A STUDY OF THE GENUS *EPHORON* FROM JAPAN (EPHEMEROPTERA, POLYMITARCYIDAE)

SHIN-ICHI ISHIWATA
Kanagawa Environmental Research Center, 842 Nakahara-Shimojuku, Hiratsuka, Kanagawa 254, Japan

Abstract

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In the genus *Ephoron* of Japan three species are recognized: *E. shigae* (Takahashi), *E. limnobium* sp.nov., and *E. eophilum* sp.nov. This study includes a key to the species, a description of each species, and maps of species distributions.

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Résumé

Nous reconnaissons trois espèces dans le genre japonais *Ephoron*: *E. shigae* (Takahashi), *E. limnobium* sp.nov. et *E. eophilum* sp.nov. La présente étude donne une clé pour chaque espèce, une description de chacune de ces espèces, et une carte de leur répartition.

INTRODUCTION

The members of the genus *Ephoron* are widespread on the continents; they are one of the most conspicuous and common mayflies in some localities because of their large body size and mass flights. Eleven species of the genus are known from the Holarctic, Oriental, Ethiopian, and Neotropical regions. Only one of them, *E. shigae*, has been recorded from Japan.

The structure of the male genitalia of this genus is generalized so it is difficult to discriminate species by these organs. As suggested by Koss (1968) and Koss and Edmunds (1974), I found that the shape and chorion sculpture of the eggs were useful characters to distinguish species of *Ephoron*.

In Japan it has been believed for many years that a single species, *E. shigae*, was distributed from Kyushu to the northern part of Honshu. However, the present study, based on the characters of nymphs, adults, and eggs, reveals that there are other new species in the Kanto plain and Lake Biwa.

MATERIALS AND METHODS

Nymphs, adults (male imagoes and female subimagoes), and eggs were studied. All specimens were preserved and examined in 75% alcohol. The wings which were removed before dipping the specimens in alcohol were observed by binocular microscope under dark field. Fully developed eggs were obtained from preserved mature female nymphs or female subimagoes. For SEM analysis, the eggs, stored in alcohol, were cleaned with an ultrasonic cleaner for 7 min, removed to 99.5% alcohol, dried, mounted on stubs with double stick tape, coated with gold for 3 min at 10 mA using an ion coater, JEOL JFC-1100E, and studied by a JEOL JSM-5400LV. Morphological nomenclature in this work follows mainly that of Edmunds et al. (1976). Egg terminology follows Koss (1968) and Koss and Edmunds (1974). The type series in this study are deposited in the collections of the National History Museum and Institute, Chiba, Japan (CM). The other specimens used in this study are deposited in the author's collections (not indicated), or the collections of the Sagamihara City Museum, Sagamihara, Japan (SM) and CM.

Abbreviations for characters are:

LB — length of body;

LC — length of cerci;

LT — length of median filament;

MWP — maximal width between lateral margins of pronotum;
MWE — maximal width between lateral margins of eyes;
LFW — length of forewings;
LHW — length of hind wings;
FF — length of forefemora;
FTB — length of foretibiae;
FTR — length of foretarsi;
LM — length of mandibular tusks;
LP — length of penis lobes (twice the measurement of a penis lobe);
NTM — number of tubercles on a mandibular tusk;
LM/MWP — ratio of LM to MWP;
MWE/MWP — ratio of MWE to MWP;
LP/MWP — ratio of LP to MWP.

EPHORON WILLIAMSON

[Japanese name: Shiro-kagerou-zoku]

Ephoron Williamson, 1802, *Trans. Amer. Philos. Soc.* 5: 71. [Type species: *Ephoron leukon* Williamson, 1802, monotype.]

Polymitarcys Eaton, 1868, *Entomol. Mon. Mag.* 5: 84. [Type species: *Ephemera virgo* Olivier, 1791, by original designation.]; synonymized by Spieth, 1940, *Canad. Entomol.* 72: 109.

Eopolymitarcys Tshernova, 1934, *Dokl. Akad. Nauk SSSR* 4: 240. [Type species: *Eopolymitarcys nigridorsum* Tshernova, 1934, by original designation.]; synonymized by Edmunds and Traver, 1954, *Proc. Entomol. Soc. Wash.* 56: 239.

Description. Mature nymph. *Head*: Maximal width between lateral margins of compound eyes (MWE) about as wide as maximal width between lateral margins of pronotum (MWP) in both sexes (Tables 1, 3, 5). Eyes black and small. Head with a median frontal process. Mandibular tusks shorter or longer than MWP (Figs. 1, 4, 7), curving downward, straight or curved upward apically as viewed laterally (Figs. 2, 8), with numerous tubercles (12–29 tubercles), with short and dense hair on upper surface near bases, with long hair on lateral surface; an acute or a blunt spine between outer and inner incisors on right mandible (Figs. 14, 15). Maxillary palpi two-segmented. Labial palpi two-segmented, held beneath and at right angles to glossae. *Thorax*: Color milky white with brown markings. Forelegs stout and fossorial with several distinct rows of long hair; femora with a row of tubercles along paraxial edge near base; tibiae flattened, with two rows of ventral tubercles, one along paraxial and one along antiaxial margins (Figs. 6, 9); foretarsi unmodified, not partially fused with tibiae. Ventral apices of hind tibiae rounded. *Abdomen*: Abdominal terga with brown markings. Gills white on abdominal segments 1–7; gills 1 single; other gills forked; each lamella of gills 2–7 with lateral margin fringed, with lateral tracheal branches pigmented or not pigmented (Figs. 3, 5, 7).

Male. *Head*: Eyes black and small, separated laterally. MWE about as wide as MWP (Tables 2, 4, 6). *Thorax*: Color pattern of body generally similar to that of nymphs. Forewings whitish and hyaline (Figs. 16, 17), with a network of tubercles (Fig. 19), with numerous crossveins and intercalaries; main vein of costal margin purplish gray; cubital area with two or more intercalaries; a strong convex vein (scv) running parallel to CuP, attached to CuA perfectly or imperfectly (Fig. 21). Hind wings whitish and hyaline, with a network of tubercles, with a blunt costal projection. Forelegs reddish brown, about as long as body; femora short; tibiae long, about four times length of femora; tarsi longer than tibiae. Middle and hind legs white, poorly developed. *Abdomen*: Color pattern of body generally similar to that of nymphs. Penes (Fig. 10) white; lobes straight and extended laterally, about as wide

as pronotum, hooked at apices (Fig. 11); forceps four-segmented. Cerci well developed; short vestigial median filament.

