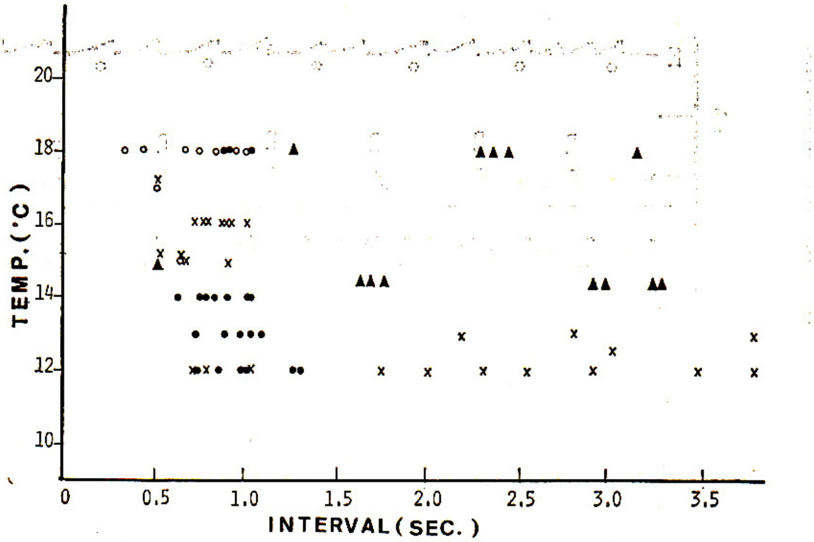


Fig. 6. Relationship of flash interval to temperature in *Hotaria parvula*. × perched or walking male, ● flying male, ○ male during male-female interaction, ▲ perched female.

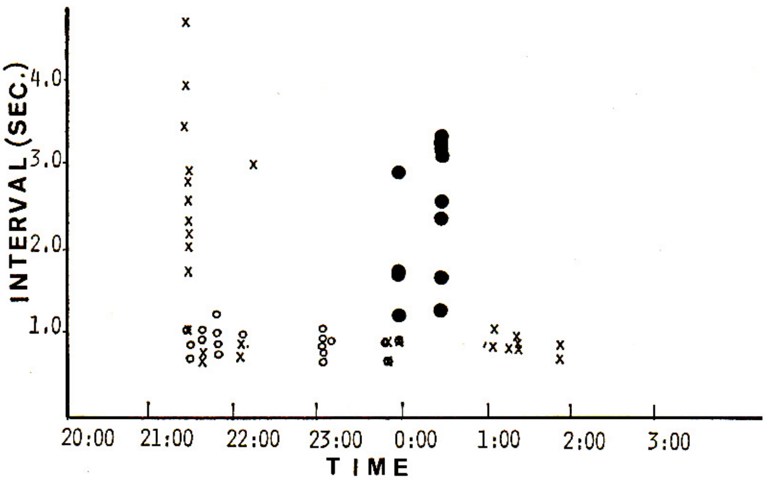


Fig. 7. Relationship of flash interval to activity time in *Hotaria parvula*. × perched or walking male, ○ flying male, ● perched female.

(Fig. 4). The female flashes were 1.26–3.18 seconds, averaging 2.34 seconds, in interval at 18°C. (Table 2). Relation between flash interval and temperature is shown in Figure 6. When a male found a female, the female flash interval gradually shortened (Fig. 7). She responded to a male flash after a short delay time (Fig. 8). Thereafter, the male copulate with the female (Fig. 5). Flash communication of this species has been reported by OHBA (1980a), except for the following observations. A female emitting characteristic flashes was placed

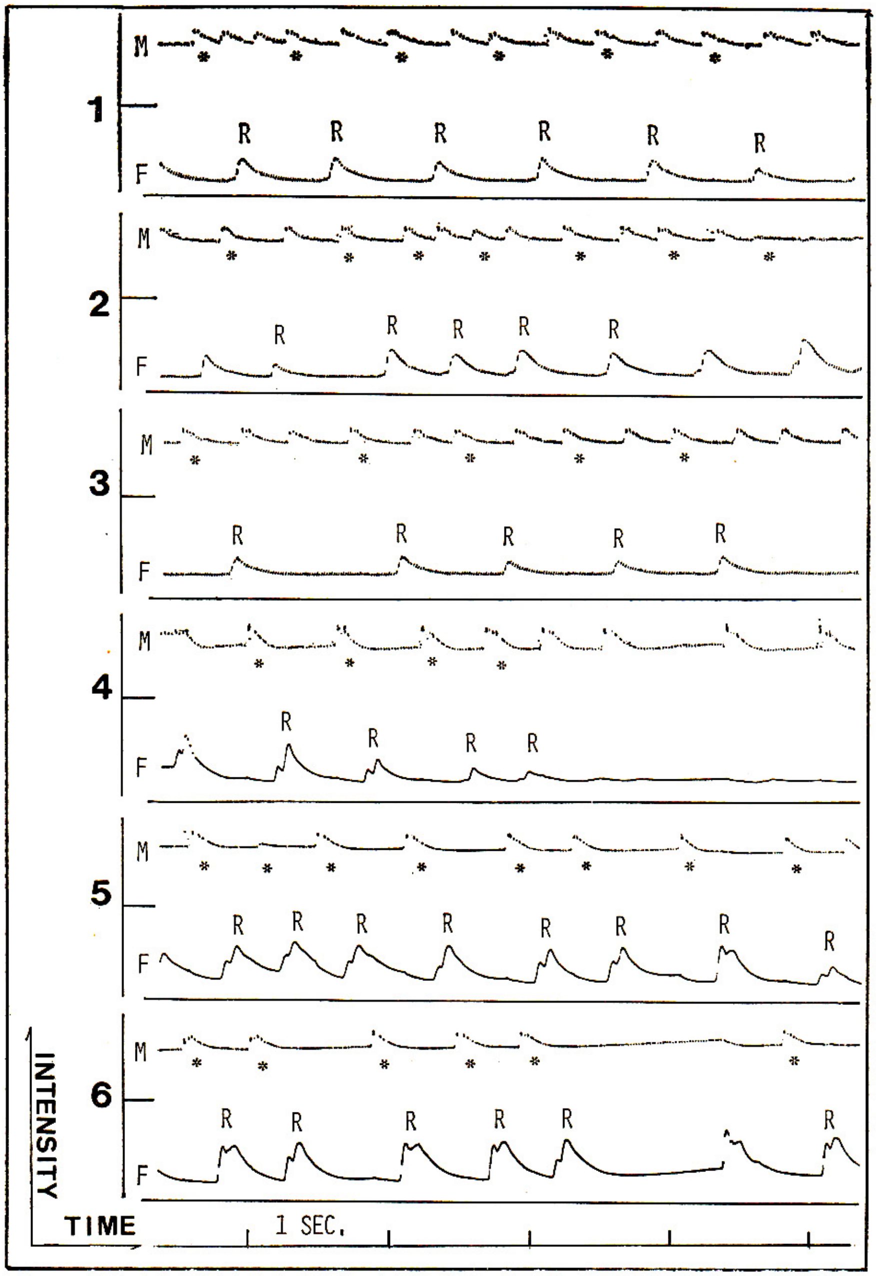


Fig. 8. Sexual communication during male-female flash interaction in *Hotaria parvula*, showing a female responding to a male flash after a short delay time. Recorded by a phototransistor system.
Light intensity was measured with a phototransistor which converted light energy into audiosignals. The latter was then recorded on tape and subsequently plotted with a pen-recorder. Read left to right.
M=male F=female R=response *=male pulse which is responded by female.

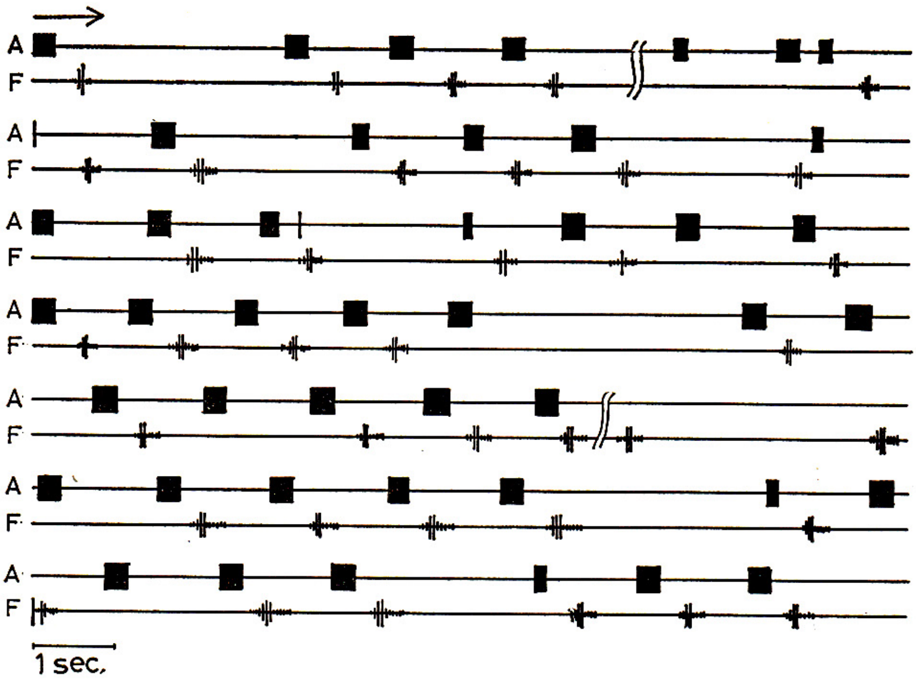


Fig. 9. Drawing from 16 mm cine-film showing flash responses of a *Hotaria parvula* to different kinds of artificial flashes.
A=artificial flashes, F=female flashes, | =bright flashes, ||| =twinkling dim-flashes.

in a clear plastic cage, and the cage was positioned near a male of the same species flying in the field. The males were definitely attracted by the flashes of the female in the plastic cage. Thereupon an attracted male emitted its own signal pulses and never flew away. When AF flashes of 2.0 seconds in interval and 0.4 seconds in duration were displayed at the same site, the AF flashes tended to attract the males. However, the male often flew away after a while. Flashing activity showed a tendency to repeat periodically and the time interval was approximately 10 minutes. When the AF flashes were emitted at the cessation of flashing activity, there was a tendency for the males to be released from the cessation.

Flash response of females from Mt. Hirugatake

Observations and experiments were conducted near the top of Mt. Hirugatake, Kanagawa Prefecture, east-central Japan on 13 July 1980, the air temperature being 13°C. Response of female flashes to red photodiode was experimented with and recorded by Method A. The result is presented in Figure 9. When a female emitting species-specific flashes was placed in the plastic cage, the female flash interval gradually shortened, and assumed a higher flash rate. When a

Table 3. Response delay time of a female *Hotaria parvula* to different kinds of artificial flashes.

ARTIFICIAL FLASHES		FEMALE RESPONSE DELAY TIME			FEMALE FLASH
INTERVAL(SEC.)	DURATION(SEC.)	MEAN(SEC.)	N	SD	DURATION(SEC.)
1.17	0.45	0.40	4	0.01	0.24
1.20	0.41	0.36	4	0.01	0.28
1.25	0.41	0.32	4	0.02	0.28
1.25	0.46	0.30	4	0.01	0.30
1.29	0.49	0.32	7	0.02	0.31
1.33	0.44	0.28	11	0.02	0.31
1.37	0.56	0.40	3	0.02	0.28

Recorded at 13℃, the top of Mt. Hirugatake, Kanagawa Prefecture. Recorded and analyzed by Method A.

female just started her characteristic flashing, the female flash response to AF flashes was of low frequency, but the response gradually increased to a higher rate in association with the passes. Usually, a female response began at 22:30, thereafter the female responded well. Then the average female response delay time was 0.34 second (Table 3).

Female flash response to the AF flashes is 0.2 second in duration, and the change in interval is from 0.2 to 1.9 seconds.

The female *parvula* population at Mt. Hirugatake was tested for its ability to discriminate between light flashes. The AF was placed 5–10 cm away from the plastic cage. The female then began to respond to it. The results are shown in Figure 11. A female responded every time to AF flashes of 1.1 seconds in interval and 0.2 second in duration. When the AF flash continued for a long time, the female was gradually allowed to rest from the response flashes. When this female was removed to a dark site without the AF flashes, it then resumed responding to artificial flashes again. A female coupled with a male did not respond to AF flashes. When the flashes were 0.1 second in interval, the female responded to the first AF flashes only. Thereafter the female did not respond to AF flashes because the interval became too short. When the AF flashes 0.35 second in interval, the female responded at three or four AF flashes apart. When the AF flash of 0.6 second in interval were presented, the female responded at two AF flashes apart. Furthermore, when AF flashes of 0.85 to 1.9 seconds in interval were presented, the female responded to the AF flashes every time.

Table 4. Waiting time of female for artificial flashes. Recorded at 13℃.

ARTIFICIAL FLASHES		WATING TIME OF FEMALE			
INTERVAL(SEC.)	DURATION(SEC.)	(SEC.)			
3.5	0.2	2.7	2.7	3.0	3.5
4.0	0.2	3.7	3.8	4.0	4.0
6.0	0.2	5.0	5.6	5.4	6.0
9.0	0.2	8.8	8.6		

Table 5. Response delay time of a *Hotaria parvula* to different kinds of artificial flashes.

AFI(SEC.)	AFD(SEC.)	N	AvFRDT(SEC.)	SD
0.12	0.12	1	0.32	----
0.25	0.20	1	0.24	----
0.54	0.32	17	0.31	0.02
0.56	0.32	18	0.31	0.01
0.74	0.13	11	0.28	0.03
0.77	0.14	6	0.27	0.01
0.79	0.14	57	0.25	0.04
0.82	0.44	17	0.24	0.00
0.82	0.44	12	0.24	0.00
0.96	0.34	18	0.30	0.06
0.80	0.30	31	0.25	0.02
1.02	0.34	30	0.24	0.03
1.06	0.32	5	0.29	0.00
1.08	0.50	8	0.26	0.01
1.36	0.51	2	0.26	----
1.38	0.79	2	0.28	----
1.46	0.64	2	0.26	----
1.53	0.32	9	0.25	0.03
1.54	0.22	3	0.15	0.04
1.56	0.76	5	0.26	0.00
1.86	1.86	14	0.25	0.04
1.88	1.04	2	0.26	----
1.88	1.26	12	0.23	0.05
2.01	1.99	6	0.23	0.01
2.08	1.94	14	0.22	0.02
2.10	2.00	5	0.23	0.00
2.86	1.98	4	0.28	0.04
4.04	1.96	1	0.24	----

AFI=artifical flash interval; AFD=artificial flash duration; N=number AvFRDT=average female response delay time. Recorded at 21.5℃.

In order to present AF flashes of long interval, the AF switch was changed from auto to manual. A female was then exposed to AF flashes of long interval. When the AF interval was over 2.7 seconds, the female flash ceased until the AF emitted the next flash. The maximum cessation time was 8.8 seconds (Table 4). Generally the female often resumed flashing naturally when the AF flashing was stopped for a while. When the interval between AF flashes was over 2.7 seconds, the female did not wait for the next AF flashes, but emitted species-specific flashes. Signals which were recorded with a photo-cell connected to a tape recorder gave the same patterns as in the case with the 16 mm cine-camera (Fig. 10). In Nagoya, female *parvula* emitted the same flash patterns as the individuals at Hirugatake. When a male flashed at a rate too fast in interval, the female responded apart to the male flashes. When the male flash interval was over 0.6 second, the female responded to the male flashes every time (Fig. 10. 3–14) and the female response delay time was almost constant (Table 5).

Response of the female to AF flashes of constant interval and variable duration

When the AF flash interval was 1.25 seconds and duration varied from 0.30 second to 5.8 seconds, the female responded to AF flashes (Fig. 12). The female responded to AF flashes every time when the AF flashes were 0.3 second in duration. When the duration were 1.3 seconds, the female responded with a short delay time to the AF flashes at the beginning of AF flashes. During AF flashes, the female often emitted individual flashes. When the AF flashes were 2.6 seconds in

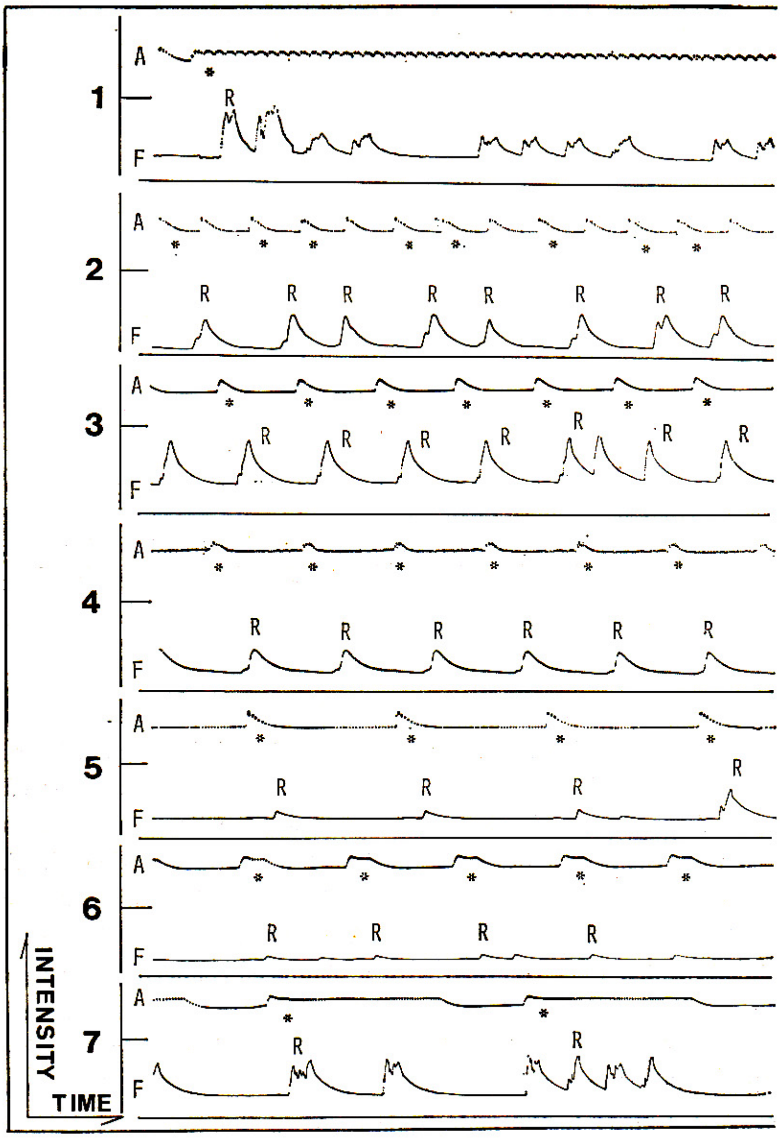
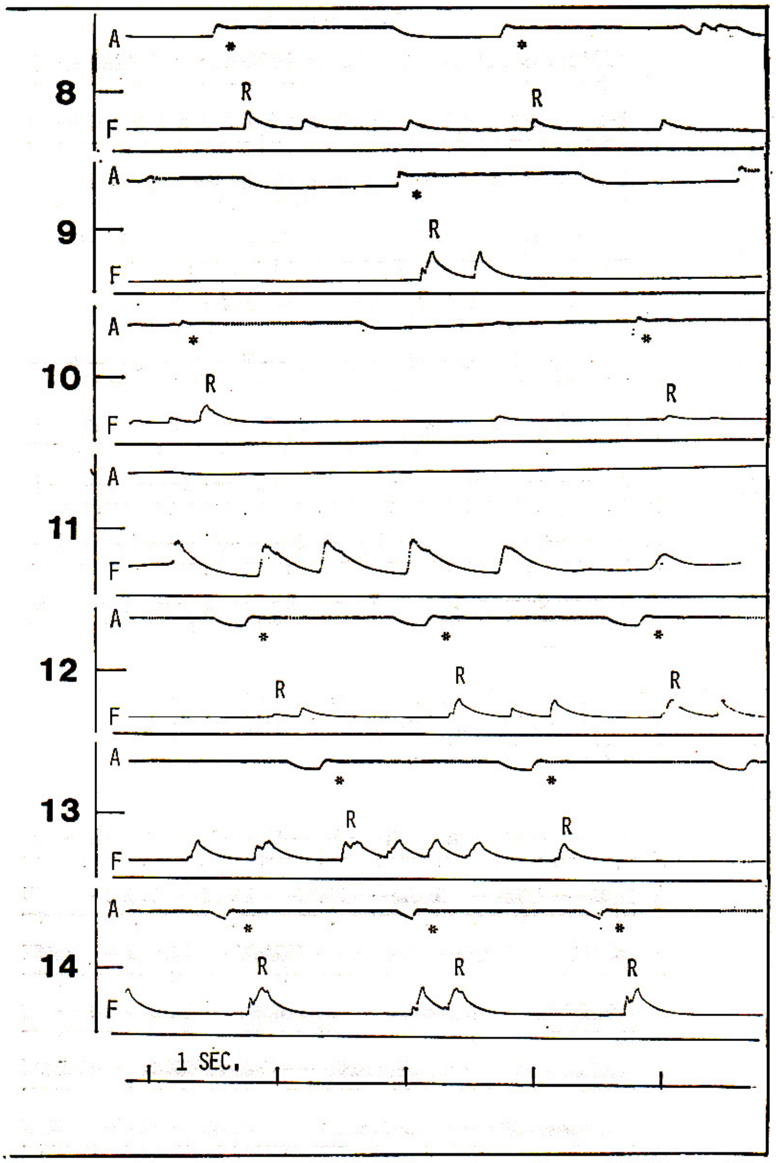


Fig. 10. Flash response of a female *Hotaria parvula* to variable flash patterns of artificial flashes.
A=artificial flashes, F=female flashes, R=response, *=male pulse which is responded by female.