Female. *Head*: Eyes black and small, separated laterally. MWE about as wide as MWP (Tables 2, 4, 6). *Thorax*: Color pattern of body and legs generally similar to those of male but darker. Wings more whitish than male, surfaced with a large number of short hairs (Fig. 20); wing venation similar to that of male except for hind wings; a vein between R1 and R2 of hind wings absent. All legs poorly developed. *Abdomen*: Color pattern of body generally similar to that of male but darker. Three developed caudal filaments.

Egg. Length without cap 183.5–458.8 μm, width 122.4–321.2 μm (Figs. 22, 23, 25, 27, 30). One polar cap with two to seven micropylar devices at capped end of egg (Fig. 28). Sperm guide poorly defined (Fig. 29); micropylar canal with "half-skullcap" (Degrange 1956). Chorionic depressions variable (Figs. 22–27). Base of cap without a chorionic collar (Fig. 28).

Discussion. The diagnosis of the genus given above is based on three Japanese species.

Edmunds and Traver (1954) reported that *Eopolymitarcys* Tshernova was a junior synonym of *Ephoron*. It needs, however, reconfirmation because they gave no explanation of the synonymy. The name *Polymitarcys nakamurae* Matsumura reported by Nakamura (1941) in his list without descriptions cannot be applied with certainty to any *Ephoron* species and does not appear in the formal listings or synonymies of *Ephoron*. No Matsumura types of *P. nakamurae* exist at Hokkaido University where most of his collection is deposited. I therefore consider *Polymitarcys nakamurae* Matsumura a **nomen dubium**.

KEY TO JAPANESE SPECIES OF *EPHORON*

Mature Nymph

1. Frontal process of head semicircular (Fig. 7) ..... *eophilum* **sp.nov.**
— Frontal process of head triangular (Figs. 1,4) 2

2. Gills on abdominal segments 2–7 with lateral tracheal branches pigmented (Fig. 3) .... *shigae*
— Gills on abdominal segments 2–7 with lateral tracheal branches not pigmented (Fig. 5) ..... *limnobium* **sp.nov.**

Male Imago

1. Wings whitish, translucent (Fig. 17) ..... *eophilum* **sp.nov.**
— Wings hyaline (Fig. 16) 2

2. Abdominal markings light brown to dark brown. Japan, Korea, and Russian Far East (Fig. 31) ..... *shigae*
— Abdominal markings usually not clearly defined. Lake Biwa (Fig. 31)..... *limnobium* **sp.nov.**

Egg

1. Egg large (length without cap 305.9–458.8 μm, width 221.8–321.1 μm) (Figs. 27, 30)..... *eophilum* **sp.nov.**
— Egg small (length without cap 183.5–282.9 μm, width 122.4–214.1 μm) (Figs. 22, 23, 25, 30) 2

2. Chorion with puncture-like impression (Figs. 23, 24) ..... *shigae*
— Chorion with large ring-like depressions (Fig. 26) ..... *limnobium* **sp.nov.**

Ephoron shigae (Takahashi)

[Japanese name: Oh-shiro-kagerou]
(Figs. 1, 2, 3, 10, 14, 22, 23, 24, 28, 29, 30, 31)

Polymitarsis shigae [sic]? Takahashi, 1924, *Annot. Zool. Japon.* 36: 379, fig. 6 [male figure; type information: unknown].

TABLE 1. Measurements and ratios for selected population samples of *Ephoron shigae*: range, mean and (standard deviation); mature nymph, measurements in mm

Locality	(*n*)	LB	LC	LT	MWP	MWE	LM	NTM	LM/MWP	MWE/MWP
Arakawa River, Kounosu-shi, Saitama										
Male	(20)	12.0–15.5	9.5–15.0	9.5–13.0	1.84–2.32	1.55–2.42	1.45–1.98	21–27	0.73–0.87	0.95–1.18
		14.3 (1.97)	11.9 (2.23)	11.2 (1.60)	2.05 (0.25)	2.07 (0.30)	1.68 (0.23)	23.7 (2.42)	0.82 (0.05)	1.01 (0.04)
Female	(20)	16.0–23.0	6.0–8.0	9.0–11.1	2.13–2.71	2.32–2.90	1.94–2.61	19–29	0.82–1.00	0.94–1.22
		19.8 (2.93)	7.0 (0.71)	10.3 (1.28)	2.52 (0.21)	2.58 (0.21)	2.25 (0.27)	24.2 (3.92)	0.89 (0.08)	1.02 (0.03)
Abukumagawa River, Date-machi, Fukushima										
Female	(20)	17.0–23.0	6.0–7.0	10.0–13.0	2.32–2.90	2.52–2.90	1.84–2.42	22–28	0.70–0.83	0.93–1.18
		20.2 (1.93)	6.75 (0.50)	11.0 (1.0)	2.70 (0.19)	2.65 (0.12)	2.03 (0.22)	23.8 (2.20)	0.75 (0.05)	0.98 (0.05)
Hijikawa River, Oozu-shi, Ehime										
Female	(20)	16.0–24.0	6.0–10.0	7.0–11.0	2.32–3.00	2.32–3.10	1.74–2.42	17–21	0.69–0.85	0.95–1.28
		20.5 (3.78)	7.4 (1.67)	9.6 (1.52)	2.71 (0.26)	2.72 (0.24)	2.14 (0.23)	19.2 (1.64)	0.79 (0.07)	0.98 (0.05)
Sagamigawa River, Sagamihara-shi, Kanagawa										
Female	(20)	18.0–23.0	6.0–8.5	9.0–12.0	2.57–3.10	2.50–2.83	1.80–2.50	19–25	0.65–0.91	0.91–0.99
		20.3 (1.60)	6.9 (0.66)	10.4 (0.85)	2.84 (0.15)	2.68 (0.11)	2.22 (0.19)	21.9 (1.77)	0.78 (0.07)	0.94 (0.03)

TABLE 2. Measurements and ratios for samples of *Ephoron shigae*: range (R), mean (M), and standard deviation (SD); male imago and female subimago, measurements in mm

	LB	CT	LT	MWP	MWE	LFW	LHW	FF	FTB	FTR	LP	MWE/MWP	LP/MWP
Male ($n = 30$)													
R	9.9–15.2	24.0–37.3	0.4–1.2	1.40–2.10	1.50–2.20	9.3–12.7	4.4–6.4	0.80–1.30	3.50–5.50	4.30–6.40	1.42–1.80	0.92–1.14	0.77–1.29
M	12.7	29.8	0.7	1.70	1.78	11.0	5.3	1.08	4.35	5.29	1.58	1.02	0.96
SD	1.29	3.73	0.18	0.21	0.20	0.75	0.48	0.15	0.47	0.55	0.10	0.06	0.10
Female ($n = 30$)													
R	13.1–19.3	8.7–18.7	6.7–12.7	1.30–2.50	1.90–2.60	13.1–18.4	5.6–8.0	0.97–2.00	1.17–2.00	0.67–1.17		0.96–1.77	
M	16.1	13.8	9.2	2.20	2.24	15.6	6.7	1.32	1.69	0.88		0.99	
SD	1.50	2.53	2.05	0.25	0.27	1.36	0.59	0.22	0.26	0.14		0.03	

Each value was measured from the samples of three localities: Arakawa River ($n = 10$, Kounosu-shi, Saitama), Obitsugawa River ($n = 10$, Kimitsu-shi, Chiba), and Yodogawa River ($n = 10$, Takatsuki-shi, Osaka).

Polymitarsis shigae [sic]?: Tsuda, 1952, *Naraken Sougou Bunka Chosahoukokusho*: 229, fig. [first nymphal description].

Polymitarcys sp. : Uéno, 1930, *Trans. Kansai Entomol. Soc.* 1: 30, figs. 17–24.

Polymitarcis shigae [sic]?: Uéno, 1931, *Annot. Zool. Japon.* 11: 189 [redescription of male]; Uéno and Okamoto, 1932, *Iconog. Insect. Japon.*: 1962, fig. 3866; Gose, 1962, *Aquatic Insects*, 1st ed.: 12, fig. 1.

Polymitarcis sp. [sic]?: Uéno, 1931, *Annot. Zool. Japon.* 11: 190, fig. 1.

Polymitarcys shigae: Lestage, 1938, *Bull. Ann. Soc. Entomol. Belg.*: 390.

Ephoron shigae: Uéno, 1973, *Freshwat. Biol. Japan*: 525; Gose, 1980, *Aquabiology* 2: 457, figs. 21–24; Nozaki, 1983, *Nat. Hist. Rep. Kanagawa* 4: 38, fig. 2 [first egg description]; Yoon, 1988, *Illust. Encycl. Fauna Flora of Korea* 30: 156, fig. 29, pl. 4; Kobayashi, 1992, *Hand. Zooben. Lake Biwa* 2: 8, fig. (nymph); (male subimago), misidentification.

Additional References. *Polymitarcis shigae* [sic]?: Uéno and Okamoto 1950; Shioyama 1978. *Ephoron shigae*: Okazaki 1984; Gose 1985; Nakamura 1985; Satoh 1987; Nakamura and Biological Research Group of Utsunomiya University 1987; Hirashima 1989; Hirashima et al. 1989; Watanabe et al. 1989; Watanabe and Takao 1991.

Description. Mature nymph. *Lengths*: Body 12.0–24.0 mm, cerci 9.5–15.0 mm (male), 6.0–10.0 mm (female), median filament 9.5–13.0 mm (male), 7.0–13.0 mm (female). Measurements and ratios for selected population samples are presented in Table 1. *Head*: Eyes black, separated dorsolaterally; ocelli black; inner margin of ocelli brown. Head with a triangular median frontal process (Fig. 1). MWE about as wide as MWP in both sexes. Mandibular tusks shorter than MWP, curving downward, straight or curved upward apically as viewed laterally (Fig. 2), with numerous tubercles (17–29 tubercles), with short and dense hair on upper surface near bases, with long hair on lateral surface: an acute spine between outer and inner incisors on right mandible (Fig. 14). Maxillary palpi two-segmented. Labial palpi two-segmented, held beneath and at right angles to glossae. *Thorax*: Color milky white with dark markings on dorsal surface. Forelegs stout and fossorial with several distinct rows of long hair; femora with a row of tubercles along paraxial edge near base; tibiae flattened, with two rows of ventral tubercles, one along paraxial and one along antiaxial margins; tubercles in paraxial and in antiaxial sides densely arranged in distal half of tibiae. Middle legs small. *Abdomen*: Color milky white with a black dot at base of each gill; abdominal terga with brown markings (Fig. 3) becoming darker and wider toward posterior end; abdominal sterna uniformly milky white. Gills white on abdominal segments 1–7; gills 1 single; other gills forked; each lamella of gills 2–7 with lateral margin fringed, with lateral tracheal branches pigmented. Three caudal filaments with intersegmental setae; median filament about as long as cerci (male), longer than cerci (female) (Table 1).

Male. *Lengths*: Body 9.9–15.2 mm, forewings 9.3–12.7 mm, hind wings 4.4–6.4 mm, cerci 24.0–37.3 mm, median filament 0.4–1.2 mm. Measurements and ratios for selected population samples are presented in Table 2. *Head*: Color light brown; ocelli and base of ocelli black; eyes black, separated laterally. MWE about as wide as MWP. *Thorax*: Color milky white with brown markings. Forewings hyaline, with numerous crossveins and intercalaries; main vein of costal margin purplish gray; outer margin with a network of tubercles ventrally along veins; cubital area with two or more intercalaries; a strong convex vein (scv) running parallel to CuP, attached to CuA perfectly or imperfectly. Hind wings hyaline, with a blunt costal projection; outer margin with a network of tubercles ventrally along veins. Forelegs reddish brown, about as long as body. Femora short; tibiae long, about four times length of femora; tarsi longer than tibiae. Middle and hind legs white, poorly developed. *Abdomen*: Color pattern of body generally similar to that of nymphs. Penes (Fig. 10) white; lobes straight and extended laterally, about as wide as pronotum, hooked at apices; forceps four-segmented. Cerci well developed; short vestigial median filament.