8
A
F
R
R
9
A
F
R
10
A
F
R
R
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12
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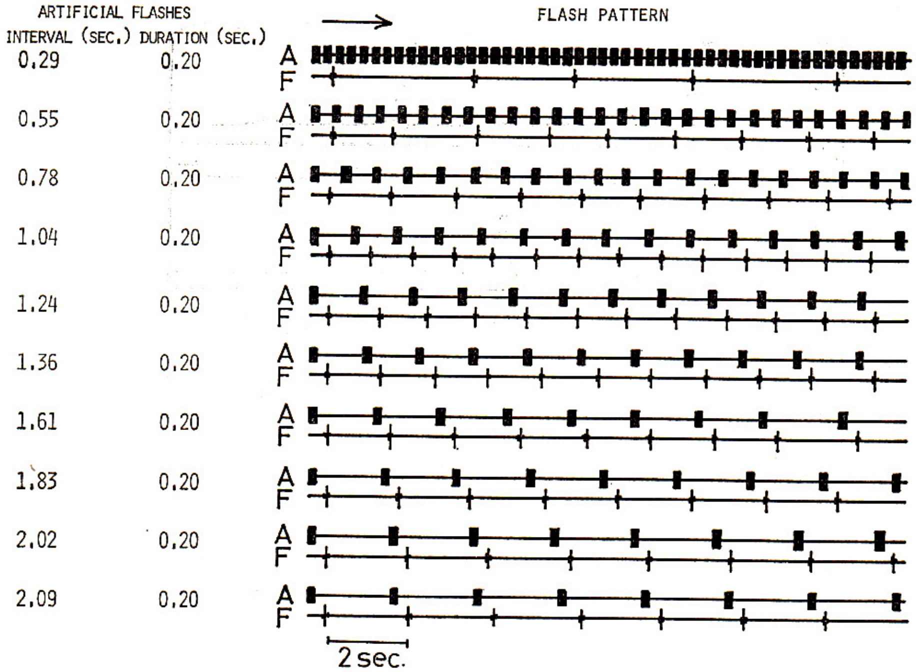

Fig. 11. Drawing from 16 mm cine-film showing flash response of a female *Hotaria parvula* to different intervals of artificial flashes. A=artificial flashes, F=female flashes.

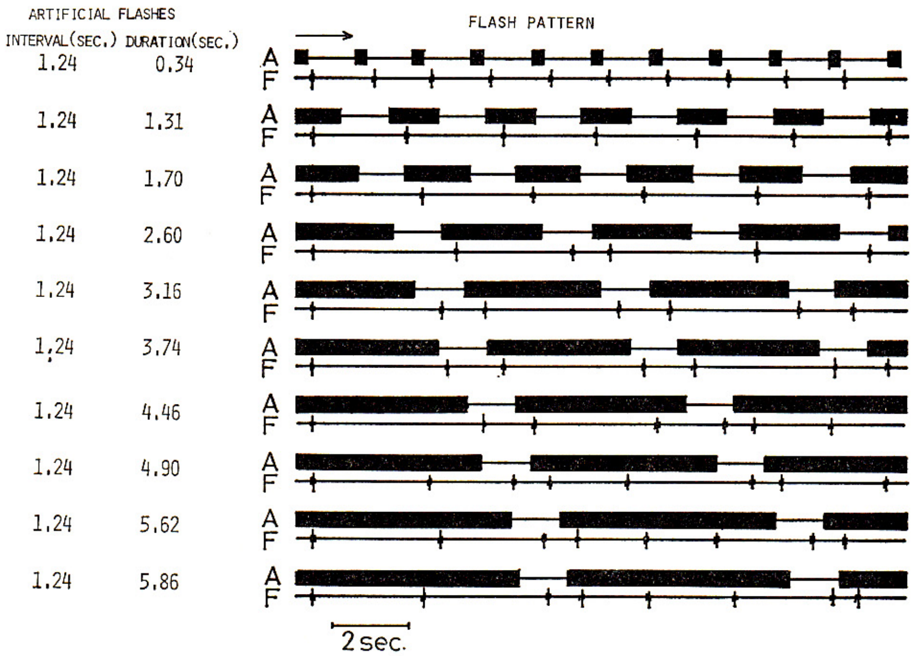

Fig. 12. Drawing from 16 mm cine-film showing flash response of a female *Hotaria parvula* to different durations of artificial flashes. F=female flashes.

duration, the female emitted species-specific flashes between the AF flashes. When AF flashes were 3.5 seconds in duration, the female emitted individual flashes during AF flashing. When AF flashes were 8 seconds in duration, the female responded to the AF flashes and emitted 2–3 pulse individual flashes. These individual flashes were released when the female was exposed to AF duration for a long time (Fig. 12). Signals recorded by Method C gave the same pattern as in the case with Method A. Females responded to various AF flashes, at which time the female response delay time was almost constant. The next female response flash was not prevented by AF flashes of long duration. Response flashes were emitted from non-coupled female only. Response flashes and individual flashes were not emitted from coupled female. Average female response delay time was about 0.25 second at 21.5°C in population of Nagoya (Table 5). This female response delay time was the same as in a natural male.

Laboratory observations

Diffraction spectrum of *H. parvula* and AF flashes

Flashes of *H. parvula* were analyzed by using an optical equipment covering the range from red to green wave length. The female responded to red, green, yellow, and the other visible wave lengths but not infrared rays.

Effect of distance between females and AF flashes on female response flashes

A female responded well to AF flashes covering distances from 5–10 cm. When the distance was over 100 cm, the female did not respond to the AF flashes. In the latter case the AF flash light was emitted from a green photodiode.

Female-female flash interaction

When a female (A) and another female (B) were placed in the same plastic cage, female-female interaction was recorded by Method C. The results are shown in Table 6 and Figure 13. This flash interaction resembled the male-female interaction in the field. However, the female-female interaction never continued for a long time. Female (A) and (B) alternately responded to each other's flashes. For example, when female (A) flashed first, female (B) responded to female (A); when female (B) flashed before female (A), female (A) responded to female (B). The response delay time of female (A) was 0.20–0.32 second, with an average of 0.28 second. The time for female (B) was the same as female (A). The response delay time (Table 6) was similar to that of a male-female interaction.

Male-male interaction

When a male in the plastic cage was placed near a female emitting individual flashes, the male emitted flash signals and tried to approach the female. When the female was replaced with another male (B), the male (A) immediately chased and attempted to mount the male (B) (Fig. 14), but copulation could not take place because of a difference in genital structure.

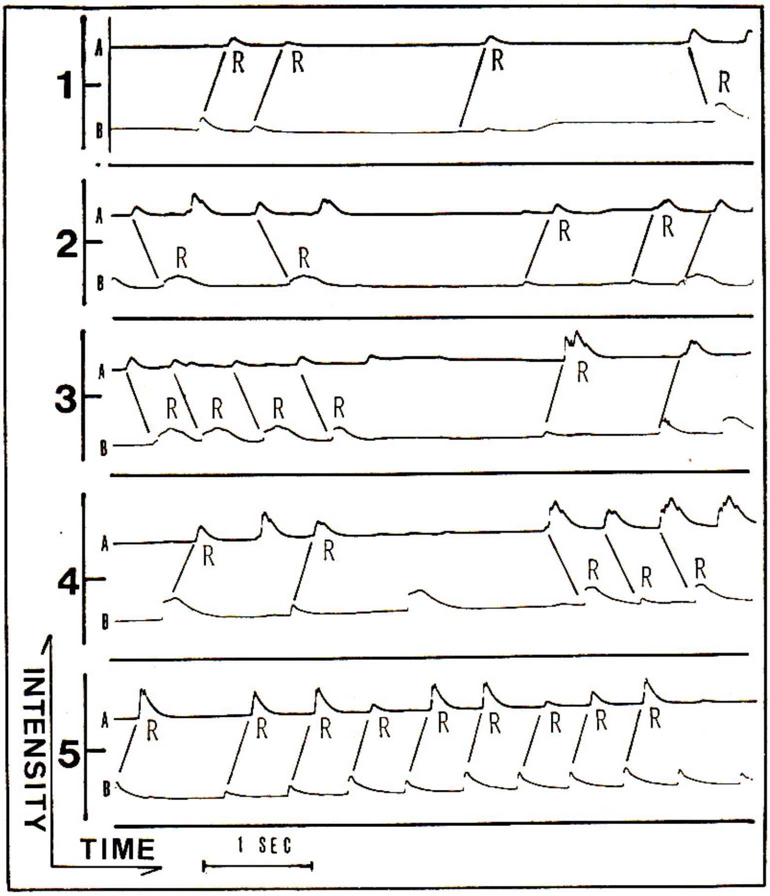

Fig. 13. Flash response during *Hotaria parvula* female-female interaction. R=response flashes. Recorded and analyzed by a phototransistor system.

Table 6. Response delay time of *Hotaria parvula* during female (A) and female (B) interaction.

FEMALE	RESPONSE DELAY TIME(SEC.)									
	MEAN	SD	RECORDED VALUE							
A	0.27	0.03	0.26	0.26	0.24	0.20	0.28	0.26	0.24	0.20
			0.24	0.24	0.22	0.31	0.31	0.31	0.32	0.30
			0.23	0.20	0.30	0.30	0.22	0.23	0.26	0.28
			0.30	0.24	0.24	0.28	0.27	0.27	0.27	0.27
			0.30	0.30	0.30					
B	0.28	0.04	0.30	0.35	0.30	0.30	0.30	0.35	0.28	0.28
			0.28	0.30	0.32	0.34	0.32	0.32	0.32	0.32
			0.24	0.26	0.32	0.26	0.26	0.26	0.26	0.26
			0.22	0.29	0.22	0.22	0.29	0.23	0.24	0.24
			0.32	0.24	0.24	0.20	0.20	0.20	0.26	0.28
			0.20	0.20	0.24	0.38	0.30	0.30	0.30	0.30
			0.30	0.32	0.30					

Recorded at 21.5°C. Recorded and analyzed by Method C.

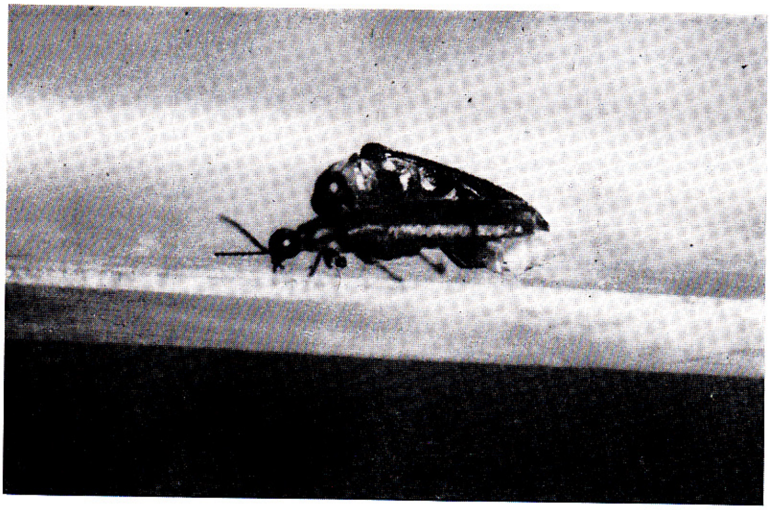

Fig. 14. Courtship display in *Hotaria parvula*, showing a male attempting to copulate with another male.

Luciola lateralis MOTSCHULSKY

Field observations

Observations and experiments were carried out at Yoshii, Yokosuka City, Kanagawa Prefecture, in east-central Japan (Pl. 1. 1). A male began flying and flashing with a single pulse at 19:40; the flashes were 0.5–1.0 second in interval, and about 1.0 second in duration. Usually, males flew 1–3 m above the ground. Several females were found in low grass, perched 10–30 cm above the ground. Females were flashing with single pulse flashes, 2.8–5.8 seconds in interval, and 1.0–1.2 seconds in duration at 23.0°C (Table 7, Fig. 15). When a male found the flashes from a female, the male immediately approached the female within 5–10 cm in distance and the flashes were converted to single flashes

Table 7. Flash pattern interval and duration in *Luciola lateralis*.

SEX	TIME	TEMP. (℃)	INTERVAL (SEC.)			DURATION (SEC.)		
			MEAN	SD	RECORDED VALUE	MEAN	SD	RECORDED VALUE
M	20:23	23.0	1.20	0.17	1.20 1.40 1.30 1.20 0.90	0.65	0.05	0.70 0.60 0.60 0.70 0.60
M	20:25	23.0	1.12	0.18	1.03 1.50 1.50 1.14 1.16 1.24 1.54 1.08 1.14 1.24 1.20 1.24 1.24 1.04 0.93 1.04 1.08 0.92 0.84 1.10 0.90 0.98 0.96 0.86 1.06	0.66	0.09	0.75 0.80 0.84 0.87 0.68 0.68 0.68 0.72 0.68 0.64 0.60 0.60 0.60 0.60 0.56 0.60 0.64 0.64 0.64 0.60 0.50 0.52
M	20:30	23.0	1.08	0.24	1.09 1.18 0.80 1.08 0.85 1.53	0.35	0.13	0.53 0.36 0.22 0.20 0.44
M	20:32	23.0	8.68	1.92	6.60 7.90 6.20 9.74	2.62	1.01	2.00 1.90 2.20 2.40 5.00 2.20 3.00 2.40
F	20:35	23.0	4.56	1.79	6.00 5.60 2.80 2.00 4.55 6.40	0.78	0.27	0.40 1.00 0.50 1.00 1.00
F	20:33	23.0	4.15	0.83	2.80 5.80 3.50 4.30 3.50 4.30 4.00 5.00	1.05	0.09	1.20 1.00 1.20 1.00 1.00 1.00 1.00 1.00

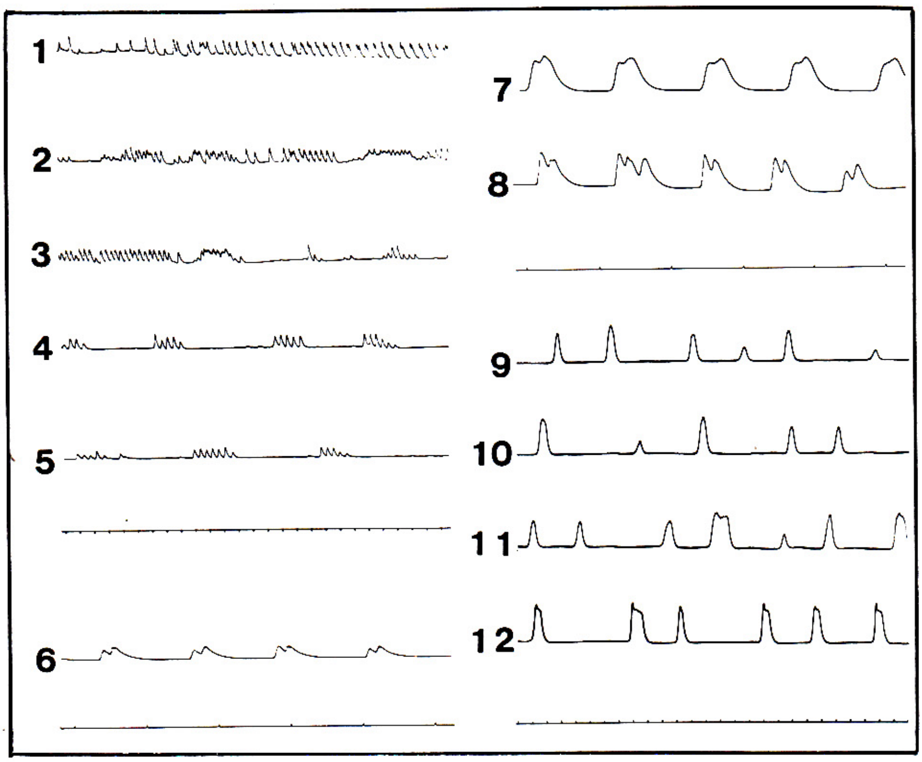

Fig. 15. Chart traces of *Luciola lateralis* recorded with a phototransistor system in the field. Recording left to right. Ordinate: relative intensity, Abcissa: time, the scale as indicating 1 second. Recording temperature is 23°C. 1–8, male flashes, 9–12, female flashes.

with twinkling. The single flashes were frequently bimodal or trimodal and the time separation of the modes varied (Fig. 15. 6–8). The duration of bimodal and trimodal flashes was variable. Flash periods or interval were also variable. Frequency of modulation during flickers varied from 0.09–1.25 Hz and it seldom remained constant for more than 1 Hz in a given flicker. When a male approached a female, the flashes of both sexes were modulated to give shorter flashes. There was a tendency for the male flashing to be released when the female emitted her individual flashes to the male. During flashes, the female flexed her abdomen in the same direction as the stimulus flashes. This female behavior indicated her calling behavior. Then the flashes were 1.2 seconds in interval and 0.4 second in duration. When the AF flashes simulated the female flashes and the instrument was placed in the field near the flying males, the males were directly attracted to the AF flashes of red and green light from the photodiode (Fig. 16). The male approached a female directly within 10–30 cm in distance, while both sexes were emitting individual flashes and attempting copulation with the AF. Males were attracted by the flashes of a female in a plastic cage

Fig. 16. Males of *Luciola lateralis* are attracted by artificial flashes (AF).

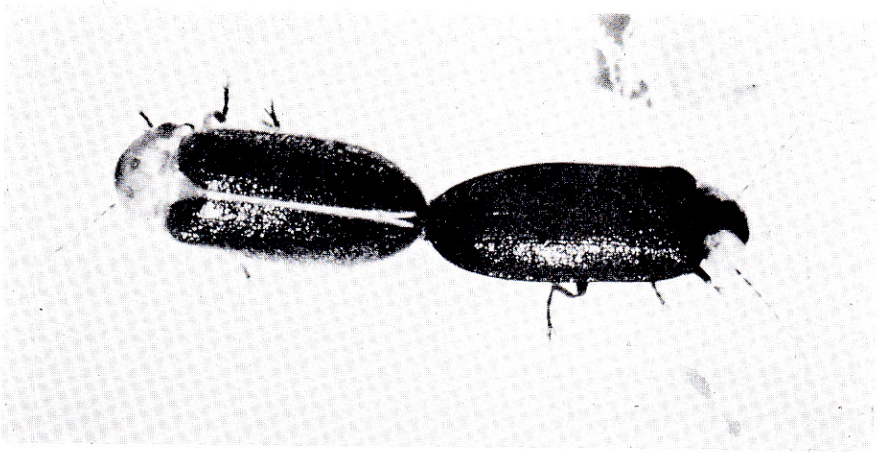

Fig. 17. Male of *Luciola lateralis* and female of Taiwanese *Luciola* firefly (left) in copulation.

and also strongly attracted by the winker light of a motor cycle. The flashes and AF flashes attracted males only within 20 m in distance. A male coupled with a female was observed on a footpath between rice fields. The peak flying activity was at about twenty o'clock, but this activity was diminished or ended by strong wind, rain, moonlight and other illuminations.

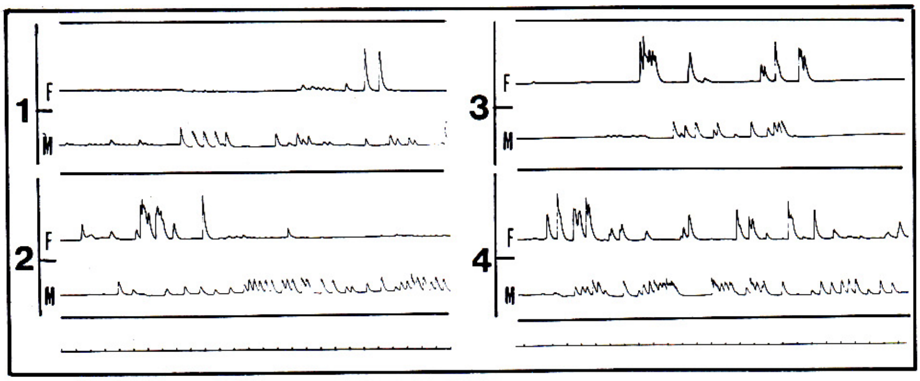

Fig. 18. Chart traces of *Luciola lateralis* recorded with a phototransistor system in the laboratory. Readings left to right. Ordinate: relative intensity, Abscissa: time, scale indicating 1 second. Male-female interaction. M=male, F=female.

Laboratory observation

AF—male flash interaction

A male was strongly attracted by single-pulsed AF flashes of 1.0 second in interval and 0.3 second in duration. When the AF was removed to another site, the male chased the AF flashes immediately. When the AF flashing was kept on for a few minutes, the male gradually display sexual behavior such as mounting and attempting to insert the genitalia toward the photodiode. If a female was placed near a male, the male was also attracted by the female and entered into sexual display. Thereafter they copulated. If a different species of Taiwanese-firefly, a *Luciola* sp. which is closely related to *L. lateralis* (OHBA, 1981b) is put near a *L. lateralis*, interaction between the species took place. Their flash patterns were similar to each other. The male *lateralis* approached the Taiwanese species and the male engaged in his sexual display such as mounting and attempting to insert the genitalia, thereupon the male copulated with the female (Fig. 17). Both species are closely related to each other in form and behavior and genital structure.

Male-female flash interaction

Male and female of *L. lateralis* emitted individual flashes to each other. It was not observed that the female responded to the male with critical timing flashes in this species. The male-female flash interaction was recorded and analyzed by Method C as shown in Figure 18.

Luciola cruciata MOTSCHULSKY

Field observations

Study was made at Nobi, Yokosuka City, Kanagawa Prefecture, on 15 June 1981, at Toyoda, Yamaguchi Prefecture, on 29 May 1975, and at other sites. At

Table 8. Flash pattern interval and duration in *Luciola cruciata*.

SEX	TIME	TEMP.(°C)	FLASH PATTERN						NOTE
			INTERVAL(SEC.)			DURATION(SEC.)			
			MEAN	SD	RECORDED VALUE	MEAN	SD	RECORDED VALUE	
M	19:36	20.0	5.59	0.58	4.5 6.1 6.1 5.3 6.3 5.5 5.3	2.70	0.31	3.3 2.6 2.6 2.7 2.9 2.8 2.2	
M	19:43	20.0	5.80	0.46	5.2 6.0 6.3	2.10	0.24	2.1 1.8 2.4	FLYING
M	20:03	20.0	4.70	0.45	5.4 4.5 4.6 4.2 4.6 4.1 5.3	2.50	0.15	2.4 2.4 2.4 2.3 2.3 2.8 2.5 2.5	FLYING
M	20:04	20.0	5.60	0.61	6.4 4.8 5.3 5.0 6.0 4.8 6.2 5.2 6.4 5.9	2.50	0.57	2.0 3.7 2.4 1.7 2.1 2.0 3.0 3.0	FLYING
M	20:42	23.5	1.90	0.12	1.9 2.0 1.8 1.7	1.10	0.20	1.5 1.0 1.0 1.2 1.0	
M	20:44	23.5	4.60	1.17	4.5 3.5 6.5 3.8	2.60	0.64	2.5 2.7 3.5 1.7	
M	20:47	23.5	1.70	0.22	1.9 1.7 1.4 1.9 2.0 1.5 1.6 1.6 1.2 1.7	1.30	0.07	1.3 1.4 1.4 1.3 1.3 1.3 1.2 1.3 1.2 1.2 1.3	
F	20:50	23.5	1.80	0.53	1.5 1.5 1.4 2.5 2.8 1.4 1.8	1.00	0.10	1.2 0.9 0.9 1.0 0.9 0.8 1.0	

Fig. 19. Luminescence of flying *Luciola cruciata*. Exposure was 30 seconds on Kodak recording film, developed at ASA 400.

Toyoda, flying and flashing fireflies were found along a clear flowing river whose banks were covered with grass and trees. The river was approximately 20 m in width, and 30–100 cm in water depth. Males began flying and flashing along the river after sunset. Their flashes were single long-pulsed flashes (Fig. 19). At Nobi, Yokosuka City, a small stream runs along a rice field, one side of which is a forest edge. The stream is 30–100 cm in width, and 5–10 cm in depth. Males began flying and flashing at about 19:30. The flash patterns were recorded by

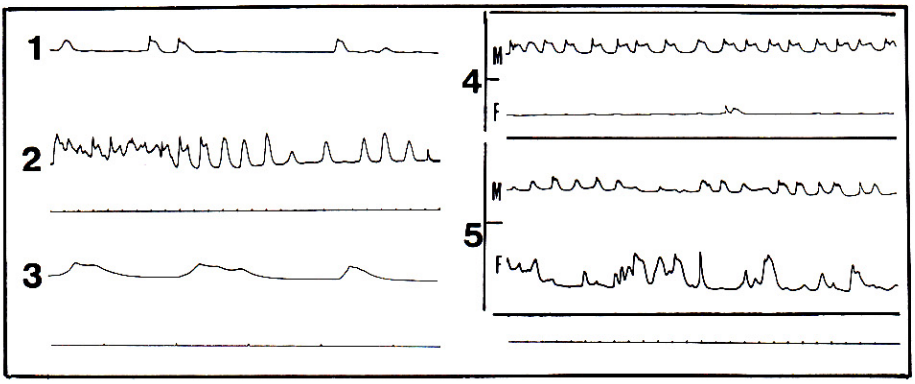

Fig. 20. Chart record of flashes of *Luciola cruciata* and male-female interactions, recorded with the phototransistor system in the field. Read left to right. Ordinate: relative intensity, Abscissa: time, scale indicating 1 second. Recording temperature 20°C. 1–2, flickering of walking male; 3, flickering of perched male; 4–5, male-female flash interaction, M=male, F=female.

Method D. Flashes of flying males were 4.5–6.1 seconds in interval with a 5.59 seconds average interval, and 2.2–3.3 seconds with a mean of 2.7 seconds in duration at 19:36, 20°C (Table 8). Males generally flew 2–3 m above the ground in a very slow leisurely flight, but occasionally flew up to 10 m above the ground. The flash pattern which consisted of a single long pulse, was emitted which the male executed the lateral and horizontal arches. When a flashing, flying male discovered another flying male, the male flew toward that male and collided with it. Female flashes were also single-pulsed flashes. Males flashed and approached females perching on leaves. Sometimes the female repeated a slow flashing when a male was absent near the female. If a male approached the female, the female sometimes responded with flashes of no critical timing (Fig. 20). There was discernible interplay of signals between sexes as found in American species using Signals System II. Many different kinds of interactions occurred between individuals. Males commonly landed a few centimeters from perched luminescing females. Perched males would sometimes begin flashing as a male or female flew over them. The most common luminescent emissions of males were flickers and single flashes. While perched, flashing males generally held up their luminous organs (Fig. 21). Male flashing activity continued for approximately one hour. Peak flying activity was reached at about 20:00. Males flashed from the perched position in the grass a few minutes before taking flight. Many males were captured and eaten by spiders as they flew in search of a female. Peak flashing activity lasted for approximately 60 minutes, although occasional males could be seen later emitting their distinctive flash patterns. Sometimes males emitted only periodically. Occasionally, a male flew

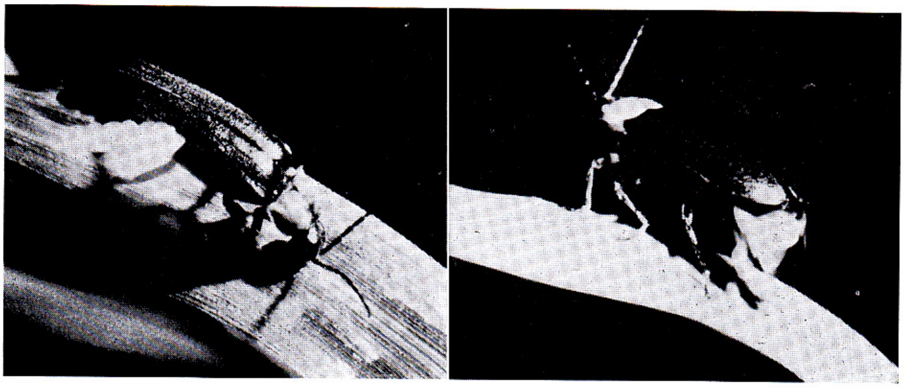

Fig. 21. Courtship display in *Luciola cruciata*, showing a male holding up his luminous organs and strongly emitting single-pulsed flashes.

down to about 10 cm above the stream, perhaps responding to the reflection of their own luminescence. Males also approached a glowing cigarette, AF flashes and the flashes of a male in a plastic cage. However the attracted males did not stay for long and generally they flew away after a few seconds.

Laboratory observation

Flash patterns of standing and walking individuals were recorded by Methods B and C. The results are shown in Figure 21 and Table 8. Sometimes strong single flashes were emitted from a standing male or female. Thus, females did not respond to males or AF flashes as in *H. parvula* using signals. When a male and a female were placed in the same plastic cage, they did not copulate immediately; they copulated after a period of more than one hour. This species and the closely related species *L. lateralis* were found together at the same site of Nobi, Yokosuka City. They were active during the same period of the evening. However, no hybrid individual of these species was found.

Luciola kuroiwae MATSUMURA

Field observations

This species was observed at Hyakuna, Okinawa Is. (Pl. 1. 7), southern Japan. Observations were made in early May. This species was active during May at Hyakuna, a large population was found at this site. Their activity continued at one or two meters above the ground, and during their display of single-pulsed flash patterns, males flashes appeared to be 0.8–1.0 second in interval and less than 0.4 second in duration at 25°C. Flash patterns of the flying male resembled those of the males of *H. parvula* (Fig. 22). Male flashing activity began at approximately 19:30, while flight was at a slow pace. Female of this species has only recently become known. A morphological note on the female has been reported (OHBA, 1979d). The female has wings, but flying females were not found in this habitat. Females emitted flash signals on

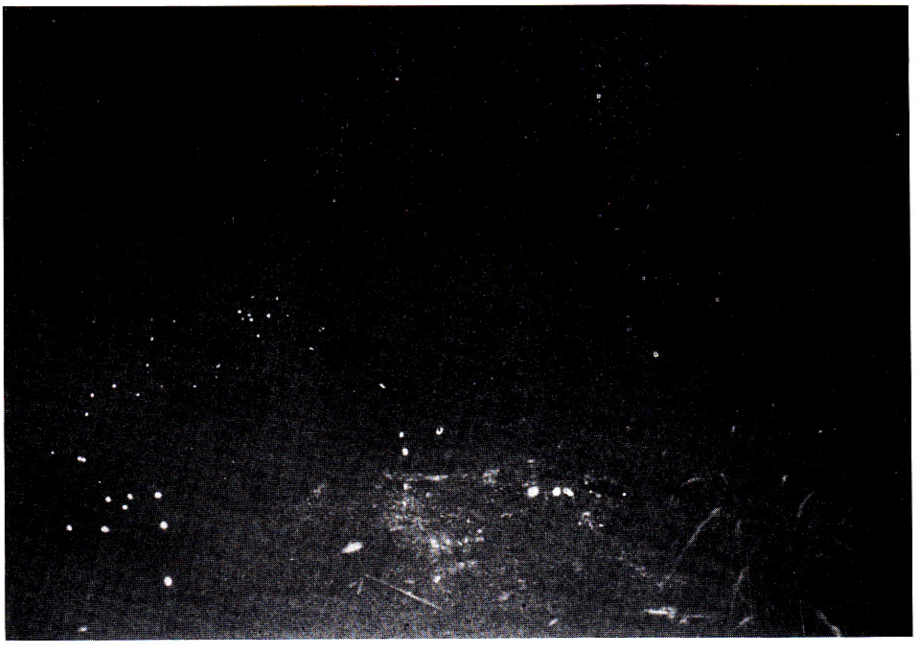

Fig. 22. Luminescence of flying *Luciola kuroiwae*. Exposure was 20 seconds on Kodak recording film, developed at ASA 400.

the leaves or the base of grass stem. Only two females were collected at this site.

Laboratory observation

Flash patterns of perched and walking males were recorded and analyzed by Methods A and B (Fig. 23. 1–3). The flash patterns resembled those of *H. parvula*. The male has large compound eyes and luminous organs, and his antenna is short and small (Pl. 5. 4).

Luciola yayeyamana MATSUMURA

Field observations

This species was seen at Mt. Banna, Ishigaki Is., Okinawa, in southern Japan on 4 May 1979 and on May 1977. Male flying and flashing activity began after sunset. The males were found in the roadside grass at the edge of a forest (Pl. 1. 6). Males emitted single-pulsed flashes which resembled those of *H. parvula*, and flew 0.7 m above the ground. Their flying activity was confined to a narrow and limmited area. During the daytime, the males perched on the leaves of a tree. Flying individuals were males only and females of this species were not found in this study. The female might be wingless. Flashes of flying male were approximately 1 second in interval, and less than 0.4 second in duration. This species closely resembles *H. parvula*.

Laboratory observations

Flash patterns of walking and standing males were recorded by Methods

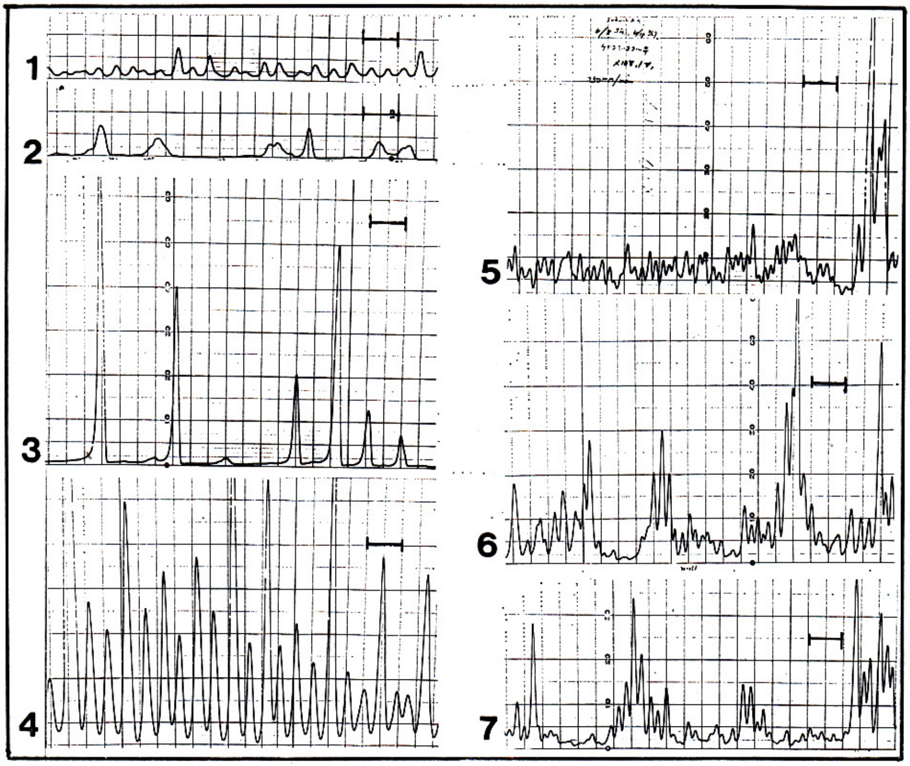

Fig. 23. Luminescent emission of *Luciola cruciata* recorded with the photomultiplier system in the laboratory. Chart record, read right to left. Ordinate: relative intensity, Abscissa: time, the thick scale indicating 5 seconds. 1–4, male flashes; 5–7, female flashes.

A, B, and D (Fig. 24. 6–8). The flash interval was approxximately 0.6 second and the duration was less than 0.4 second at 24°C. Thus, flash patterns were similar to those of *H. parvula.*

Curtos costipennis GORHAM

Field observations

This species is widely distributed in Ryukyu Isls., and Amami Isls., southern Japan. *C. costipennis* was observed in Iriomote Is., Mt. Banna, Ishigaki Is., and Miyako Isls., Okinawa, (Pl. 1. 5–6). In Iriomote Is., the season of adult activity was from early May to late August. This species was found along the roadside forest edge. Dems were moderate in size, each were seen with 50–200 mates around a rush in a roadside ditch. Male flight path was a long arc. Generally, males flew straight, and slowly at 1–5 m above the ground, and traversed approximately 1 m long between flashes. Females were found on leaves in a grove of trees or at the tip of grass 10–50 cm above the ground. The flash patterns consisted of single slow pulses and apeared to be 2–3 seconds in duration at 26°C. Mean

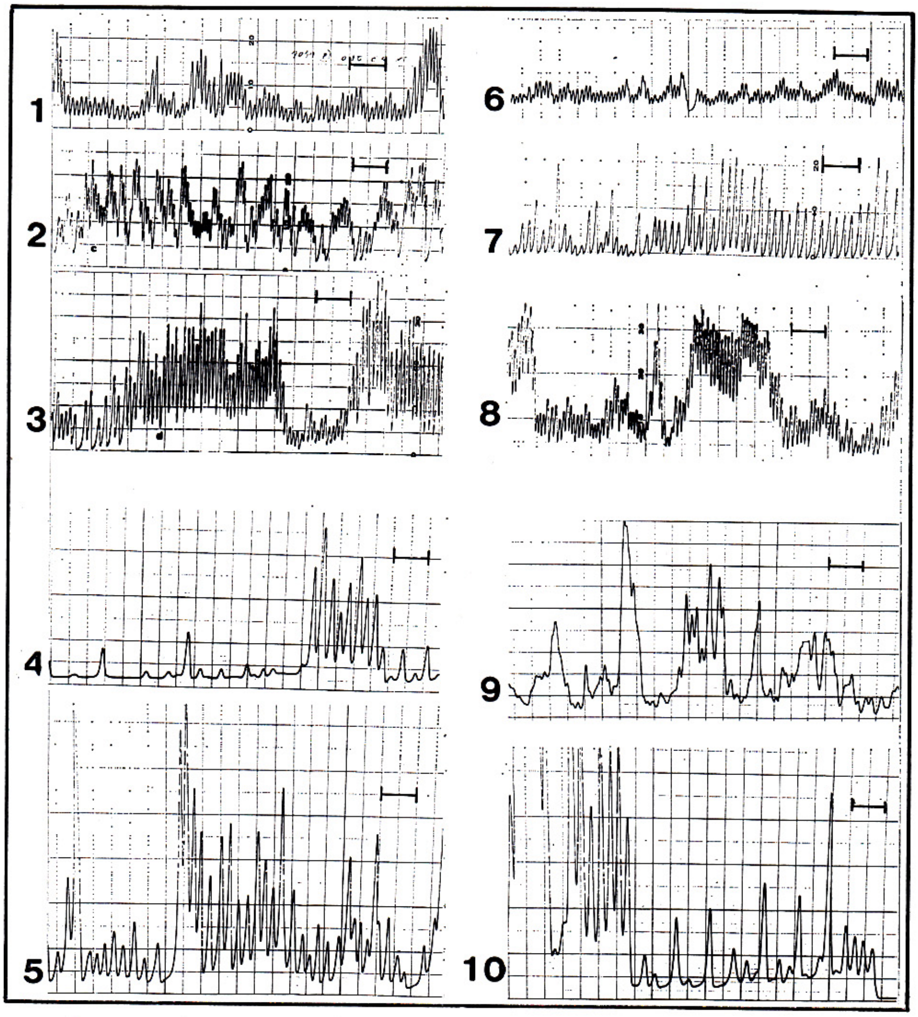

Fig. 24. Chart traces of luminescent emission of *Luciola kuroiwae*, *L. yayeyamana* and *Curtos costipennis* recorded with a photomultiplier system in the laboratory. Chart record, read right to left. The thick scale indicating 5 seconds. Recording temperature 24°C.
1–3, walking male *L. kuroiwae*; 6–8, *L. yayeyamana*; 4–5, walking male *Curtos costipennis*; 9–10, female *C. costipennis*.

flash interval was 3 seconds. Males were attracted by female and AF flashes (interval, 1.0–1.5 seconds; duration, 0.5–0.8 second) (Fig. 25).