Female. *Lengths*: Body 13.1–19.3 mm, forewings 13.1–18.4 mm, hind wings 5.6–8.0 mm, cerci 8.7–18.7 mm, median filament 6.7–12.7 mm. Measurements and ratios for selected population samples are presented in Table 2. *Head*: Color pattern of ocelli and eyes similar to those of male. Eyes separated laterally; MWE about as wide as MWP. *Thorax*: Color pattern of body and legs generally similar to those of male but darker. Wings more whitish than male, surfaced with a large number of short hairs; wing venation similar to that of male except for hind wings; a vein between R1 and R2 of hind wings absent. All legs poorly developed. *Abdomen*: Color pattern of body generally similar to that of male but darker. Three developed caudal filaments.

Egg. Length without cap 183.5–282.9 μm, width 122.4–214.1 μm (Figs. 22, 23, 30). Chorion with puncture-like impression (Figs. 23, 24). One polar cap with two to four micropylar devices at capped end of egg (Fig. 28). Sperm guide poorly defined (Fig. 29); micropylar canal with "half-skullcap". Chorionic depressions geographically variable (Figs. 22, 23). Base of cap without a chorionic collar.

Diagnosis. Nymphs of this species can be distinguished from those of *E. eophilum* by the relatively short mandibular tusks (Fig. 1), an acute spine on the right mandible (Fig. 14), the triangular frontal process (Fig. 1), the relatively wide markings on the abdominal terga (Fig. 3), and the length of the cerci, which are about as long as the median filament (male nymph, Table 1). Adults of this species are distinguished from those of *E. eophilum* by the hyaline wings (male) and by the wide brown markings on the abdominal terga (both sexes). Eggs of this species can be easily distinguished from those of *E. eophilum* by the typically small size (Fig. 30). *Ephoron shigae* and *E. limnobium* are closely related and nearly indistinguishable morphologically. The nymphal stages of these species are very similar, but *E. shigae* may be distinguished by the pigmented gills in mature nymphs and the brown markings on the body. Most adults of *E. shigae* possess dark brown markings on the body, but the markings on the body of *E. limnobium* are often not distinctly defined. The most reliable character for recognizing *E. shigae* is its punctured chorion sculpture. Eggs having the chorion with large and ring-like depressions are referable to *E. limnobium*.

Type Series. HOLOTYPE. Not designated. Type information unknown, probably lost.

Other Material Examined. Japan: [Honshu] Aichi. Otogawa River, Okazaki-shi, 4-VII-92, N. Ban, 10N; Shimoshidamibashi, Shonaigawa River, Moriyama-ku, Nagoya-shi, 21-IX-93, K. Hatta, Light, 55♀♀. Chiba. Iwatabashi, Obitsugawa River, Kimitsu-shi, 26-VIII-86, N. Kobayashi, 1N (CM); Kanamori, Obitsugawa River, Kimitsu-shi, 15-IX-93, S. Ishiwata, Light, 30♂♂ 10S♂♂ 40♀♀. 1N, 24-IX-93, S. Ishiwata, 2N; Shinkoudabashi, Yorogawa River, Komagome, Ichihara-shi, 24-IX-93, S. Ishiwata, Light, 5♀♀; Shiobuchibashi, Isumigawa River, Horinouchi, Ootaki-machi, 24-IX-93, S. Ishiwata, Light, 20♂♂ 20S♂♂ 50♀♀. Fukushima. Datebashi, Abukumagawa River, Date-machi, ?-VIII-92, ?, 5N; Abukumagawa River, Fukushima-shi, 19-IX-92, ?, 3♂♂ 2♀♀. Hiroshima. Ootagawabashi, Ootagawa River, Asaminami-ku, 6-VI-87, S. Ishiwata, 1N, 10-VI-93, S. Ishiwata, 5N. Hyogo. Shosha, Yumesaki River, Himeji-shi, 10-IX-89, T. Ueno, Light, 1♂ 1♀. Ibaraki. Oogatabashi, Kinugawa River, Kamaniwa, Chiyokawa-mura, 5-IX-92, S. Ishiwata, Light, 20♀♀; Sendaibashi, Nakagawa River, Naka-machi, 11-IX-91, S. Ishiwata, Light, 6♀♀. Kanagawa. Sagamigawa River nr the Tomei Expressway, Atsugi-shi, 11-IX-92, S. Ishiwata, Light, 8♀♀, 14-IX-93, S. Ishiwata, Light, 10♀♀; Showabashi, Sagamigawa River, Sagamihara-shi, 8-IX-94, H. Moriya, 24N (SM). Kyoto. Ochi, Takedagawa River, Fukuchiyama-shi, 4-VI-87, S. Ishiwata, 3N. Ujigawabashi, Ujigawa River, Uji-shi, 8-IX-94, S. Ishiwata, Light, 1♂ 10♀♀. Mie. Onoki, Ichishi-cho, 12-IX-77, A. Sugiyama, Light, 8♂♂ 11♀♀. Miyagi. Eaegawa River, Wakuya-cho, 3-X-92, N. Yokoyama, 10♀♀. Niigata. Yasudabashi, Aganogawa River, Yasuda-machi, 20-IX-90, S. Togashi, 30♀♀. Okayama. Asahigawa River nr the Shinkansen line,