Laboratory observations

Flash patterns of walking and perched individuals were recorded by Method B (Fig. 24. 4–5, 9–10). The most common luminescent emission of male was flickers and single flashes.

Fig. 25. Luminescence of flying *Curtos costipennis*, showing males are attracted by AF flashes.

Curtos okinawana MATSUMURA

Field observations

Studies were made on this species at two localities in Nago City, and at Hyakuna, Okinawa Is., southern Japan. A large population was present at Hyakuna, on 6 May 1979. This species was found along the road side in hedges, bushes and at the edge of mesophytic forest. Male flashing activity began approximately at 19:30. Both sexes flew 1–3 m above the ground. This species and *L. kuroiwae* were found together at the same site. They were active during the same period of the evening. However, no interaction was observed between *C. okinawana* and *L. kuroiwae*. The flying male flashes were a single slow-pulsed flashes of 2–3 seconds in interval and 1–2 seconds in duration. Several females were seen flying together with males, but most individuals were found above the ground or lying within 60 cm above the base level of grass stems. *L. kuroiwae* was also seen frequently at the same site.

Laboratory observations

Male and female flash patterns were recorded by Method B (Fig. 26. 1–5). The flash patterns consisting of a single flash emitted during walking or standing, were similar to *C. costipennis*. The larva of this species emitted continuous light.

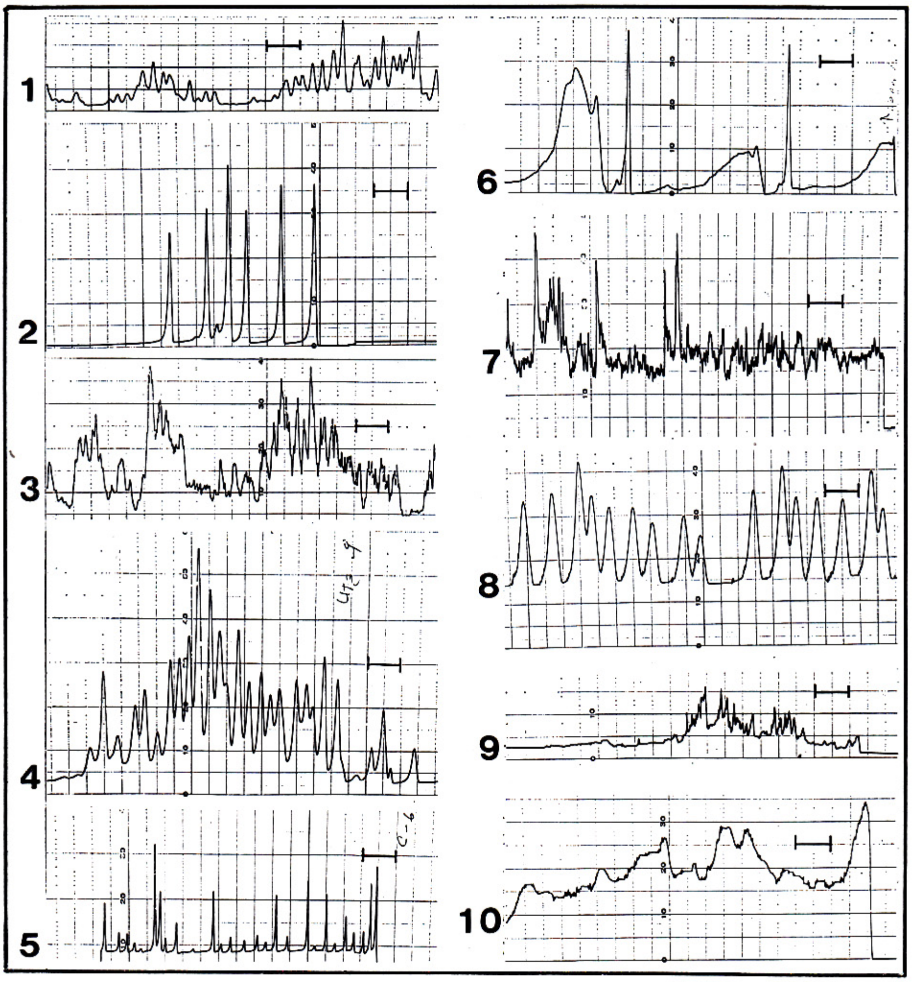

Fig. 26. Chart traces of luminescent emission of *Curtos okinawana* and *Pyrocoelia rufa*. Chart read right to left. Scale as indicated by 5 seconds. Recording temperature 22°C.
1–2, walking male *C. okinawana*; 3–5, walking female *C. okinawana*; 6–7, walking male *P. rufa*; 8–10, walking female *P. rufa*.

Pyrocoelia rufa OLIVIER

Field observations

Studies were made at the three sites on this species, at Izuhara, Kyozuka, and Sasuna, Tsushima Is., Nagasaki Prefecture, during 15–17 October 1980. Male flashing activity began at 19:30 and it continued for approximately 1 hour. Generally, the habitat was open land situated along a river or stream. A large population was seen at Kyozuka, 7–9, October 1979. This species distributed only in Tsushima Is., Japan. Many males flew around a deserted house, grass field and rice field, 1–3 m above the ground while emitting a continuous glow of light. As female emitted continuous light from their luminous organ, they flexed their abdomens, usually in the direction of the stimulating emission. Several flying males approaching females were observed. The female of this species was wingless and could not fly. A female on a tip of grass or on a rock was associated with the flying activity of a male. Peak flashing activity lasted for approximately 60 minutes, although occasionally males could be seen giving their distinctive continuous light. This species possessed a unique morphology and behavior such as adults of this species appear in autumn. Males were observed earlier than females. During this investigation, several females were found on the base of grass stem. Male emission was diminished or ended by rain, strong wind, moonlight or other illuminations, and also by temperatures under 12°C. Males were attracted by female emissions.

Laboratory observations

Male and female flash patterns were recorded by Method B (Fig. 26. 6–10). Both sexes glowed continuously. Fresh specimens of the firefly glowed well, but a few days later the luminescent emission of this species decreased to a low; furthermore, 10 days later, this species became almost nonluminescent. Female adults and larvae of this species live within the same site and their emissions were similar to each other, but the forms of their luminous organs were distinctly different between the adult female and larva (Fig. 27, Pl. 6. 9, 11, 24). When several males were placed a few centimeter from a fresh female, the males immediately became excited, and sexual display occurred. Males frequently chased a female in order to mount and copulate, but the female often attempted to escape from the male. Courtship in *P. rufa* appeared identical. The male approched a female from behind or from the side with his head in a prognathous position. Display was always directed toward the apex of the females abdomen. The male maxillary palpi were placed on the femal's body as he mounted. Males frequently mounted and attempted to insert their genitalia. When a male mounted a female, the male retreated along the back of the female and attempted to copulate. When the male failed to copulate with the female, the male repeated its attempt to climb the back of the female or the side of her and rubbed her head with his maxillary palpi, then the female gradually became quiet and finally the male coupled with the female (Pl. 3. 3). If a dead female 10 days old was placed near a male, the male was also attracted by the female and demonstrated display immediately. The male rubbed the head of the female with his maxillary palpi (Pl. 3. 6), and retreated along the female, then the male attempted to insert its genitalia (Pl. 3. 7). However, the male was not attracted to a female that had been dead for a year.

Fig. 27. Luminescent emission of a female *Pyrocoelia rufa* from her luminous organs.

Pyrocelia miyako NAKANE

Field observations

This species was seen in Kurima Is., Miyako Isls., Okinawa, in southern Japan, on 6 May 1979 and 5–6 Nov. 1979. It was found abundantly in this island. A large population was observed in Kurima Is., on 5 May 1979. Adults of *P. miyako* were active from October to May. Male glowing activity began at approximately 19:30 and males flew 1–3 m above grass field, farms, and around a house. The females were wingless, thus the flying individuals were males only. It was very difficult to locate females. No female was seen in this study. Flying and glowing activity continued for approximately 1 hour, then they gradually congregated at the bases of grass. Flying males were seen in the same number as *L. cruciata*, and in this respect they rather resemble *P. rufa*. A difference in behavior between *P. miyako* and *P. rufa* was seen as follows. The males of the former flew several times above a field or near a house in the daytime, but the latter was never seen during the day. Larvae of *P. miyako* emitted continuous light from a pair of luminous organs while in a bush or grass.

Laboratory observations

Fresh females were obtained by breeding (OHBA, 1981a). The form and behavior of the female were similar to those of *P. rufa* (Pl. 2. 16, 18; Pl. 5. 9–10, 17–18), but the size of the female luminous organ was rather small compared to *P. rufa*. Both sexes strongly emitted a continuous light during a period of a few days, but after ten days, little luminous emission remained. If a male and a female were placed in a small plastic cage, the male immediately attempted to mount and copulate with the female as seen in *P. rufa*. This species resembled *P. rufa* closely in mating behavior and form, especially, with respect to their genitalia (Pl. 2. 16, 18).

Pyrocoelia atripennis LEWIS

Field observations

Studies were made of this species in Iriomote Is., Okinawa, in southern Japan, on 1 Nov. 1979. This species appeared from October to April (based on Museum materials). In Iriomote Is., they were found in a field of sugar cane (Pl. 1. 4), a grass field or around a house. Many flying and glowing males were seen 1–2 m above the ground. Male glowing activity began approximately at 19:40. Female of this species usually glowed on the ground or lying within 10–20 cm above the ground at the base of grass stems, rolling their abdomens away from the stimulus of glowing light in the manner described for other brachypterous females. During this time the flying male glowed actively. The glowing activity continued for 1 hour and ended 2 hours later. Then the males lay at the base of grass. The luminescent pattern of this species was of continuously glowing light. It was difficult to distinguish *P. atripennis* from *P. miyako* by their behavior and luminescent patterns. Generally, flying and glowing males were not seen in so many number as *L. cruciata*. Females of this species were more difficult to capture than females of *P. rufa*. Larvae of *P. atripennis* were seen at the same site and emitted a glow of light from a pair of luminous organs located at the last abdominal segment. Occasionally, a male flying actively was observed during the day but no female was seen in the field during this study.

Laboratory observations

Several fresh females were obtained by breeding. The female adult resembled the larval form. The female luminous organs were smaller than those of the male and the forms were much different from those of the male (Pl. 6. 10, 12). The luminescent patterns were recorded and analyzed by Method B (Fig. 28). Both sexes emitted a continuous glow light and the luminescent patterns resembled those of *P. miyako* and *P. rufa*. When a female and a male were placed in a small plastic cage, the male became immediately excited, and sexual display took place. Sexual display of this species was similar to that of *P. rufa* and *P. miyako*. The male approached the female from behind or the side with his head in a prognathous position (Pl. 4. 1–2, 5). Display was always directed toward the middle leg (Pl. 4. 2) or to the apex of the female abdomen. The maxillary palpi of the male were typically placed on the female's body as he mounted. The display alternated with orientation as well as with mounting periodically. Males fre-

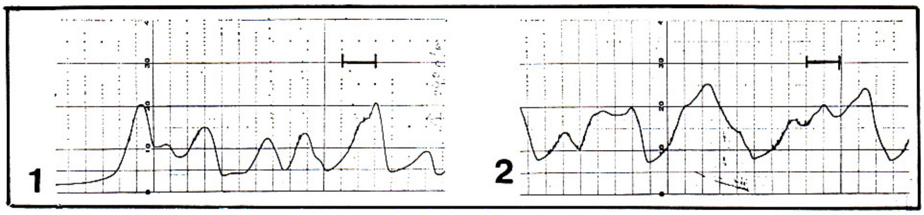

Fig. 28. Chart traces of luminescent emission of *Pyrocoelia atripennis* recorded with a photomultiplier system in the laboratory. Chart read right to left. The scale, 5 seconds. Recording temperature 20°C. Walking male.

quently mounted and attempted to insert the genitalia, and after a while copulation occurred (Pl. 4. 8). When a male mounted a female, the male retreated along the back of the female and attempted to copulate with her (Pl. 4. 7). When the male failed to copulate, he repeated its attempt to climb the back or the side of the female (Pl. 4. 4) and rubbed her head with the maxillary palpi and then they copulated. Males were not attracted to the larvae of this species. Courtship in *P. atripennis* appeared identical. The male immediately attempted to copulate in the manner described for other brachypterous

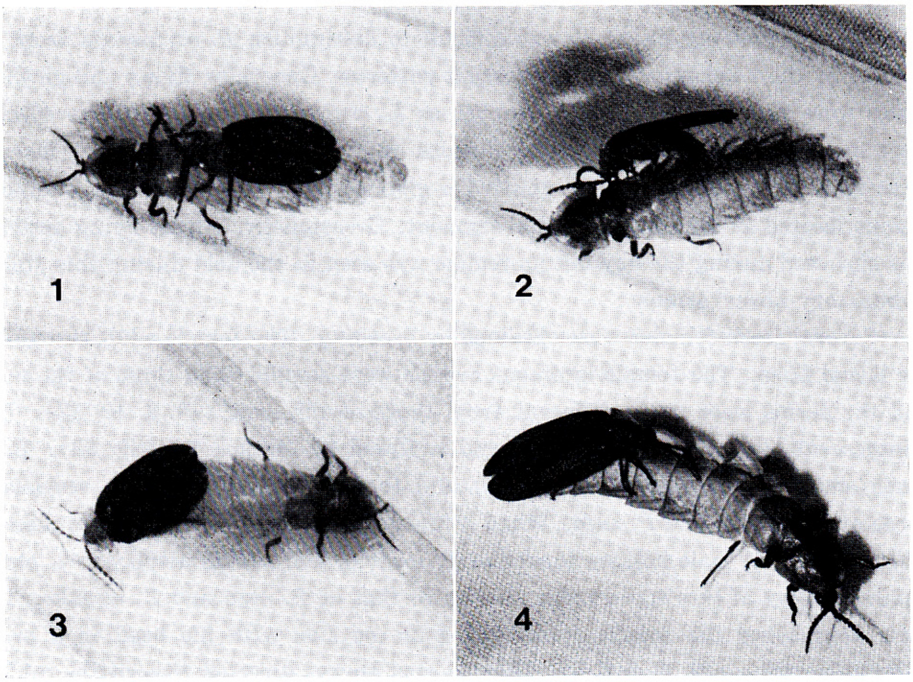

Fig. 29. Courtship display of *Pyrocoelia atripennis* and *P. miyako*. 1, showing a male *P. miyako* mounting a female *P. atripennis*; 2, male *miyako* rubbing body of female *atripennis*; 3, male *miyako* attempting to copulate with female *atripennis*; 4, copulating.

species. When a different species, a male of *P. miyako*, was placed near a female of *P. atripennis*, sexual behavior was observed (Fig. 29). Their luminescent patterns were the same. The male *miyako* approached the female *atripennis* and the male commenced his sexual display such as palpilation, mounting, and attempting to insert its genitalia, and thereafter they copulated (Fig. 29. 4). Both species resemble each other in form, behavior and genitalia (Pl. 2. 16–17; Pl. 5. 10–11, 18–19; Pl. 6. 10, 12).

Pyrocoelia abdominalis NAKANE

Field observations

This species was seen in Mt. Omoto, Ishigaki Is., Okinawa, on 30 April 1977 and at Yonehara, Ishigaki Is., Okinawa, on 30 October 1978. In Mt. Omoto, the male slowly flew 1–2 m above the ground, on a mountain path with grassy sides

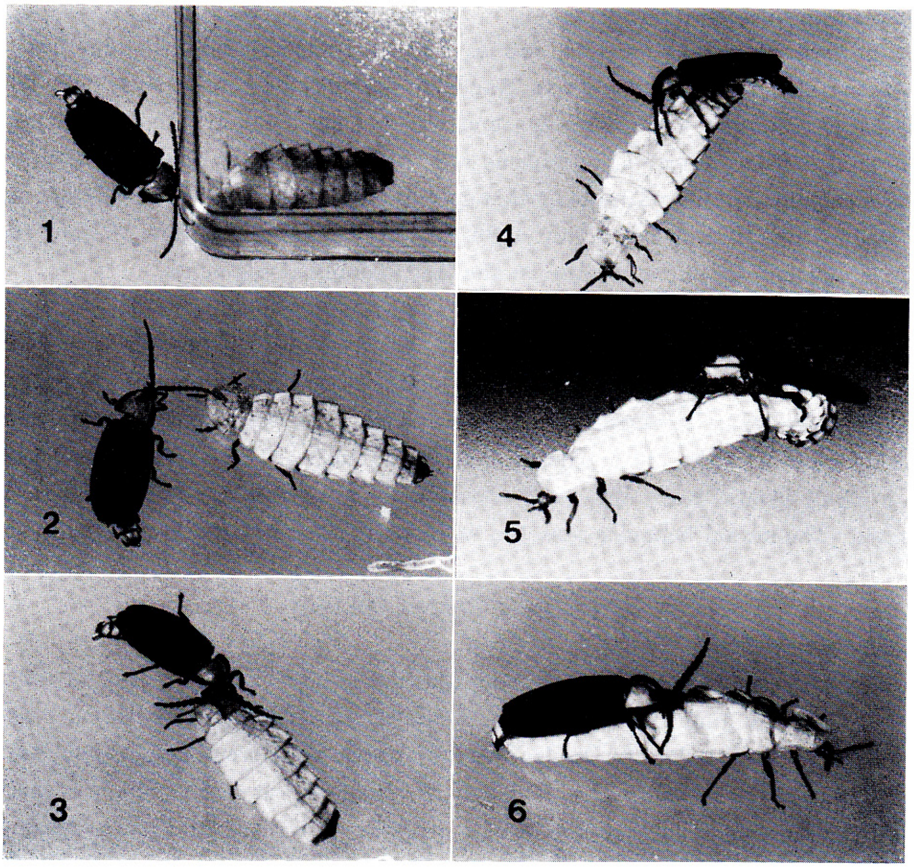

Fig. 30. Courtship display in *Pyrocoelia abdominalis*. 1, showing male attracted by female under a plastic cover; 2, male approaching to female; 3, male attempting to mount; 4, mounting; 5, male attempting to copulate; 6, male and female in copulation.

in the daytime. On the other hand, several larvae of this species were found at Yonehara. Adults of this species were weakly luminescent. The larvae emitted a continuous light from their luminous organs on the last abdominal segment.

Laboratory observations

Several females were obtained by breeding. Larva, pupa, and adult of this species emitted a weak continuous glow of light. Both sexes were placed in a small plastic cage and were tested for male-female interaction. When a male approached a female, the male attempted to insert its genitalia in the manner described for other brachypterous species (Fig. 30). Both sexes had a pair of vestigial luminous organs. Male antennae were well developed, and the compound eyes were small (Pl. 5. 27) and the male genitalia resembled those of *P. rufa*.