Okayama-shi, 11-IX-88, N. Watanabe, Light, 2♂♂, 4-IX-92, N. Watanabe, 3N, 17-IX-93, I. Yoshitaka, 3♂♂ 10♀♀. Tottori. Sanogawashusuientei, Hinogawa River, Furuichi, Mizokuchi-cho, 19-VIII-79, S. Tanaka, 10N. Osaka. Hirakataohashi, Yodogawa River, Banda, Takatsuki-shi, 4-IX-86, N. Kobayashi, 1N, 25-IX-93, S. Ishiwata, Light, 20♂♂ 20S♂♂ 50♀♀. Saitama. Araibashi, Arakawa River, Arai, Kitamoto-shi, 10-IX-93, S. Ishiwata, 13N (11 exuviae), 10-IX-93, S. Ishiwata, Light, 80♂♂ 20S♂♂ 100♀♀, 27-VII-94, S. Ishiwata, 3N; Kaiheibashi, Arakawa River, Hirakata, Ageo-shi, 6-IX-93, S. Ishiwata. 1N (exuvia); Nukadabashi, Arakawa River, Nukada, Kounosu-shi, 10-IX-93, S. Ishiwata, Light, 3♂♂, 17-VIII-94, 11N, Light, 100♂♂ 150♀♀; Oashibashi, Arakawa River, Oashi, Fukiage-machi, 10-IX-93, S. Ishiwata, Light, 1♂; Oshikiribashi, Arakawa River, Oshikiri, Kounan-cho, 6-IX-93, S. Ishiwata, Light, 2♂♂ 5♀♀, 10-IX-93, S. Ishiwata, Light, 2♂♂ 5♀♀. Tochigi. Utsunomiya, Kinugawa River, Utsunomiya-shi, 13-IX-86, K. Nakamura, 1♀, 15-IX-86, 4♀♀; Mukadabashi, Arakawa River, Mukada, Karasuyama-machi, 11-IX-91, N. Koibuchi, 10♀♀. Tokyo. Tamagawa River nr the Hachikosen line, Hino-shi, 4-IX-94, S. Sasaki, Light, 5♂♂ 10♀♀; the irrigation channel nr Tokoji Temple, Sakae-cho, Hino-shi, 4-IX-94, S. Sasaki, Light, 10♂♂ 20♀♀. [Shikoku] Ehime. Torikubibashi, Hijikawa River, Torikubi, Oozu-shi, 13-IX-85, K. Kuwata, 3♂♂ 15♀♀. Kagawa. Kawagebashi, Kotogawa River, Kawabe-machi, 20-IX-93, N. Watanabe, 6♀♀. Kochi. Kakinoue, Shimantogawa River, Nishitosa-mura, 11-IX-87, Y. Horiuchi, 1N; Toitajimabashi, Monobe River, Noichi-cho, 14-IX-88, Y. Horiuchi, Light, 44♀♀; Shimantogawabashi, Shimantogawa River, Nakamura-shi, 11-IX-87, Y. Horiuchi, 1N. Tokushima. Aizonobashi, Yoshinogawa River, Aizumi-cho, 9-IX-93, Y. Tokuyama, 30♀♀. [Kyushu] Oita. Shiratakibashi, Onogawa River, Oita-shi, 12-IX-88, S. Satoh, 4♀♀, 7-VIII-92, S. Satoh, 1N; Oitagawa River, Oita-shi, 21-IX-92, K. Hisaeda, Light, 1♀. Saga. Kamimutsuro, Kamimutsurogawa River, Fuji-cho, 20-V-94, K. Ogata, 1N. **Korea:** At street light nr Han River, Myongil-dong, Seoul, 15-IX-83, Y.J. Bae, 4♀♀; Talchon River, Chungju Chungchongbuk-do, 12-VI-83, Y.J. Bae, 1N. **Russian Far East:** Razdolnaya River nr Pokrovka village, Primorye Territory, 6-IX-91, T. Vshivkova, 3♂♂ 1♀; Ussuri River, 1.5 km lower Podgornoye village, Primorye Territory, 22-IX-91, T. Tiunova, 2♂♂ 1♀; Arsenjevka River, nr Beltsovo village, Primorye Territory, 18-VII-91, T. Tiunova, 4N.

Distribution (Fig. 31). Japan (Honshu, Shikoku, Kyushu), Korea, Russian Far East.

Biology. This is the most widespread species of Japanese *Ephoron*, occurring throughout most of the large rivers. Based on specimens that have been studied, the nymphs are generally found in gravel and sand shoals of large rivers (Shioyama 1978). Adults emerge mainly from August to September. Mass flights (mating flights) occur over rivers in the evening (after sunset). In this study many individuals were collected from Japan. But no males or only a few males were found in some rivers (Sagamigawa River, Kinugawa River), where the populations are probably parthenogenetic.

Discussion. No type specimens were designated by Takahashi, nor were localities presented clearly; there was, however, a note on the distribution of this species in his text, "Shiga and Shanuki (Kagawa)". I have collected specimens from Kyushu to the northern part of Honshu, including the localities in Takahashi's note. Only specimens of *E. limnobium* were collected from Shiga, and those of *E. shigae* were collected from Shanuki and the other localities. Although Takahashi's original description is relatively incomplete, examination of material in my study justifies the treatment in the present paper because the color pattern of the thorax and abdomen nearly agree with that described for *E. shigae* by Takahashi (1924).

Ephoron shigae has a wider geographical distribution than does *E. eophilum* or *E. limnobium*. *Ephoron eophilum* has been found from the lower reaches of large rivers in the Kanto plain (Arakawa River, Tonegawa River, and its tributary) and *E. limnobium* only from

Lake Biwa. In those rivers *E. shigae* and *E. eophilum* occur sympatrically indicating they are specifically distinct. A similar test of sympatry is not known for *E. shigae* and *E. limnobium* and the morphological differences between this pair are not as great as between *E. shigae* (or *E. limnobium*) and *E. eophilum*. However, *E. limnobium* has unique features in the chorion surface, in the color pattern of the body, and in the nymphal gills so that treating it as a distinct species is reasonable.

I collected mainly shallowly depressed eggs (Fig. 23) from three localities of Chiba: Isumigawa River, Obitsugawa River, and Yorogawa River. The eggs collected from other localities had almost deep depressions. Occasionally, a few of them (Chiba and the other localities) had deep and shallow depressions in the same population. Consequently, I conclude that the degree of depression is interspecific variation.

Nymphs, male imagoes, and eggs were examined in the Korean species (*E. shigae*) and the Far Eastern Russian species [*Ephoron virgo* (Olivier)]. I assign these specimens from Korea and Russia to *E. shigae*, because nymphal characters (except for the character of pigmented gills), male characters, and egg characters were the same as in the Japanese specimens of this species. It may be that the pigmentation of gills is variable. Immature nymphs of *E. shigae* often show no pigmentation. Judging from the figure of Yoon (1988, p. 156, fig. 29-4), there is no pigmentation in Korean specimens studied by him. More nymphal specimens from Korea and Russia should be examined to clarify the problem of pigmentation.

Degrange (1960) reported that the egg size of the European *E. virgo* was 266 μm in length (without polar cap), 175 μm in width, and the chorion was smooth. The egg size of *E. shigae* (Fig. 30) is similar to that of *E. virgo*. The chorion surface of *E. shigae*, however, differs from that of *E. virgo* in having punctures (Fig. 24).

Ephoron shigae seems to be closely related to *Polymitarcys nanchangi* (Hsu 1936) from China based on venation and the size of the eyes. *Polymitarcys virgo* from China by Uéno (1941) is also related to this species, judging from the wing figure. Kobayashi (1992) gave two figures under the name of *E. shigae* (Takahashi). One was a nymph from the Yodogawa River and the other was a male subimago from Lake Biwa (Nishino, personal communication). The figure of the male subimago was misidentified by Kobayashi and it is actually of *E. limnobium*.

Ephoron limnobium **sp.nov.**

[Japanese name: Biwako-shiro-kagerou]
(Figs. 4, 5, 6, 11, 12, 16, 18, 25, 26, 30, 31)

Ephoron shigae: Kobayashi, 1992, *Hand. Zooben. Lake Biwa* 2: 8, fig. (male subimago); (nymph), misidentification.

Description. Mature nymph. *Lengths*: Body 14.0–22.0 mm, cerci 9.0–10.5 mm (male), 5.2–6.0 mm (female), median filament 8.0–10.5 mm (male), 9.0–11.1 mm (female). Measurements and ratios for samples are presented in Table 3. *Head*: Eyes black, separated dorsolaterally; ocelli black; inner margin of ocelli brown. Head with a triangular median frontal process (Fig. 4). MWE about as wide as MWP in both sexes. Mandibular tusks shorter than MWP, curving downward, straight or curved upward apically as viewed laterally, with numerous tubercles (16–27 tubercles), with short and dense hair on upper surface near bases, with long hair on lateral surface; an acute spine between outer and inner incisors on right mandible (Fig. 12). Maxillary palpi two-segmented. Labial palpi two-segmented, held beneath and at right angles to glossae. *Thorax*: Color milky white with slight markings on dorsal surface. Forelegs stout and fossorial with several distinct rows of long hair; femora with a row of tubercles along paraxial edge near base; tibiae flattened, with two rows of ventral tubercles, one along paraxial and one along antiaxial margins (Fig. 6); tubercles in

TABLE 3. Measurements and ratios for a population sample of *Ephoron limnobium*: range, mean and (standard deviation); mature nymph, measurements in mm

Locality	(*n*)	LB	LC	LT	MWP	MWE	LM	NTM	LM/MWP	MWE/MWP
Lake Biwa, Biwa-cho, Shiga										
Male	(20)	14.0–16.0	9.0–10.5	8.0–10.5	1.84–2.13	1.83–2.08	1.35–1.55	16–24	0.63–0.75	0.92–1.12
		15.2 (0.93)	10.0 (0.55)	9.9 (0.94)	1.96 (0.12)	1.95 (0.10)	1.41 (0.08)	20.5 (2.66)	0.70 (0.05)	0.99 (0.04)
Female	(20)	16.0–22.0	5.2–6.0	9.0–11.1	2.18–2.56	2.18–2.27	1.55–1.74	20–27	0.66–0.77	0.93–1.11
		19.0 (1.75)	5.8 (0.32)	9.8 (0.75)	2.29 (0.12)	2.25 (0.07)	1.62 (0.08)	23.9 (2.85)	0.71 (0.04)	0.98 (0.03)

TABLE 4. Measurements and ratios for a population sample of *Ephoron limnobium*: range (R), mean (M), and standard deviation (SD); male imago and female subimago, measurements in mm

	LB	LC	LT	MWP	MWE	LFW	LHW	FF	FTB	FTR	LP	MWE/MWP	LP/MWP
Male ($n = 15$)													
R	9.8–14.7	26.0–33.8	0.5–1.3	1.67–2.00	1.66–2.00	9.6–12.0	4.8–5.9	1.20–1.40	4.20–4.90	4.90–6.20	1.61–1.92	0.92–1.10	0.82–1.02
M	12.5	30.5	0.9	1.77	1.77	10.9	5.3	1.29	4.52	5.78	1.69	1.00	0.96
SD	1.34	2.60	0.24	0.12	0.10	0.75	0.21	0.07	0.27	0.54	0.10	0.04	0.05
Female ($n = 15$)													
R	11.7–19.3	10.4–16.3	5.3–13.0	2.00–2.70	2.10–2.60	13.0–15.3	4.9–5.9	1.00–1.50	1.33–2.00	0.60–1.07		0.93–1.03	
M	14.0	13.2	9.6	2.26	2.24	13.3	5.5	1.26	1.70	0.84		0.99	
SD	2.32	2.57	2.47	0.26	0.20	0.74	0.34	0.13	0.20	0.17		0.03	

Each value was measured from the samples of Lake Biwa (Biwa-cho, Shiga).

paraxial and in antiaxial sides densely arranged in distal half of tibiae. Middle legs small. *Abdomen*: Color milky white with a black dot at base of each gill; abdominal terga with light brown markings; tergum 1–4 without markings; tergum 10 with slightly broad marking covering entire segment (Fig. 5); abdominal sterna uniformly milky white. Gills white on abdominal segments 1–7; gills 1 single; other gills forked; each lamella of gills 2–7 with lateral margin fringed, with lateral tracheal branches not pigmented. Three caudal filaments with intersegmental setae; median filament about as long as or slightly shorter than cerci (male) or longer than cerci (female) (Table 3).