Pyrocoelia matsumurai NAKANE

Field observations

Several specimens of this species were collected during the daytime by sweeping along the roadside grass, Nago City, Okinawa Is., on 6 May 1979. This species distributed in Okinawa Is., and was not seen at any other localities in this study. The number of specimens seen in Museum collections indicates that it is a common species. Larvae of this species were seen along the roadside grass in Nago City (Pl. 1. 8), on 6 Nov. 1980. The larvae emitted a glow of light from a pair of small luminous organs on the last abdominal segments.

Laboratory observations

Adults of this species were obtained by breeding for testing male-female interaction. Both sexes were very weak luminescent. The female of this species was a larval form; it resembled *P. abdominalis*. The larva and pupa emitted a weakly glow of light. If a pair of male and female of this species was placed in a small plastic cage, the male immediately attempted to copulate with the female. The sexual behavior was the same as in *P. abdominalis*.

Pyrocoelia fumosa GORHAM

Field observations

This species was studied at Juniso, Kamakura City (alt. approximately 20 m) (Pl. 1. 2), on 20 June 1975, and in Mt. Adatara (alt. 1000 m), Fukushima Prefecture, on 23 July 1975. At Juniso, several males were seen. Males flew 1–2 m above the ground during the daytime. *P. fumosa* was early summer species and active during the first two weeks in June in Kamakura City. Flying individuals were males only. No female was found in this study in the field observations. At night, larvae of this species walked on the ground or leaves, and climbed stem of grass. They emitted a continuous light from a pair of small luminous organs on the last abdominal segments 30 minutes after sunset.

This species is mainly distributed in northern Honshu. *P. fumosa* closely resembles *P. discicollis*, but the latter is distributed in southwest Honshu only. *P. fumosa* displayed the same behavior as *P. matsumurai*.

Laboratory observations

Fresh females were obtained by breeding. The female resembled *P. abdominalis*. (Pl. 5. 12, 27). This species had a pair of small luminous organs which emitted a very weak yellowish green light. If a male was placed in a plastic cage with another male, the male attempted to mount the latter. A glow of light was emitted from their luminous organs. When a female was put in the cage, males were attracted to the female. This sexual behavior was the same as in *P. abdominalis*.

Lucidina biplagiata MOTSCHULSKY

Field observations

This species was observed in Mt. Ohgusu (alt. 200 m), Yokosuka City, and Mt. Tanzawa (alt. 1000 m), Kanagawa Prefecture. In Mt. Ohgusu, they were found in small colonies in moist areas along the roadside ditches among lush vegitation. On June 1981, flying males were seen. Flying of males was observed in the daytime. The adult of this species was non-luminescent. Males flew slowly, 0.5–1.5 m above the ground. Several coupling individuals were seen on the leaves in the daytime. This species flew well on cloudy days rather than on fine days.

Laboratory observations

Both sexes were almost non-luminescent; the light was never visible to the naked eye, but very weak luminescent light was detected with a highly sensitive photomultiplier appratus. The luminescence was a very weak glow of light (Fig. 31. 3–4). When a male and a female were placed in a small plastic cage,

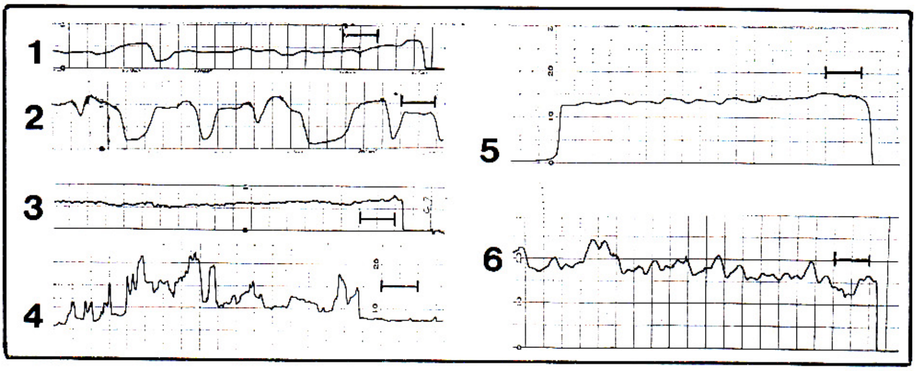

Fig. 31. Chart traces of luminescent emission of fireflies in the laboratory, recorded with a photomultiplier system. Chart read left to right. The scale 5 seconds. Recording temperature 20°C. 1–2, walking male *Cyphonocerus ruficollis*, 3–4, walking male of *Lucidina biplagiata*; 5–6, walking female *Drilaster ohbayashii*.

the male immediately became excited and shook his antennae and chased the female, whereupon mating behavior took place. The male mounted on the back of the female and attempted to couple. Occasionally, a male chased another male and attempted the same.

Lucidina accensa GORHAM

Field observations

This species was observed in Mt. Tanzawa (alt. 1000 m), Kanagawa prefecture, on 9 July 1979. Several males were seen flying 1–3 m above the ground. In the Tanzawa Mts., they were found in small colonies along the roadside at the edge of a forest. This species occurs most frequently at altitudes above 1000 m. They were observed in small colonies along a path through a forest. On 7 July 1979, flying males and females were observed in the daytime. Both sexes were non-luminescent when seen by the eye, and they flew slowly 1–2 m above the ground.

Laboratory observations

This is a diurnal species. The antennae are well developed, and have very small compound eyes (Pl. 5. 26). When a male and a female were placed in a plastic cage, the male immediately attempted to couple and excitedly shook his antennae. After 1 or 2 minutes, they copulated. Form and behavior of this species resemble those of *L. biplagiata*.

Cyphonocerus ruficollis KIESENWETTER

Field observations

Studies were made on this species at Juniso, Kamakura City, Kanagawa Prefecture (Pl. 1. 2), on 15 June 1976. This species was found on the tips of grass in wet forest. Coupling males and females were found on leaves or at the base of grass stems 5–20 cm above the ground (Fig. 32). Occasionally one female would be mounted by 2 or 3 males. They were observed in small isolated colonies at this site. Other species, *Lucidina biplagiata, Pyrocoelia fumosa,* and *Drilaster axillaris* also lived at the same site. However, the peak season for the adult stage differed somewhat. Males often flew slowly in the daytime 0.5 m above the ground. The flying males were not so plentiful as *Luciola cruciata*. Most of them were sedentary during the daytime. At night, larvae of this species emitted a glow of light from a pair of luminous organs.

Laboratory observations

Both sexes emitted a weak continuous light after sunset from a pair of vestigial luminous organs. When the adults were placed in a small plastic cage, the female was immediately chased and mounted by the males. Thereafter, the male attempted to couple and projected his genitalia toward the side of his abdomen. Both sexes burrowed a small hole and spent time in it. Several females laid

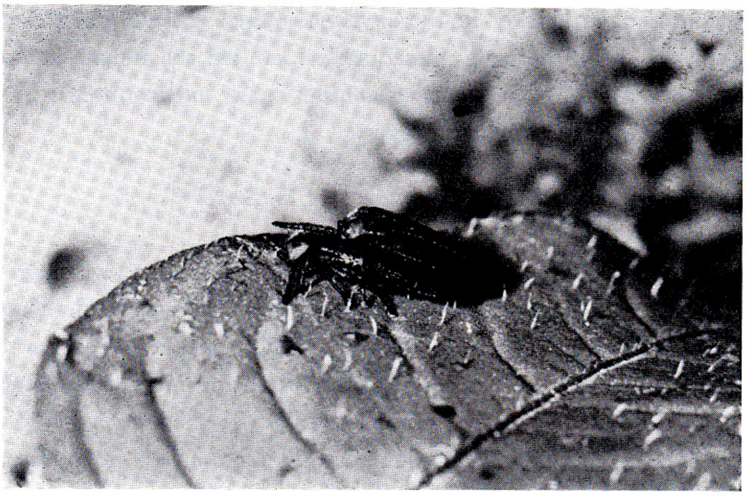

Fig. 32. Courtship display in *Cyphonocerus ruficollis*, showing male and female in copulation on the leaf of grass in the daytime.

eggs in the hole. Sometimes a male chased another male and attempted to couple. The luminescent patterns were recorded by Method B (Fig. 31. 1–2). The males have small compound eyes and a developed antennae (Pl. 5. 21–22).

Drilaster axillaris KIESENWETTER

Field observations

This species was seen at Juniso, Kamakura City, Kanagawa Prefecture (Pl. 1. 2), on 15 June 1976. In the daytime several males were seen perched on the leaves of grass or flying within 1 m above the ground. They were present in small isolated colonies at the forest edge. At Juniso, the season for adult activity was from early to the middle of May. The adults were non-luminous, while the status of the larvae is unknown.

Drilaster fuscicollis NAKANE

Field observations

Studies were carried out on this species in Nago City, Okinawa Is. (Pl. 1. 8), in southern Japan, on 6 Nov. 1979. No adult was found there, but many larvae were found in the roadside grass. They emitted continuous light from a pair of small luminous organs. Four species of lampyrid larvae were found at this site, namely, *Pyrocoelia matsumurai, Curtos okinawana, Luciola kuroiwae*, and *Drilaster fuscicollis*.

Laboratory observations

Adults were obtained by breeding and tested for sexual behavior. Both sexes emitted a very weak continuous light from a pair of vestigial luminous organs. However, the adult became non-luminous one day after emerging. The adults flew and walked briskly in the daytime. When a male and a female were placed in a plastic cage, the male immediately mounted the female and attempted to couple. Several times, a male chased another male and mounted it. The males of the species have small compound eyes.

Drilaster ohbayashii M. SATÔ

Field observations

Several specimens were collected during the daytime by sweeping along the roadside in Ishigaki Is., Okinawa Isls. (Pl. 1. 6). This species was not seen at any other localities during three springs of field work. Several larvae of this species were seen along a shallow roadside ditch in Mt. Banna, Ishigaki Is. (Pl. 1. 6), on 5 May 1977 and 30 October 1979. It may be a glade or marsh species. The larvae emitted a weak glow of light from a pair of minute luminous organs.

Laboratory observations

Adults of this species were obtained by breeding (OHBA, 1981a). The pupa also emitted a continuous light from a pair of luminous organs. Newly transformed adults emitted a very weak glow of light (Fig. 31. 5, 6), but they became nonluminous after one or two days following their emergence. They flew slowly and walked in the daytime. This is a diurnal species and resembles *D. fuscicollis* in form and behavior. When a male and a female were placed in a small plastic cage, similar behavior to *D. fuscicollis* was observed.

Pristolycus sagulatus GORHAM

Field observations

One specimen of this non-luminescent species was collected during the daytime by sweeping the marshy grounds at Sengokuhara of Hakone (alt. 1000 m), Kanagawa Prefecture, on 21 July 1979. A male flew above the tip of a blade of grass in the daytime. The male's antennae were well developed and compound eyes were very small (Pl. 5. 28).

Discussion

Communication systems of Japanese fireflies

1. Communication system in *Hotaria parvula* (HP system)

Flash of a female during male and female interaction

The flash communication system of *H. parvula* has been studied previously in the field (OHBA, 1980a). According to the findings, the female *parvula* responds to the flashing of a male with a short delay time. This female delay time is constant at approximately 0.24 second at 16°C. This is the first flash communication system recognized in Asian fireflies (OHBA, 1980a). Sexual behavior of this species was found to involve peculiar flash patterns during the male-female interaction. The flashing activity of males might be controlled by a circadian rhythm because their flashing activity begins almost at a constant time after sunset. A coupled female never responds to male flashes, therefore the female flash response serves not only to let the male know that "I am here" but also to let him know that "I have not coupled yet". The female begins emitting peculiar flashes which are associated with the males beginning their flying and flashing activity. When the male is not present near the female or the male has ceased flashing, the female begins to emit peculiar flashes. From this fact, it may be considered that the female flashes attract the male and bring about the male flashing. The twinkling associated with the peculiar female flashes plays an important role in sexual communication.

Effect of artificial flashes on the female

The female flash response is induced by variable AF flashes (Figs. 9 to 13). The minimum AF flash interval for a female *parvula* is 0.4 second. If the interval is under 0.4 second, the female cannot respond to the flashes. Generally, the female flash response is 0.16–0.21 second in duration (OHBA, 1980a). Therefore, the above AF flashes are at a rate too fast for the female to respond. If the AF flashes are 0.2 second in duration and this fast rate is given to the female for a while, the peculiar female flashes are gradually induced. The above facts suggest that the fast AF flashes are recognized as a continuous light by the female. On the other hand, a female never ceases to respond to a male flashes in the field. Generally, male-female interaction does not take place for a long time, they invariably copulate within a few minutes when an obstruction is absent. Just before copulating, the female flash response interval gradually shortens, and finally the flashes of both sexes are almost synchronized and then they copulate. Therefore, the critical timing of flashes is needed for this species in sexual communication. It seems that a female recognizes a male that is qualified for copulating as a mate. It is difficult to maintain this critical timing by AF flashes. Therefore, it is difficult to produce a male's copulating behavior by AF flashes.

Significance of female flashes

When the AF flash interval is gradually extended, the peculiar female flashes are induced as shown in Figures 11 and 12. This peculiar female flashes also appear during the interaction between native male and female. The peculiar female flashes (interval, 2–4 seconds; duration, 0.13–0.21 second) are induced by AF flashes of long duration or interval, and the flashes stop. Generally, if the AF flashes are over about 2.7 seconds, the peculiar female flashes are induced. It means that peculiar female flashes act to initiate the male flashes, to make him known her position and to attract males. In field observations, non-coupled females also emit the peculiar flashes when a male is absent. It may be a female calling signal since several males are attracted by the female after several minutes. The female flashes also induce male flashes. If AF flashes are presented to a female which emits this peculiar flashes, the female immediately responds to the AF flashes. Generally, a male flash interval is over approximately 2.7 seconds and female *parvula* is able to initiate a male to flash. This flash interval is in agreement with the peculiar flash interval. These facts suggest that the peculiar female flashes influence a male to begin flashing.

Key of female flash response

Female flash response is induced starting with the male or AF flashes. When the flash interval lengthens, the female response interval also lengthens. This is the same for female response patterns as with the natural male flashes. The foregoing is evident from the results of recording and analyzing carried out in this study on the female response flashes to AF flashes of long duration (Fig. 12). Female *parvula* recognizes the AF flashes which are a simple flickering of light flashes of visual color. Non-flickering light never induces a female flash response. The key to the female flash response is flickering of visual light. AF flash patterns for inducing the female flash response varies widely. However, the female responds well to AF flashes of 0.7–1.0 second interval and 0.2–0.6 second duration. Copulated females never emit the peculiar flashes, because there is no need to attract males or to copulate with a male. The most important role for a copulated female is to lay eggs. Female response flashes are not only induced by orderly flickering of AF flashes but also optionally (Figs. 9–13). When the temperature and the activity time are fixed, the female response delay time becomes almost constant (Tables 3 and 5). This fact supports the hypothesis that the male recognizes the critical timing of the female flash response, and also the peculiar female twinkling flashes as a calling signal. The compound eyes of this species are very large (Pl. 5. 1, 13) and serve as a photosensor.

Amended flash response to male flashes or AF flashes

The female response to a male involves critical timing. However, if the timing suffers a time lag, the female emits flashes at almost the same time or just after AF flashes. When the female emits peculiar flashes as soon as AF flashes are emitted or just after them, the female immediately responds to them. However, the timing or the response often suffers a time lag. Under such circumstances, the female emits a flash response once again immediately (Fig. 10. 7, 14). It seems that the female flashes is amended by the time lag. In order to communicate with such a critical timing requirement, it is necessary that the flash possesses distinct and intermittent flash patterns. Therefore, *Hotaria parvula* uses distinct flashes for sexual communication.

Presumption of communication system

Flash patterns, structure of the compound eyes, and antennae and luminous organs are intimately involved in the communication systems of fireflies (OHBA, 1978). The following species are grouped under the HP system based on the above characteristics, behavior, and the results of the previous studies of Japanese fireflies (MATSUMURA, 1928; NAKANE, 1970; CHÛJÔ and SATÔ, 1971; OHBA, 1975, 1976a, 1979c, 1979d): *Luciola kuroiwae* MATSUMURA, *L. yayeyamana* MATSUMURA and *Hotaria tsushimana* NAKANE.

2. Communication system of *Luciola lateralis* (LL system)

When a male *lateralis* is walking or standing, it emits single-pulsed flashes of light with twinkling, but the female emits only single-pulsed flashes of light (Fig. 15). Thus, the flash patterns of *L. lateralis* are different from those of male and female *H. parvula*. The flashes produced by this species are not suitable for communication with critical timing because the interval and duration of the former are longer than those of the latter. The sexual behavior of the former begins with the male flying and flashing. A single flash with approximately 1 second in interval and duration is produced. The female then begins flashing with peculiar flashes 2.8–5.8 seconds in interval and 0.5–1.2 seconds in duration. It is possible that the male's flying and flashing activity is induced by the female's peculiar flashes. When a flying male observes a female's peculiar flashes, it approaches the female within 5–10 cm distance. The peculiar flash of the female plays an important role in attracting males. In the next step, the male converts his flash pattern into single flashes with twinkling (Fig. 15. 1–8) and emits the flashes direct to the female. Twinkling single flashes are regarded as an inducer of female calling behavior. A single male flash consists of 3–4 pulses (Fig. 15. 6–8). In the last step, both sexes keep on emitting their peculiar flashes and thereafter they copulate. Experimental results with male response to AF flashes which simulate the female peculiar flashes indicate that green, yellow, and red colored AF flashes induce their copulation. In this species, key to mating behavior is the flicker of light. Males are directed to induce sexual behavior by the light. Therefore, the signal system is of the most simple type. No critical timing of female response flashes is seen in this species. They emit individual flashes and recognize each other. Therefore, different species which are similar in behavior and structure to *Luciola lateralis* are able to couple with *L. lateralis* (Fig. 17). The following species are grouped under the LL system based on this study and on the previous studies of these species (OHBA, 1978, 1979b, 1981c, 1981d; CHÛJÔ and SATÔ, 1970b, 1971): *Curtos okinawana* MATSUMURA and *C. costipennis* GORHAM.

3. Communication System of *Luciola cruciata* (LC system)

The flash patterns of this species involve slow intermitent flashes as shown in Figure 19. Such flashes are less suitable for communication than those of

H. parvula, but are more suitable than *Pyrocoelia* fireflies. *Luciola cruciata* emits flashes with various flash patterns as in the case of *Luciola obsoleta* (LLOYD, 1972b). Female flash response with critical timing was not observed in this study. YAJIMA (1978) described a female response to male flashes, but the female flash response is not dependent on critical timing flashes as in *H. parvula.* The female response does not always occur in sexual communication. The communication system of this species is presumed to be as follows. The female emits single pulsed flashes of light which are associated with the male flying and flashing. When the male finds a female, the male approaches the female. Occasionally the female responds to male flashes and the male emits flashes with variable flash patterns while approaching and walking near the female, thereafter they couple. This flash communication system is similar to the complex system described previously (LLOYD, 1972b). Non-sexual flash communication has been observed in this species. Females gather at the same site on the moss beside a river in order to lay eggs. The female emits peculiar flashes and attracts another female (KURIBAYASHI, 1980; YUMA, 1981). Similar behavior in this species has been reported by KAUFMANN (1965). He found distinct flashes produced by the female of *Luciola discollis,* an African species, that directed females ready to oviposit to the sites of previously existing populations. The behavior of this female is similar to that of *L. cruciata.* However, the method of attracting females is unknown. Male *cruciata* is attracted by another male or female or by AF flashes. The male has a tendency to repeat its flashing periodically. Synchronous flashing is observed in certain species of Southeast Asia. Great numbers gather in certain trees and flash in apparent synchrony (BUCK, 1938; HANEDA, 1966; BASSOT and POLUNIN, 1967; LLOYD, 1973a, b). The behavior of synchronous flashing may partly occur in *L. cruciata.*

4. Communication system of *Pyrocoelia rufa* (PR system)

Males and females are indistinguishable from each other in their luminescent patterns. The female is wingless and cannot fly; she can only crawl on the ground. She emits a continuous light which is similar to that of the larva. The male may be recognized by the form and size of the luminous organ, and by the different luminousity from the female. No male has been attracted by the light of larvae in field observations. The form of the luminous organ of female is largely different between the larva and the adult male (Pl. 6. 9, 11, 24). These facts support the above idea. Continuous light is impossible to send signals with critical timing. Such luminescent signals make known their position only. The female attracts males by the light and it is presumed that sex pheromone participates in the mating behavior of this species, which is supported by experimental observations shown in Pl. 3. If two male adults and a larva are placed in a small plastic cage, the male never attempts to copule with each other or with the larva. Furthermore, a dead female 10 days after death attracts the males, but dry female specimens dead for one year never attract males. These facts support the above idea. In this species, the compound eyes are large in size and antennae are well developed (Pl. 5). These facts indicate that this species uses luminescent and chemical signals in sexual communication. This communication system is similar to that found in *Phausis* and *Lampyris* fireflies. The communication system in these fireflies has been reported as belonging to Signal System I by LLOYD (1966a). The following species are grouped under the PR system based on this study and on the previous studies of these species (HASAMA, 1942; CHÛJÔ and SATÔ, 1970; OHBA, 1978, 1979a, 1979b, 1980b, 1980c, 1981a, 1981c; NAKANE, 1970, 1981) : *Pyrocoelia miyako* NAKANE and *P. atripennis* LEWIS.