Male. *Lengths*: Body 9.8–14.7 mm, forewings 9.6–12.0 mm, hind wings 4.8–5.9 mm, cerci 26.0–33.8 mm, median filament 0.5–1.3 mm. Measurements and ratios for samples are presented in Table 4. *Head*: Color light brown; ocelli and base of ocelli black; eyes black, separated laterally. MWE about as wide as MWP. *Thorax*: Color milky white with light brown markings. Forewings hyaline (Fig. 16), with numerous crossveins and intercalaries; main vein of costal margin purplish gray; outer margin with a network of tubercles ventrally along the veins; cubital area with two or more intercalaries; a strong convex vein (scv) running parallel to CuP, attached to CuA perfectly or imperfectly. Hind wings hyaline, with a blunt costal projection; outer margin with a network of tubercles ventrally along veins. Forelegs reddish brown, about as long as body. Femora short; tibiae long, about four times length of femora; tarsi longer than tibiae. Middle and hind legs white, poorly developed. *Abdomen*: Color pattern of body generally similar to that of nymphs. Penes white; penis lobes straight and extended laterally, about as wide as pronotum, hooked at apices (Fig. 11); forceps four-segmented. Cerci well developed; short vestigial median filament.

Female. *Lengths*: Body 11.7–19.3 mm, forewings 13.0–15.3 mm, hind wings 4.9–5.9 mm, cerci 10.4–16.3 mm, median filament 5.3–13.0 mm. Measurements and ratios for samples are presented in Table 4. *Head*: Color pattern of ocelli and eyes similar to those of male. Eyes separated laterally; MWE about as wide as MWP. *Thorax*: Color pattern of body and legs generally similar to those of male but darker. Wings more whitish than male, surfaced with a large number of short hairs; wing venation similar to that of male except for hind wings; a vein between R1 and R2 of hind wings absent. All legs poorly developed. *Abdomen*: Color pattern of body generally similar to that of male but darker. Three developed caudal filaments.

Egg. Length without cap 214.1–260.0 μm, width 137.6–183.5 μm (Figs. 25, 30). One polar cap with two to four micropylar devices at capped end of egg. Sperm guide poorly defined; micropylar canal with "half-skullcap". Chorion with ring-like depressions, about 10 μm in diameter (Fig. 26).

Diagnosis. Nymphs of *E. limnobium* are very similar to those of *E. shigae*, but *E. limnobium* may be distinguished by the gills with no pigmentation in mature nymphs and by the slightly brown markings of the body. Male adults of this species are also similar to those of *E. shigae*, however, they are separable from *E. shigae* by the color characters. Adults of this species are usually lighter than *E. shigae*. Eggs of *E. limnobium* and *E. shigae* can be easily distinguished by the chorion surface. Nymphs of *E. limnobium* can be distinguished from those of *E. eophilum* by the relatively short mandibular tusks (Fig. 4), an acute spine on the right mandible, the triangular frontal process (Fig. 4), the slight markings on the abdominal terga (Fig. 5), and the length of the cerci, which are about as long as the median filament (male nymph, Table 3). Adults of this species are distinguished from those of *E. eophilum* by the hyaline wings (male) and the light markings on the abdominal terga (both sexes). Eggs of this species can be easily distinguished from those of *E. eophilum* by the typically small size (Fig. 30).

Etymology. The species name *limnobium* is derived from the Greek *limne* meaning lake, and *bioo* meaning live.

Type Series. HOLOTYPE. A female nymph with eggs (alcohol), CBM-ZI 33880, labeled/ Hayazaki, Lake Biwa, Biwa-cho, Shiga, Japan 3-IX-1993 S. Ishiwata/ determined by S. Ishiwata and deposited in CM. PARATYPES. A male imago (alcohol), CBM-ZI 33881, labeled/ Hayazaki, Lake Biwa, Biwa-cho, Shiga, Japan 3-IX-1993 S. Ishiwata, Light/ determined by S. Ishiwata and same deposition as holotype. PARATYPES. Four female nymphs with eggs (alcohol), CBM-ZI 33882-33885, same data and deposition as holotype.

Other Material Examined. Hayazaki, Lake Biwa, Biwa-cho, 3-IX-93, S. Ishiwata, 18N, Light, 3♂♂ 7S♂♂ 50♀♀; Imazuhama, Lake Biwa, Imazu-cho, 10-IX-86, H. Nishida, Light, 14♂♂ 2♀♀, 3-IX-93, S. Ishiwata, 30♂♂; Ogami, Lake Biwa, 10-IX-86, M. Nishino, Light, 1♂.

Distribution (Fig. 31). Japan (Honshu). This species is known only from Lake Biwa (Shiga, near Kyoto).

Biology. The nymphs of this species are found in gravel and sand shoals of Lake Biwa. Mass flights (mating flights) occur in the evening after sunset.

Discussion. After careful study of eggs collected from all over Japan, I conclude that the specimens from Lake Biwa represent a new species, *E. limnobium*. Although the adults and nymphs of this species are similar to those of *E. shigae*, the unique characteristics of the eggs have prompted me to describe the species. The eggs of this species are easily distinguished from the eggs of the other known species in the genus by the ring-like depressions on the chorion. The eggs of *E. virgo* and *Ephoron album* (Say) have a smooth chorionic surface (Degrange 1956, 1960; Koss 1968), those of *Ephoron leukon* Williamson have a large-mesh reticulation (Koss 1968), and those of *Ephoron nigridorsum* (Tshernova) have two polar caps (unpublished data). Kobayashi's (1992) male figure of *E. shigae* (Takahashi) was misidentified and is actually *E. limnobium*.

Ephoron eophilum sp.nov.