5. Communication system of *Cyphonocerus ruficollis* (CR system)

Flying activity of this species occurs in the daytime, just after the sunset. The male and female emit continuous light. The male of this species has small eyes with a little facets that receive light from a narrow angle. The weak continuous light is not suitable for communication. This species might be using sex pheromone for sexual communication instead of flash signal. However, the weak light is regarded as fulfilling the function for aiding their communication when male and female approach and attempt to copulate at a dark site such as the base of a grass stem just after sunset. The area of activity narrows the distance over which sex attraction has to take place. Communication in this species is summarized in Figure 33. It is presumed that the following species are classifiable as possessing a CR system based on field observations, experiments and the previous studies of this species (SATÔ, 1976; NAKANE, 1967; OHBA, 1976b, 1981a, 1981c): *Cyphonocerus marginatus* LEWIS, *C. inegens* NAKANE, *C. yayeyamensis M.* SATÔ, *Pyrocoelia fumosa* GORHAM, *P. discicollis* KIESENWETTER, *P. matsumurai* NAKANE and *P. abdominalis* NAKANE.

6. Communication system of *Lucidina biplagiata* (LB system)

The adult of this species is non-luminescent, but the larva of this species emits continuous light from a pair of small luminous organs. Male and female flying activity begins during daytime. Antennae in this species are well developed and the compound eyes are small. These facts support the hypothesis that the species uses sex pheromone in sexual communication. Generally, its flying area is narrow and limited. It is logical that a flying male seeks and copulates a mate and a female attracts males by pheromone. The following species are grouped under the LB system based on morphology, behavior, and the previous studies (NAKANE and OHBAYASHI, 1949; NAKANE, 1950, 1961, 1977, 1981; CHÛJÔ and SATÔ, 1972, 1976; OHBA, 1978, 1981c; KANDA, 1935; OHBAYASHI and SATÔ, 1963) : *Drilaster axillaris* KIESENWETTER, *D. unicolor* LEWIS, *D. shibatai* M. SATÔ, *D. anomalus* NAKANE, *D. okinawensis* NAKANE, *D. ohbayashii* M. SATÔ, *D. fuscicollis* NAKANE, *D. bicolor* M. SATÔ, *D. iokii* M. SATÔ, *Stenocladius yoshikawai* NAKANE, *S. shirakii* NAKANE, *S. azumai* NAKANE, *Lucidina biplagiata* MOTSCHULSKY, *L. accensa* GORHAM, *L. okadai* NAKANE et OHBAYASHI, *L. natsumiae* CHÛJÔ et SATÔ, *Prystolycus sagulatus* GORHAM and *P. shikokensis* OHBAYASHI et M. SATÔ.

Comparison of communication systems

The communication systems of Japanese fireflies are classified into 6 types, namely, HP system (Signal System II), LL system, LC system (Complex System), PR system (Signal System I), CR system and LB system (Fig. 33). All of these communication systems are correlated with morphology and behavior of the fireflies (Table 9). For example, the compound eyes of the HP group are the largest in size compared with the LL, LC, PR, CR, and LB systems, accompanied by an activity change from diurnal to noctural. Sex pheromone is probably concerned in the PR, CR, and LB systems. The courtship pattern in *Pyrocoelia rufa* resembles most the pattern in *Lampyris noctilca*. Luminescent signals are con-

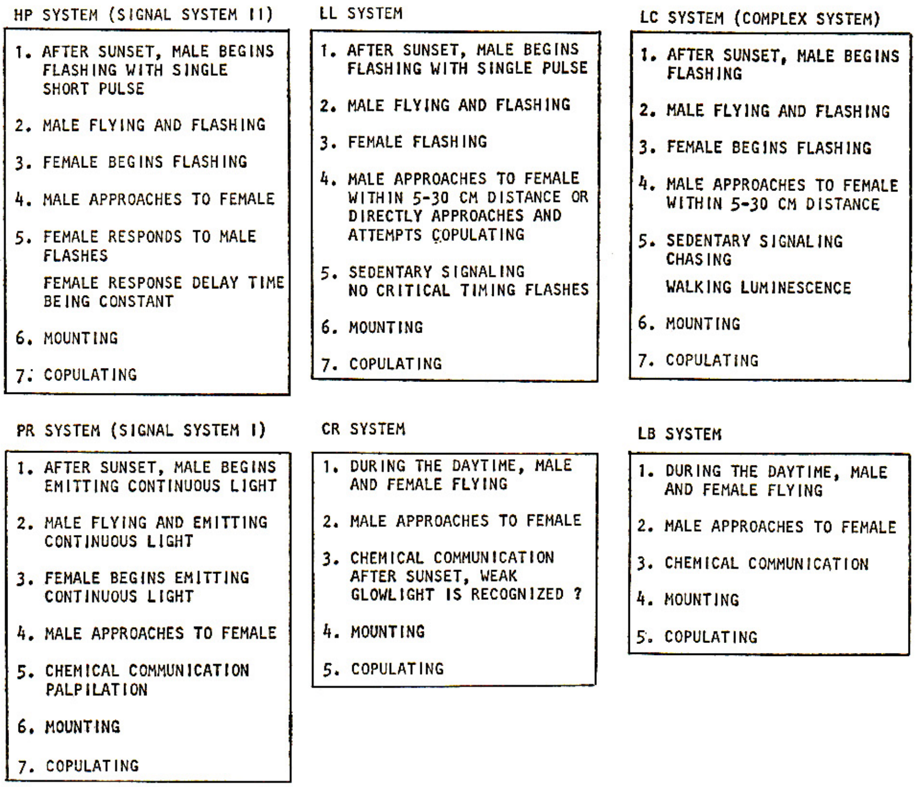

Fig. 33. Communication systems of Japanese fireflies.

Table 9. Comparison of communication systems associated with behavior and morphology in the Japanese fireflies.

COMMUNICATION SYSTEM		HP SYSTEM (SIGNAL SYSTEM II)	LL SYSTEM	LC SYSTEM (COMPLEX SYSTEM)	PR SYSTEM (SIGNAL SYSTEM I)	CR SYSTEM	LB SYSTEM
SIZE OF COMPOUND EYE e/p (OHBA, 1978)		0.80 - 0.70	0.80 - 0.70	0.70 - 0.65	0.45 - 0.27	0.30 - 0.27	0.22 - 0.20
SIZE OF ANTENNA log a/p (OHBA, 1978)		0.59 - 0.45	0.85 - 0.78	1.11 - 0.85	1.49 - 1.18	1.58 - 1 11	1.70 - 1.11
LUMINOUSTY	LARVA	++	++	+++	++++ - +	++ - +	++ - ±
	ADULT	++++	++++	+++++	++++ - ++	+	±
LUMINESCENT PATTERN		SINGLE SHORT PULSE	SINGLE PULSE	SINGLE LONG PULSE	CONTINUOUS LIGHT	CONTINUOUS WEAK LIGHT	NONLUMINESCENCE
ACTIVITY		NOCTURNAL	NOCTURNAL	NOCTURNAL	NOCTURNAL	AMPHIPETAL	DIURNAL
LUMINESCENT SIGNAL		CRITICAL TIMING FLASHES	NO CRITICAL TIMING FLASHES	NO CRITICAL TIMING FLASHES	+++++	+	-
CHEMICAL SIGNAL		-	-	±	+++++	+++++	+++++
SIZE OF LUMINOUS ORGAN		+++++	+++++	+++++	+++++ - ++	+	±
NOTE					FEMALE WINGLESS		

cerned in the systems designated as HP, LL, LC, PR, and CR. However, the CR system mainly depends on sex pheromone. The HP system has been known on the American *Photinus* fireflies (LLOYD, 1966a). This flash communication system involves a process of critical timing of the female flash response to male flashes. In the LL system, the mating behavior of males is induced by flickering of light. In the LC system, males display various behavior patterns, for example, approaching or going away from a female, and emitting various flash patterns. The female recognizes a male display and various flash patterns. This communication system is similar to that found in *Luciola obsoleta*. The PR system resembles Signal System I. Most fireflies in this group emit a glow light. Therefore, they can only recognize their position by the light. The flying male is attracted by the female light and thereafter the male displays palpitation. These fireflies use sex pheromone in sexual communication. The CR and LB system fireflies use sex pheromone, but the former emits a very weak glow light which is not suitable to communicating between males and females. Understanding of this behavior is important since some of these anatomical features are used in their classification and are correlated with species identification. The enlarged palpi of male of several species, and slight modification of the antennae in others, are associated with tactile display, considering that members of this group are so similar anatomically.

Geographical distribution and habitat isolation

Most geographical distribution data are based on Museum specimens. Much of the additional information is based on field observations. Geographical distri-

Table 10. Geographical distribution of Japanese fireflies. Localities are shown in Figure 34.

PSH	PSA	PS	LN	LO	LA	LB	PAD	PK	PMA	PF	PD	PA	PM	PR	CO	CC	HT	HP	LK	LP	LJ	LL	LC	SA	SS	SY	DI	DB	DF	DOK	DAN	DS	DU	DA	CY	CI	CM	CR	SPECIES
		+				+																+												+					HOKKAIDO
		+			+	+				+								+				+	+											+				+	NORTH EAST HONSHU
		+		+	+	+					+							+				+	+											+		+		+	SOUTH WEST HONSHU
+						+					+							+				+	+											+			+	+	SHIKOKU
					+	+					+							+			+	+	+										+	+			+	+	KYUSHU
						+								+			+					+	+															TSUSHIMA Is.
						+												+				+											+						YAKUSHIMA Is.
																+																							TOKARA Is.
												+			+	+			+									+			+	+							AMAMI OHSHIMA
									+						+	+			+					+	+				+	+									OKINAWA Is.
													+			+																							MIYAKO Is.
							+					+				+																			+				ISHIGAKI Is.
							+					+				+										+													IRIOMOTE Is.

CR=*Cyphonocerus ruficollis*, CM=*C. marginatus*, CI=*C. inelgans*, CY=*C. yayeyamensis*, DA=*Drilaster axillaris*, DS=*D. shibatai*, DAN=*D. anomalus*, DOK=*D. okinawaensis*, DF=*D. fuscicollis*, DB=*D. bicolr*, DI=*D. iokii*, SY=*Stenocladius yoshikawai*, SS=*S. shirakii*, SA=*S. azumai*, LC=*Luciola cruciata*, LL=*L. lateralis*, LJ=*L. japonica*, LP=*L. praeusta*, LK=*L. kuroiwae*, DO=*D. ohbayashii*, HP=*Hotaria parvula*, HT=*H. tsushimana*, CC=*Curtos costipennis*, CO=*C. okinawana*, PR=*Pyrocoelia rufa*, PM=*P. miyako*, PA=*P. atripennis*, PD=*P. discicollis*, PF=*P. fumosa*, PMA=*P. matsumurai*, PK=*P. matsumurai kumejimensis*, PAD=*P. abdominalis*, LB=*Lucidina biplagiata*, LA=*L. accensa*, LO=*L. okadai*, LN=*L. natsumiae*, PS=*Prystolycus sagulatus*, PSA=*P. sagulatus amami*, PSH=*P. sagulatus shikokensis*, DU=*D. unicolor*.

bution of Japanese fireflies is summarized in Table 10. The *Cyphonocerus* group is primarily distributed widely in Japan where four species occur except in Hokkaido. The most widespread species is *C. ruficollis*, distributed from Kyushu, Shikoku, to Honshu in Japan. However, the other species of this group are uncommon in the most arid regions of Japan. Exceptions are *C. inelegans*, known only from Mie Prefecture, central Japan and *C. yayeyamensis* from around Iriomote Is., Okinawa. Geographical and habitat isolations have occurred in this group. In the genus *Drilaster*, nine species are known from Japan. The most widespread species is *D. axillaris*, distributed from Kyushu, Shikoku to Honshu. Other of this genus are distributed only in the Southwestern Islands of southern Japan; they are, *D. shibatai*, *D. anomalus* and *D. biocolor* distributed in Amami Isls., *D. ohbayashii*, known from Ishigaki Is., and *D. okinawaensis* and *D. fuscicollis* known from Okinawa Is. Habitats of these species are narrow and limited. Among *Luciola* fireflies, the most widespread species is *L. lateralis*, distributed from Hokkaido, Honshu, Shikoku, to Kyushu and other areas. Another *Luciola* group is distributed in southern Japan. Only one or two specimens of *L. japonica*

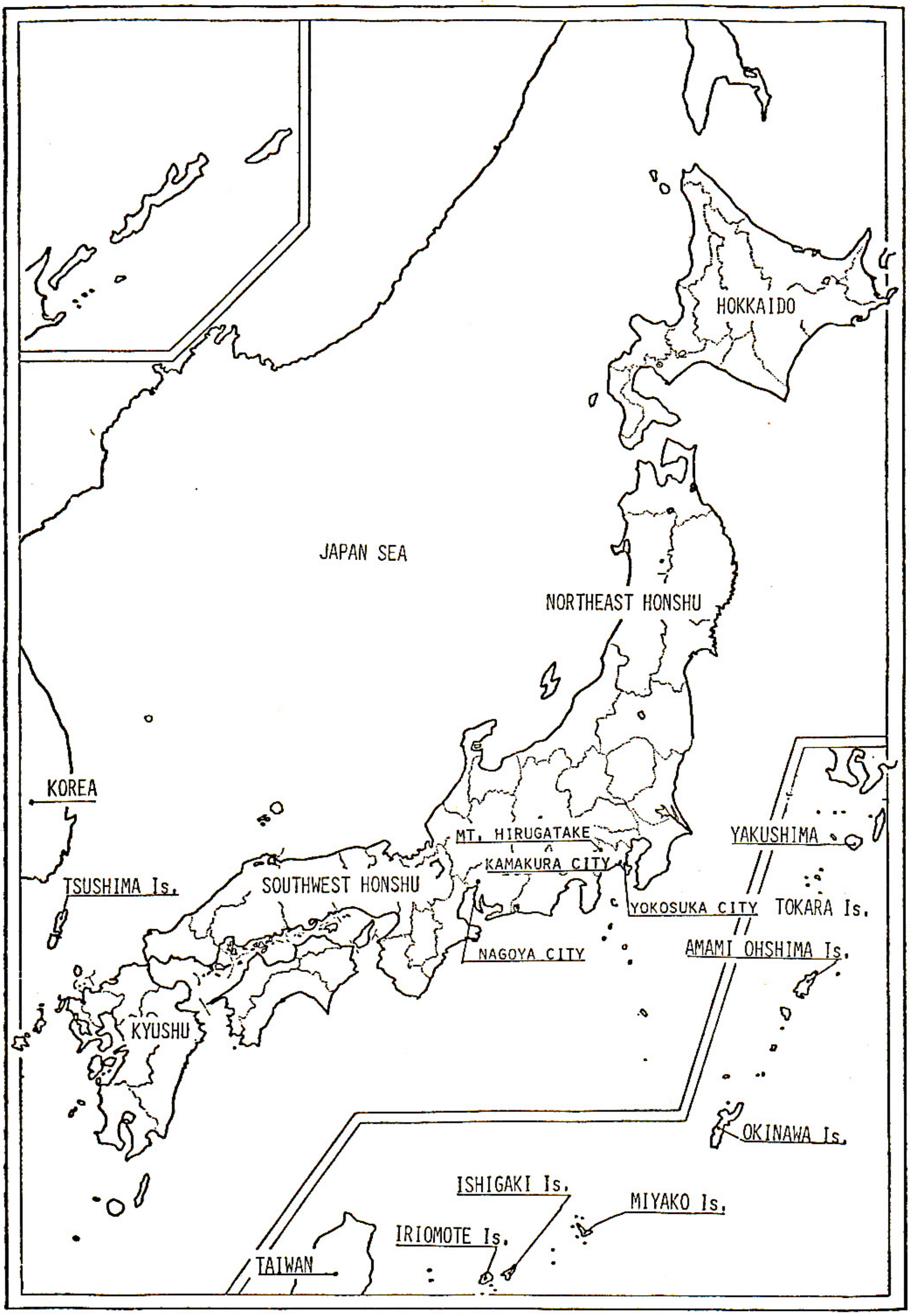

Fig. 34. Map showing localities in this study.
Read Tokara Isls. for Tokara Is.

and *L. praeusta* have been collected from a narrow site of Kyushu, therefore their geographical distribution and habitats are unknown. *L. kuroiwae* is found in Okinawa and Amami Isls. and *L. yayeyamana* is known from Iriomote Is. and Ishigaki Is. These species are isolated geographically. In the genus *Hotaria, H. parvula* is widely distributed in Honshu, Shikoku and Kyushu. However, their habitats are limited areas. *H. tsushimana* is known only from Tsushima Is., Nagasaki Prefecture. *L. cruciata* lives near a stream or river, but *L. lateralis* lives in rice fields. They are isolated in habitat. In the genus *Curtos, C. costipennis* is distributed in the Southwestern Islands of southern Japan. Both species do not live in the same site. These species are isolated by habitat. In the *Pyrocoelia* firefly, eight species are known from Japan. *P. rufa* is found only in Tsushima Is., Nagasaki Prefecture, *P. miyako* occurs only in Miyako Isls., and *P. atripennis* is known from Ishigaki Is. and Iriomote Is., Okinawa. They are perfectly isolated geographically. *P. fumosa* and *P. discicollis* are also isolated geographically. The former is distributed mainly in Northeast Honshu and the latter in Southwest Honshu. Three other species are distributed in the Southwestern Islands of southern Japan. They are also isolated geographically. In the *Lucidina* group, four species are known from Japan. The most widely distributed are *L. biplagiata* and *L. accensa*, found in Honshu, Shikoku, Kyushu, and Hokkaido. However, the former species is common between 1–1500 meter in elevation and latter above 1000 m in Tanzawa Mts., Kanagawa Prefecture. They seem to be isolated by habitats. *L. okadai* is known from a narrow site in central Japan. This species is very rare and its habitat is a limited site. *L. natsumiae* is observed only from Iriomote Is., Okinawa. They are again isolated by habitat. In the *Pristolycus* group, two species are known from Japan. *P. sagulatus* is widely distributed in Hokkaido, Honshu, and Kyushu, and *P. shikokensis* is known only from Shikoku. Habitat differences are obviously important in spatially separating breeding colonies. At one location, *Luciola cruciata* and *L. lateralis* were found within a few meters of each other. However, the former was found along a stream or at the edge of woods along a stream, and *L. lateralis* was found in the rice field beside the stream. At two other locations, demes of *L. yayeyama* were found in the lush grass and weeds along the edge of woods and *C. costipennis* was found along the edge of woods, about 50 m from the *yayeyamana* site. In the *Pyrocoelia* group, their genitalia and behavior are similar to each other (Pl. 2). From experimental observations, these species may be discriminated sharply by females of different species that do not meet under natural conditions. These species are separated each other by geographical and habitat isolation. This genus distributed mainly in Southeast Asia, therefore their distribution may have been enlarged along two passages, one is from China to Tsushima Is. and the other is from Taiwan to the Southwestern islands. Geographical speciation appears to have occurred thereafter in each locality.

Seasonal distribution

Seasonal distribution of adult fireflies summarized in Fig. 35. Most species are active during summer. An exception is *L. lateralis* which becomes active somewhat later. The following species are active during spring: *P. matsumurai*, *P. abdominalis*, *Drilaster ohbayashii* and *D. fuscicollis*. The range of dates for collecting can substantially depend on the range of elevation. For example, *H. parvula* has been collected near the Tosashimizu, Kochi Prefecture, as early as 15 April, and in Mt. Kamiyama of Hakone, Kanagawa Prefecture, in early August. Adults of *P. fumosa*, *D. axillaris*, *C. ruficollis*, and *L. biplagiata* were collected near Juniso, Kamakura City, Kanagawa Prefecture, in early June, and in the Tanzawa Mts. (alt. about 1000 m), Kanagawa Prefecture, in the middle of July. *P. rufa* is active during autumn, while *P. miyako* and *P. atripennis* are active in the autumn late and the early part of the next spring. The wide seasonal range of *P. atripennis* and *P. miyako* in these area is probably concerned with the emergence dates depending on local conditions. Most lampyrids occurrence is roughly correlated with the rainfall and climate.

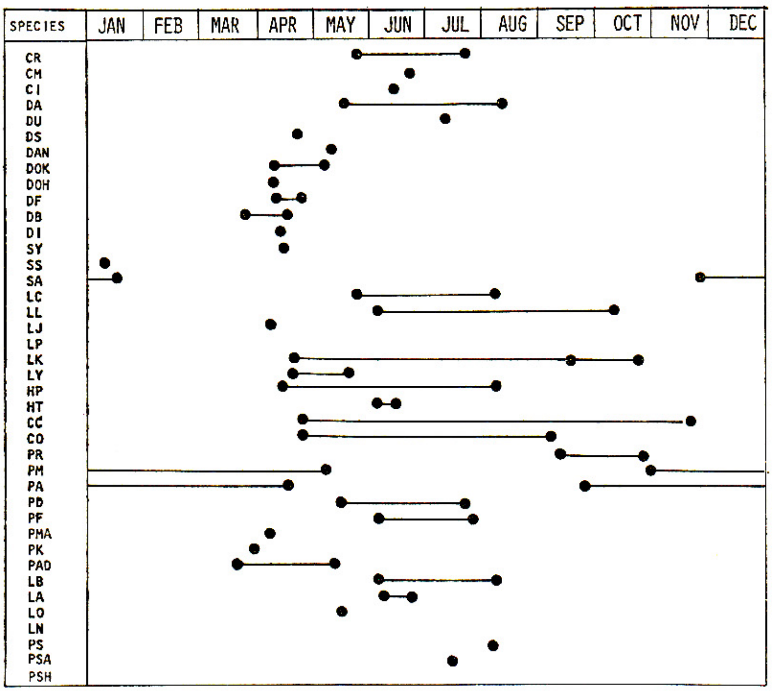

Fig. 35. Seasonal distribution of adult Japanese fireflies. From CR to PSH are shown in Table 10.

Siginificance of System II in the Japanese firefly, *Hotaria parvula*

Many species of *Photinus* and *Photuris* fireflies use System II in sexual communication and live in the same locality (LLOYD, 1966a, 1966b; BUSCHMANN, 1972). Under the circumstances, a struggle for existence should occur among these species. They need to use critical timing flashes for sexual communication in order to maintain their population. Among the Japanese fireflies, several species are similar to each other live in the same site, although their hybrids were not found in the field. Under the circumstances they do not appear to have a need for Signal System II in Japan for sexual communication. Most Japanese species do not use critical timing flashes in sexual communications with the exception of *H. parvula, H. tsushimana, L. yayeyamana,* and *L. kuroiwae*. Thus these species resemble each other in morphology and behavior. It appears from the above that these species originated mainly in Southeast Asia. It is believed that many species in that region resemble each other in form and behavior, and so they need the use of critical timing flashes for their sexual communication in order to recognize the mates to couple. From the geographical distribution of fireflies possessing the HP system, it might be inferred that the ancestor of *H. parvula* spread through two passages; one was Southeast Asia→China→Korea→Tsushima→Kyushu→Honshu and the other was Southeast Asia Taiwan→Okinawa Isls. Thereafter, they became isolated and speciated during the course of geographical isolation in each locality. It could be that *H. parvula* acquired the use of System II from its ancestors that have since disappeared from each locality. Therefore, it is presumed that several fireflies using Signal System II will be discovered in Southeast Asia in the near future.

Conclusion

The communication systems of Japanese fireflies are grouped into 6 systems. All of these communication systems are correlated with their morphology and behavior. Differences in the signals of various species of Japanese fireflies serve to prevent interspecific attraction. Signal exchange between a male and a female of different species may be prevented if the female is not stimulated to respond to the male. In nocturnal species, some of them use critical timing flash signals in sexual communication. In *Hotaria parvula,* the female responds to male flashes after a short delay time. This communication system is the same as Singgal System II in the American firefly *Photinus*. Such species have large compound eyes and small antennae. Others use no critical timing flash signals. The male is directly attracted by female flashes. Complex system is observed in *Luciola cruciata*. This species is closely related to *L. obsoleta* which is found in New Guinea. In *Pyrocoelia* fireflies, most of the species utilize luminescent and chemical signals in sexual communication. Such a communication system is the same as that in *Lampyris noctiluca*. These species have rather small compound eyes compared with *Luciola* fireflies. In amphipetal species, they all use chemical signals and very weak luminescent signals in sexual communication. Such species have small compound eyes, large antennae, and vestigial luminous organs. Diurnal species use chemical signals in sexual communication. Such species have small compound eyes, large antennae, and vestigial luminous organs. Diurnal species use chemical signals in sexual communication. Generally, the habitat of these species is narrow and limited. All of the Japanese fireflies are isolated from each other in their communication systems, function of male genitalia, and in geographical and seasonal distributions. In *Hotaria parvula*, the species developed the ability to utilize Signal System II from an ancestor which has since disappeared from each locality. Therefore, fireflies that use Signal System II are likely to be found in Southeast Asia in the near future. In *Pyrocoelia* fireflies, various communication system are present. *P. fumosa* might be an endemic species. This study would be of importance in investigating speciation and adaptive evolution in Japanese fireflies.

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日本産ホタルのコミュニケーションシステムの研究

大 場 信 義

日本産ホタル類は夜行性で強く発光する種から昼行性のほとんど発光しない種まで知られている。しかし，これらの交信システムについての研究はきわめて不充分であった。本論文では日本産ホタルのコミュニケーションシステムを 16 mm シネカメラ，フォトトランジスター光増幅記録装置，光電子倍増管を用いた高感度光増幅記録装置そして電子発光装置などを駆使して観察，実験し解析した。更に発光パターン，習性，形態などの知見から日本産ホタル類のコミュニケーションシステムの推定および類型化を試みるとともに，ホタルの生殖的隔離機構について，コミュニケーションシステム，生息地，分布，発生期そして生殖器官の形態と機能などの観点から論議した。この研究により，次の点が明らかにされた。

1) 日本産ホタルのコミュニケーションシステムは次の6型に大別される。
a. ヒメボタル *Hotaria parvula* に代表されるシステムは雄の発光信号に対し，雌が一定時間後に応答発光する。このシステムを HP システムとする。HP システムは北米に広く分布する *Photinus* 属ホタルのそれ (Signal System II) に相当する。**b.** ヘイケボタル *Luciola lateralis* に代表されるシステムは雌の一定範囲の明滅信号により，雄が直ちに接近，交尾行動が解発される。このシステムを LL システムとする。LL システムは HP システムにみられる雌の明瞭な応答発光が認められない。**c.** ゲンジボタル *Luciola cruciata* に代表されるシステムは雄の様々なパターンの発光信号，接近歩行発光などの誇示性行動の後に交尾に至る。このシステムを LC システムとする。LC システムはニューギニアに分布する同属種の *Luciola obsoleta* のそれ (Complex System) に相当する。**d.** アキマドボタル *Pyrocoelia rufa* に代表されるシステムは雌の連続発光信号により雄が誘引された後，発光器の形態を識別し，更に性フェロモンにより雄の交尾行動が解発される。このシステムを PR システムとする。PR システムは欧州に広く分布する *Lampyris noctiluca* のそれ (Signal System I) に相当する。**e.** ムネクリイロボタル *Cyphonocerus ruficollis* に代表されるシステムは昼間に飛翔活動するホタルに認められ，雄が雌に接近した後に性フエロモンが関与して交尾行動が解発される。こうしたシステムを有するホタル類は生息地が狭く限定され，交尾行動の機会を高めている。微弱な連続光は日没後に補助的な交信信号の役割を果していると推定される。このシステムを CR システムとする。**f.** オバボタル *Lucidina biplagiata* に代表されるシステムは CR システムに似るが，発光信号が雌雄のコミュニケーションに全く関与していない。このシステムを LB システムとする。

2) ホタルのコミュニケーションシステムは形態，習性，発光パターンなどと密接な相関関係が認められる。即ち夜行性のホタルは複眼が大きく発達するが，触角は細く短い。また発光器がよく発達し，強い断続光を放つ。こうしたホタル類は発光信号をコミュニケーション手段とし，HP システムに属する。昼行性ホタルは触角が大きく発達する一方複眼は小さい。発光器は退化しほとんど発光しない。こうしたホタルは主として性フェロモンをコミュニケーション手段とし，LB システムに属する。両行性ホタルは夜行性および昼行性ホタルの中間的形質を有し，発光器は小さく，弱い連続光を放つ。こうしたホタルは性フェロモンおよび光信号をコミュニケーション手段とし，CR システムに属する。ホタル類は夜行性から昼行性へ連続的な形質変化が認められ，発光パターンも断続光から弱い連続光に変わり，それに伴いコミュニケーションシステムも HP, LL, LC, PR, CR, そして LB システムと変わる。

3) 日本産ホタルはコミュニケーションシステムの相違，生息地，分布，発生期，生殖器官の形態

と機能の相違により，生殖的隔離が維持されている。

4)　PR および LL システムを有するホタルは同属種相互の形質がきわめて類似し，異種間で交尾行動が解発される。こうしたホタルは主に地理的隔離により生殖隔離が維持されている。

5)　日本産ホタルのコミュニケーションシステムに HP システムが存在する事実は次の様に解釈される。HP システム即ち Signal System II を有するホタルは北米に *Photinus* 属ホタルをはじめ多種知られている。こうしたホタル類は同所的に近縁種が多数生息することから，厳密に定まった発光パターンの光を放ち交信システムを特殊化させている。しかし日本では同所的に少数の，近縁種が生息するのみであり，HP システムの様にコミュニケーションシステムを特殊化させる心要はない。このシステムを有するホタル類は対馬，沖縄にも分布することから，HP システムを有するホタルの祖先種が東南アジアのある地域から次の 2 系路で日本に分布拡大した後，地理的隔離により種分化を起したとみなされる。

その一系路として東南アジア→対馬→本州，他は東南アジア→台湾→沖縄。従って，HP システムを有するホタルは今後の研究により，東南アジアから新たに発見される可能性が高い。

Explanation of plates 1–6

Plate 1

1. Yoshii, Yokosuka City, Kanagawa Prefecture, *Luciola cruciata* and *L. lateralis* were studied.
2. Juniso, Kamakura City, Kanagawa Prefecture, *Cyphonocerus ruficollis*, *Pyrocoelia fumosa*, *Lucidina biplagiata*, and *Drilaster axillaris* were studied.
3. Top of Mt. Hirugatake, Kanagawa Prefecture, *Hotaria parvula* was studied.
4. Ohhara, Iriomote Is., Okinawa Isls., *Pyrocoelia atripennis* was studied.
5. Kurima Is., Miyako Isls., Okinawa, *Pyrocoelia miyako* was studied.
6. Mt. Banna, Ishigaki Is., Okinawa Isls., *Luciola yayeyamana*, *Pyrocoelia atripennis*, *P. abdominalis*, *Curtos costipennis*, and *Drilaster ohbayashii* were studied.
7. Hyakuna, Okinawa Is., *Pyrocoelia matsumurai*, *Luciola kuroiwae*, *Curtos okinawana*, were studied.
8. Nago City, Okinawa Is., *Pyrocoelia matsumurai*, *Luciola kuroiwae*, *Curtos okinawana*, and *Drilaster fuscicollis* were studied.

Plate 2

1. Male genitalia of *Curtos costipennis*.
2. Male genitalia of *Curtos okinawana*.
3. Male genitalia of *Luciola cruciata*.
4. Male genitalia of *Luciola kuroiewae*.
5. Male genitalia of *Drilaster axillaris*.
6. Male genitalia of *Luciola lateralis*.
7. Male genitalia of *Luciola yayeyamana*.
8. Male genitalia of *Pyrocoelia discicollis*.
9. Male genitalia of *Lucidina biplagiata*.
10. Male genitalia of *Pyrocoelia fumosa*.
11. Male genitalia of *Pyrocoelia matsumurai*.
12. Male genitalia of *Lucidina accensa*.
13. Male genitalia of *Pristolycus sagulatus shikokensis*.
14. Male genitalia of *Hotaria parvula*.
15. Male genitalia of *Cyphonocerus ruficollis*.
16. Male genitalia of *Pyrocoelia miyako*.
17. Male genitalia of *Pyrocoelia atripennis*.
18. Male genitalia of *Pyrocoelia rufa*.
19. Male genitalia of *Pyrocoelia abdominalis*.

Plate 3

1. Courtship display in *Pyrocoelia rufa*, showing the male rubbing the head of the female with his maxillary palpi.
2. Courtship display in *Pyrocoelia rufa*, showing the male touching abdomen of the female with his maxillary palpi.
3. Courtship display in *Pyrocoelia rufa*, showing copulation.
4. Courtship display in *Pyrocoelia rufa*, showing a female attracting four males.
5. Courtship display in *Pyrocoelia rufa*, showing males gathered and induced into copulating behavior besides a female dead for 10 days.

6. Courtship display in *Pyrocoelia rufa*, showing a male rubbing the head of a female dead for 10 days with his maxillary palpi.
7. Courtship display in *Pyrocoelia rufa*, showing male attempting copulate with a dead female after 10 days death.
8. Courtship display in *Pyrocoelia rufa*, showing males attracted by a female in a saran net cage.

Plate 4

1. Courtship display in *Pyrocoelia atripennis*, showing the male approaching the female from the side of her body.
2. Courtship display in *Pyrocoelia atripennis*, showing the male touching the female's body.
3. Courtship display in *Pyrocoelia atripennis*, showing the male attracted to the site of a female's middle leg.
4. Courtship display in *Pyrocoelia atripennis*, showing the male attempting to mount from the side of female's body.
5. Courtship display in *Pyrocoelia atripennis*, showing the male rubbing the female pronotum with his maxillary palpi.
6. Courtship display in *Pyrocoelia atripennis*, showing the male attempting to mount from the female's head.
7. Courtship display in *Pyrocoelia atripennis*, showing the male attempting to copulate with a female.
8. Courtship display in *Pyrocoelia atripennis*, showing the male and the female in copulation.

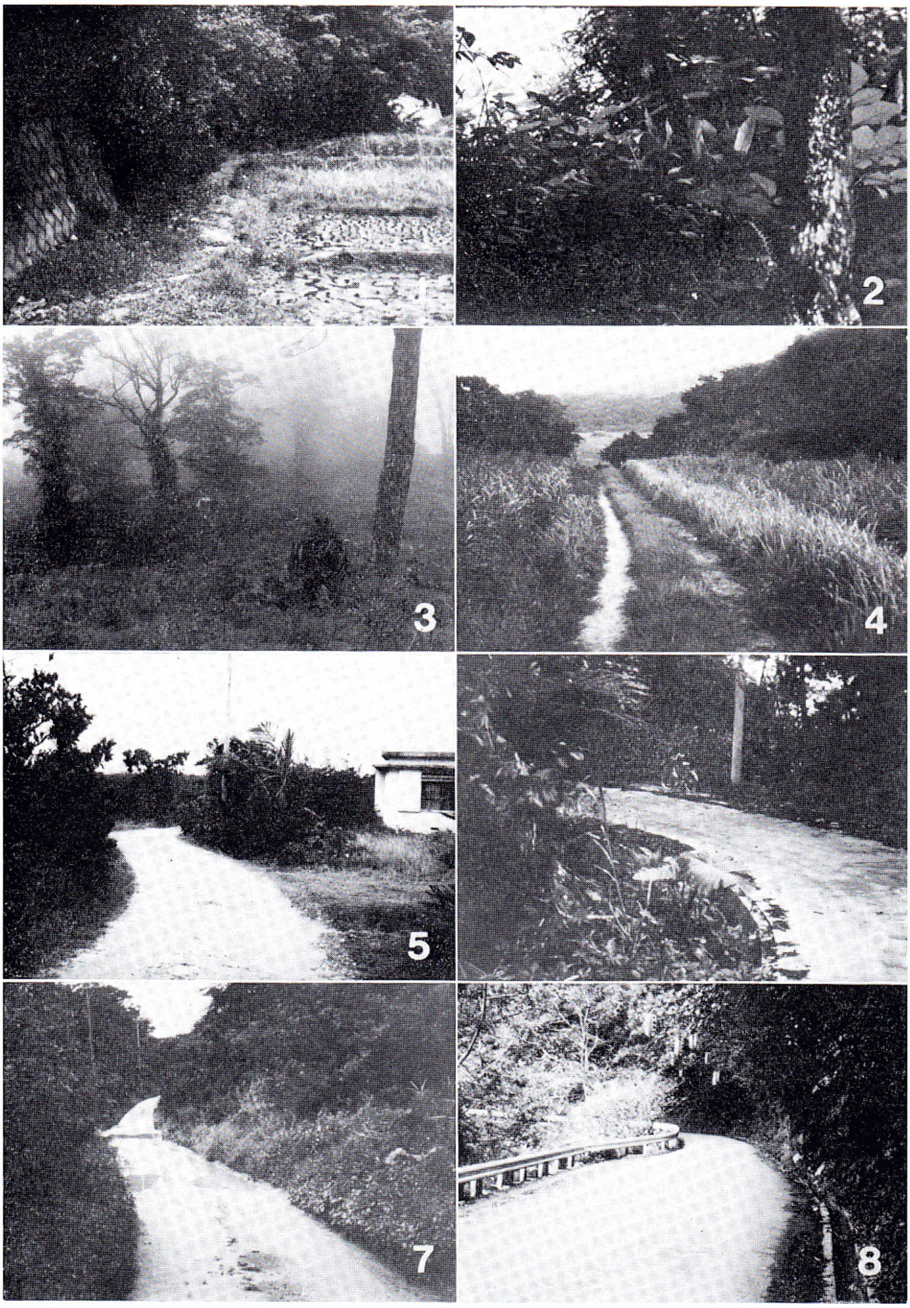
Plate 5

1. Head of *Hotaria parvula* (male).
2. Head of *Hotaria tsushimana* (male).
3. Head of *Luciola yayeyamana* (male).
4. Head of *Luciola kuroiwae* (male).
5. Head of *Curtos costipennis* (male).
6. Head of *Curtos okinawana* (male).
7. Head of *Luciola cruciata* (male).
8. Head of *Luciola lateralis* (male).
9. Head of *Pyrocoelia rufa* (male).
10. Head of *Pyrocoelia miyako* (male).
11. Head of *Pyrocoelia atripennis* (male).
12. Head of *Pyrocoelia fumosa* (male).
13. Head of *Hotaria parvula* (female).
14. Head of *Curtos costipennis* (female).
15. Head of *Luciola cruciata* (female).
16. Head of *Luciola lateralis* (female).
17. Head of *Pyrocoelia rufa* (female).
18. Head of *Pyrocoelia miyako* (female).
19. Head of *Pyrocoelia atripennis* (female).
20. Head of *Pyrocoelia matsumurai* (female).
21. Head of *Cyphonocerus ruficollis* (male).
22. Head of *Cyphonocerus ruficollis* (female).
23. Head of *Drilaster axillaris* (male).
24. Head of *Drilaster ohbayashii* (female).
25. Head of *Lucidina biplagiata* (male).

26. Head of *Lucidina accensa* (female).
27. Head of *Pyrocoelia abdominalis* (male).
28. Head of *Prystolycus sagulatus* (male).

Plate 6

1. Luminous organ of adult *Hotaria parvula* (male).
2. Luminous organ adult *Hotaria tsushimana* (male).
3. Luminous organ of adult *Luciola yayeyamana* (male).
4. Luminous organ of adult *Luciola kuroiwae* (male).
5. Luminous organ of adult *Curtos costipennis* (male).
6. Luminous organ of adult *Curtos okinawana* (male).
7. Luminous organ of adult *Luciola cruciata* (male).
8. Luminous organ of adult *Luciola lateralis* (male).
9. Luminous organ of adult *Pyrocoelia rufa* (male).
10. Luminous organ of adult *Pyrocoelia miyako* (male).
11. Luminous organ of adult *Pyrocoelia atripennis* (male).
12. Abdomen of adult *Pyrocoelia fumosa* (male).
13. Luminous organ of adult *Hotaria parvula* (female).
14. Luminous organ of adult *Luciola cruciata* (female).
15. Luminous organ of adult of *Curtos costipennis* (female).
16. Luminous organ of *Luciola lateralis* (female).
17. Abdomen of adult *Pyrocoelia fumosa* (male).
18. Abdomen of adult *Lucidina accensa* (female).
19. Abdomen of adult *Pyrocoelia okinawana* (female).
20. Luminous organ of larva *Pyrocoelia atripennis*.
21. Abdomen of adult *Cyphonocerus ruficollis* (male).
22. Abdomen of adult *Drilaster ohbayashii* (male).
23. Abdomen of adult *Drilaster axillaris* (male).
24. Luminous organ of larva *Pyrocoelia rufa*.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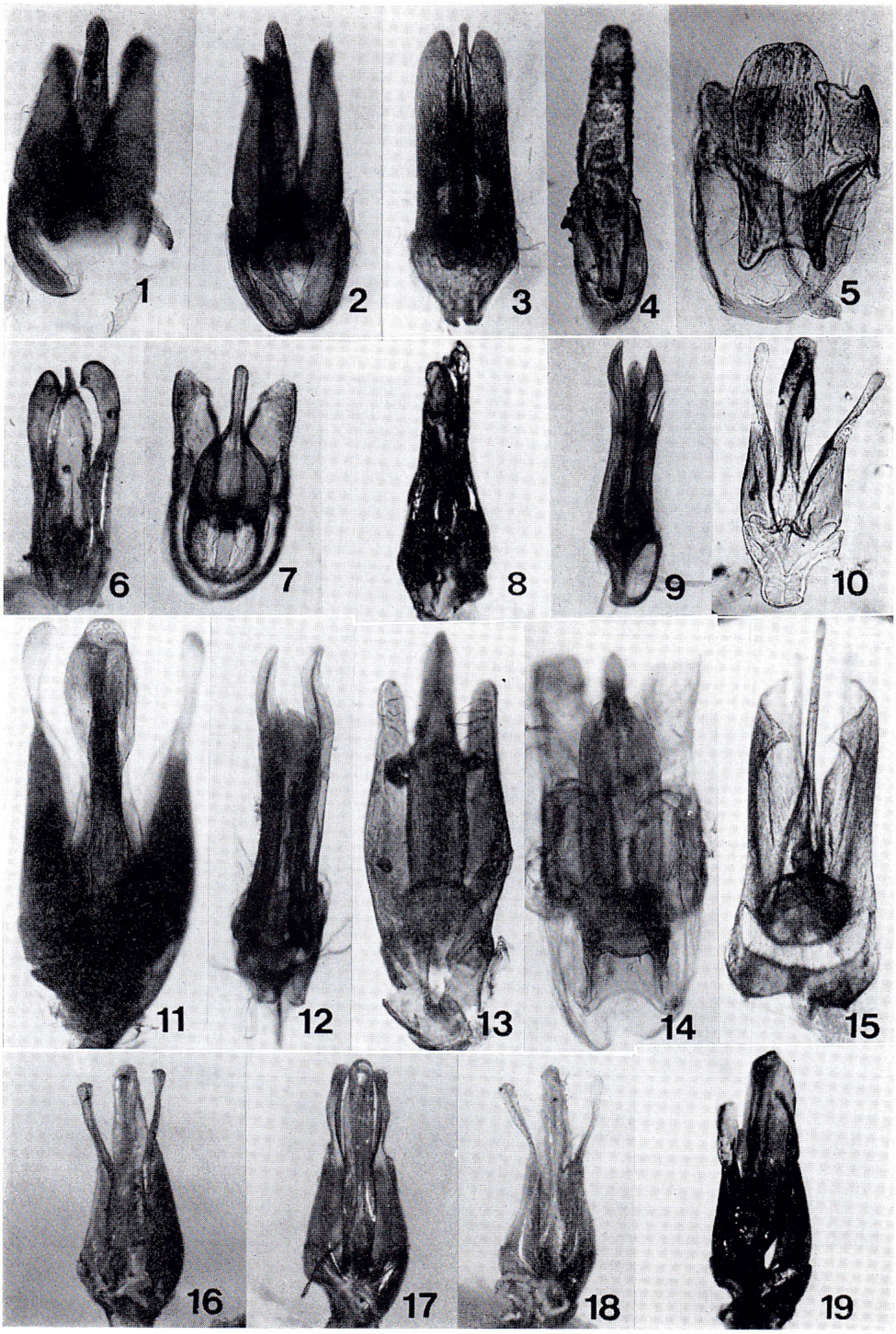
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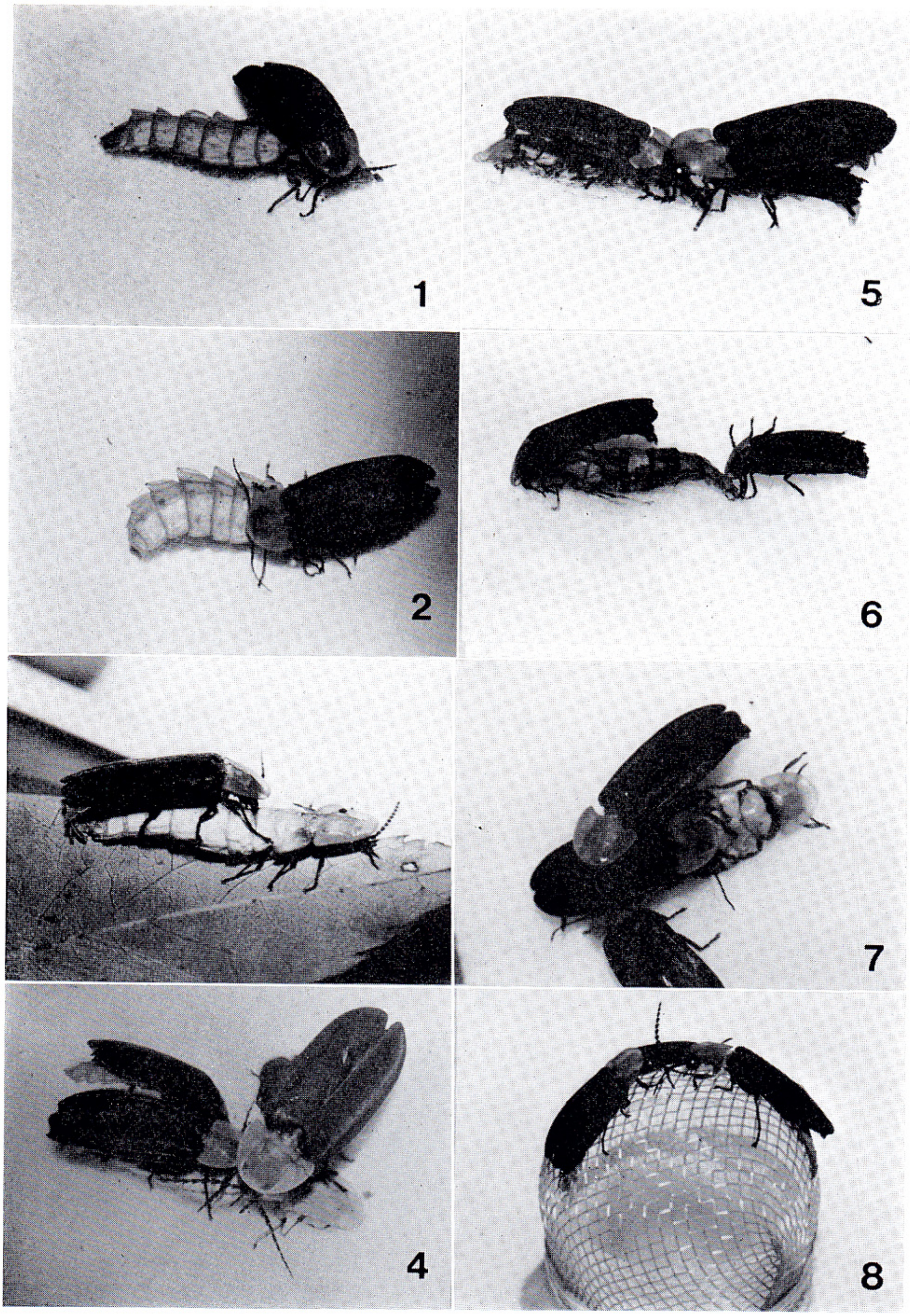
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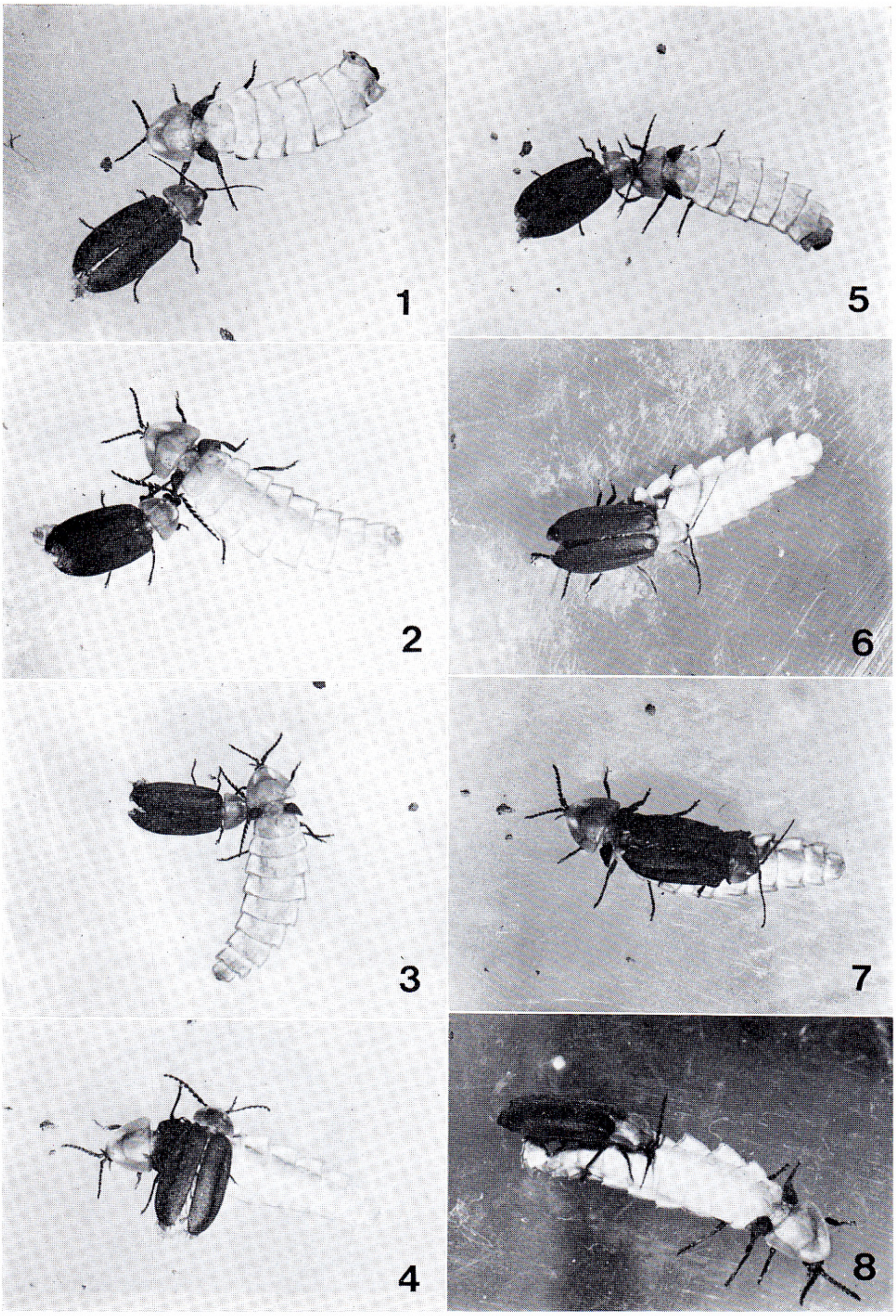
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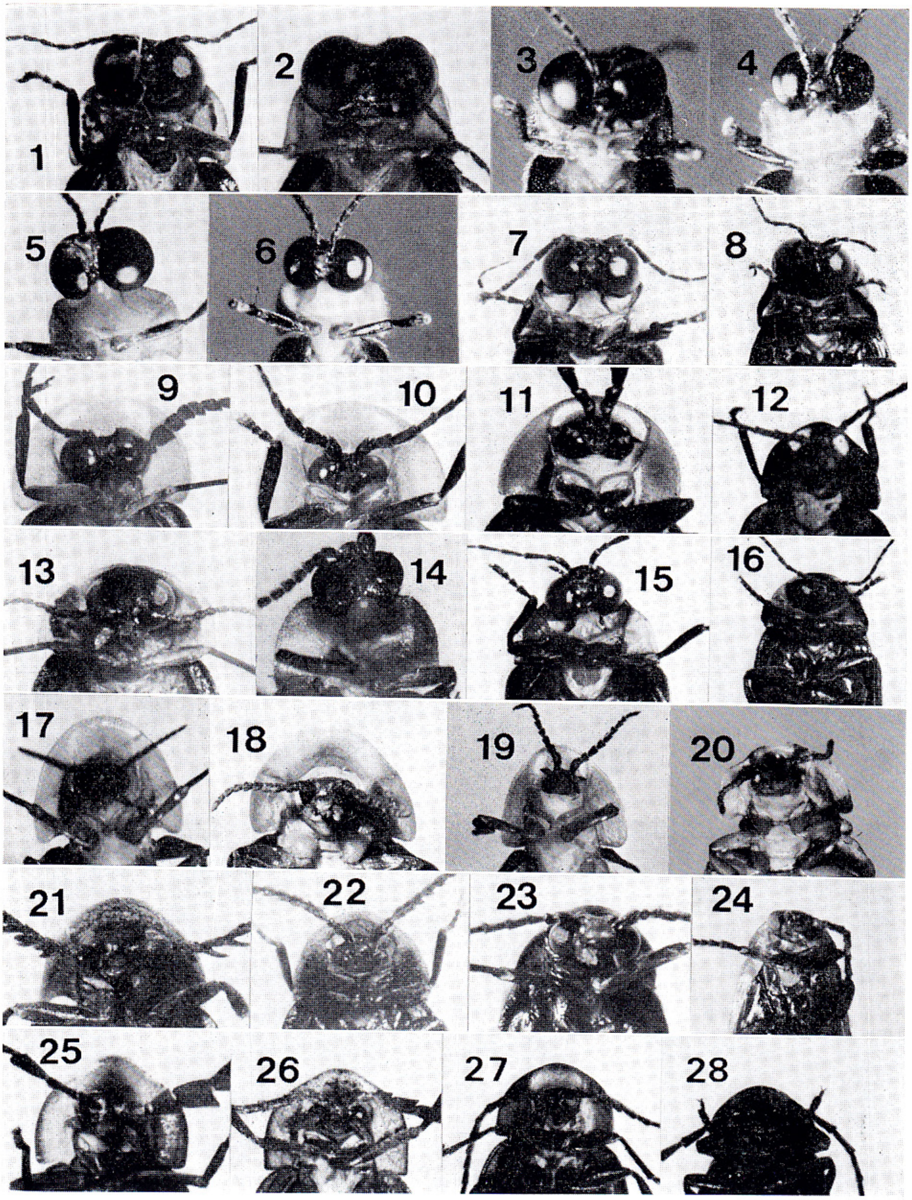
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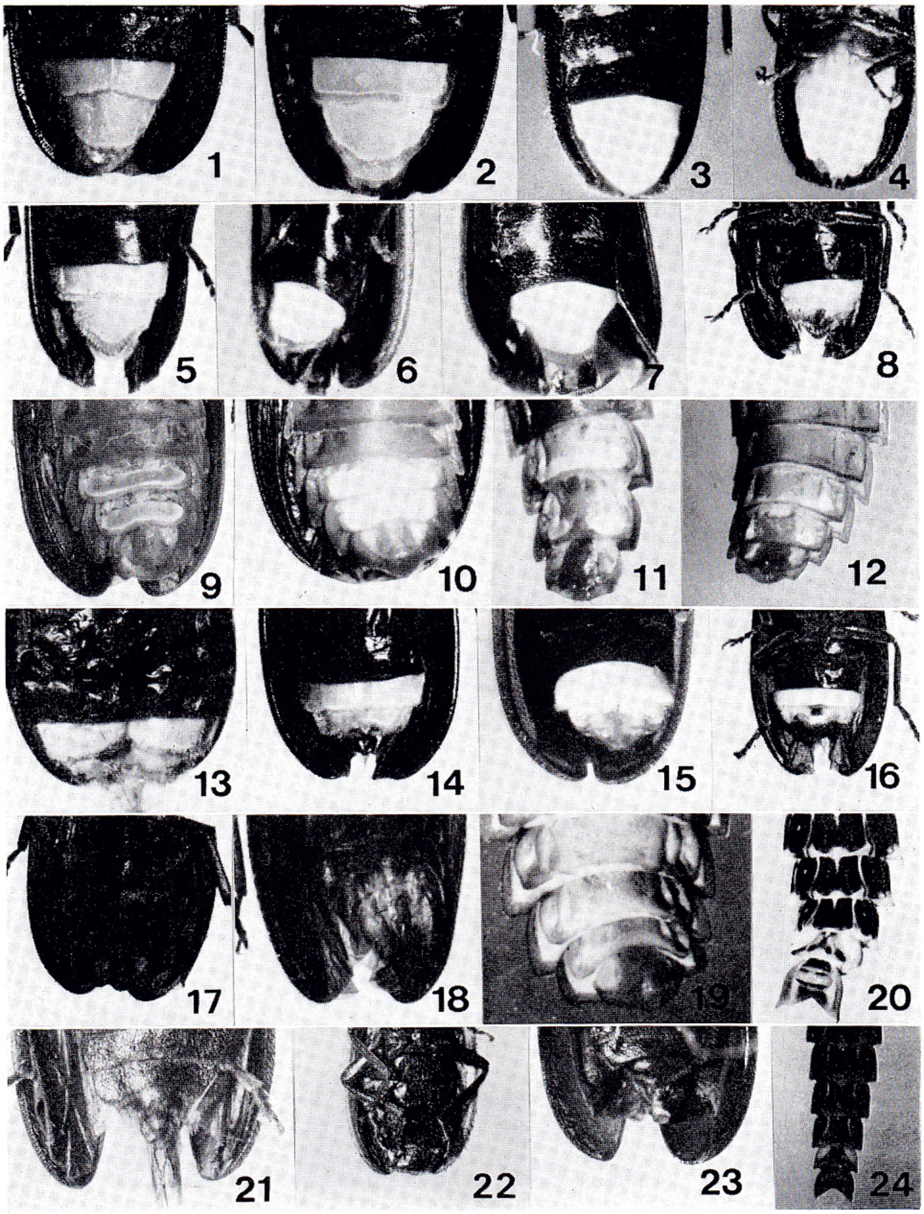
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