[Japanese name: Akatsuki-shiro-kagerou]
(Figs. 7, 8, 9, 13, 15, 17, 19, 20, 21, 27, 30, 31)

Description. Mature nymph. *Lengths*: Body 17.5–29.1 mm, cerci 12.0–18.0 mm (male), 5.2–9.5 mm (female), median filament 6.5–11.0 mm (male), 6.0–12.0 mm (female). Measurements and ratios for selected population samples are presented in Table 5. *Head*: Eyes black, separated dorsolaterally. Ocelli black; inner margin of ocelli brown. Head with semicircular median frontal process (Fig. 7). MWE about as wide as MWP in both sexes. Mandibular tusks longer than MWP (Fig. 7), curving downward, curved upward apically as viewed laterally (Fig. 8), with rows of tubercles (12–25 tubercles), with short and dense hair on upper surface near bases, with long hair on lateral surface; a blunt spine between outer and inner incisors on right mandible (Fig. 15). Maxillary palpi two-segmented. Labial palpi two-segmented, held beneath and at right angles to glossae. *Thorax*: Thorax milky white with slight markings on dorsal surface. Forelegs stout and fossorial with several distinct rows of long hair; femora with a row of tubercles along paraxial edge near base; tibiae flattened, with two rows of ventral tubercles, one along paraxial and one along antiaxial margins; tubercles on paraxial side sparsely arranged in less than distal half of tibiae (Fig. 9). Middle legs small. *Abdomen*: Color milky white, with a black dot at base of each gill. Abdominal terga milky white with brown markings becoming darker and wider toward posterial end. Abdominal sterna only milky white. Gills white on abdominal segments 1–7; gills 1 single; other gills forked; each lamella of gills 2–7 with lateral margin fringed and with lateral tracheal branches not pigmented. Three caudal filaments with intersegmental setae; median filament shorter than cerci (male) or longer than cerci (female).

TABLE 5. Measurements and ratios for two population samples of *Ephoron eophilum*: range, mean and (standard deviation); mature nymph, measurements in mm

Locality	(*n*)	LB	LC	LT	MWP	MWE	LM	NTM	LM/MWP	MWE/MWP
Arakawa River, Kitamoto-shi, Saitama										
Male	(20)	17.5–22.0	13.0–18.0	7.0–11.0	2.13–2.90	2.23–3.39	2.42–3.39	12–20	0.96–1.36	0.92–1.25
		20.1 (1.12)	14.4 (1.22)	9.4 (0.80)	2.52 (0.21)	2.51 (0.22)	3.00 (0.24)	16.2 (2.35)	1.18 (0.11)	1.00 (0.04)
Female	(20)	22.0–29.1	5.5–9.5	9.0–12.0	2.61–3.68	2.71–3.48	3.39–4.35	14–25	1.11–1.55	0.93–1.34
		25.2 (1.84)	6.7 (1.02)	10.3 (0.94)	3.10 (0.26)	3.05 (0.19)	4.01 (0.26)	19.1 (2.55)	1.30 (0.11)	0.98 (0.04)
Kinugawa River, Ishige-machi, Ibaraki										
Male	(20)	17.5–20.5	12.0–13.0	6.5–8.5	2.22–2.32	2.18–2.22	2.13–2.42	13–15	0.92–1.09	0.91–1.22
		18.8 (1.03)	12.4 (0.38)	8.08 (1.24)	2.26 (0.05)	2.21 (0.03)	2.28 (0.12)	14.3 (0.82)	1.01 (0.06)	0.98 (0.05)
Female	(20)	20.5–27.0	5.2–6.5	6.0–10.0	2.63–2.97	2.57–2.97	2.67–3.24	13–20	1.00–1.09	0.92–1.31
		22.8 (2.46)	5.94 (0.47)	8.80 (1.60)	2.72 (0.11)	2.67 (0.14)	2.81 (0.20)	15.5 (2.59)	1.03 (0.03)	0.98 (0.04)

TABLE 6. Measurements and ratios for samples of *Ephoron eophilum*: range (R), mean (M), and standard deviation (SD); male imago and female subimago, measurements in mm

	LB	LC	LT	MWP	MWE	LFW	LHW	FF	FTB	FTR	LP	MWE/MWP	LP/MWP
Male ($n = 20$)													
R	10.3–16.7	28.0–39.3	0.7–1.3	1.63–2.23	1.77–2.13	11.3–13.7	4.8–6.6	1.20–1.33	4.67–5.60	5.87–7.73	0.90–1.23	1.00–1.16	0.90–1.25
M	13.8	33.1	0.9	1.94	2.06	12.4	6.0	1.27	5.09	6.91	1.06	1.06	1.09
SD	1.43	3.04	0.20	0.19	0.18	0.66	0.39	0.07	0.28	0.47	0.10	0.05	0.09
Female ($n = 20$)													
R	16.0–26.1	12.0–17.3	8.0–14.0	2.20–3.17	2.23–2.95	14.0–20.0	5.5–8.7	1.17–1.67	1.33–2.57	0.83–1.27		0.93–1.03	
M	19.3	15.5	11.4	2.65	2.63	17.4	7.1	1.44	1.92	1.07		0.99	
SD	2.29	4.70	1.52	0.24	0.19	1.41	0.60	0.14	0.26	0.11		0.03	

Each value was measured from the samples of two localities: Arakawa River ($n = 10$, Kounosu-shi, Saitama) and Kinugawa River ($n = 10$, Ishige-machi, Ibaraki).

Male. *Lengths*: Body 10.3–16.7 mm, forewings 11.3–13.7 mm, hind wings 4.8–6.6 mm, cerci 28.0–39.3 mm, median filament 0.7–1.3 mm. Measurements and ratios for selected population samples are presented in Table 6. *Head*: Color brown; ocelli and base of ocelli black; eyes black, separated laterally. MWE about as wide as MWP. *Thorax*: Color milky white with brown markings. Forewings whitish and translucent (Fig. 17), surfaced with a network of tubercles (Fig. 19) ventrally and dorsally, with numerous crossveins and intercalaries; main vein of costal margin purplish gray; cubital area with two or more intercalaries; a strong convex vein (scv) running parallel to CuP (Fig. 21), attached to CuA perfectly or imperfectly. Hind wings whitish and translucent, with a blunt costal projection, surfaced with a network of tubercles ventrally and dorsally. Forelegs about as long as body; femora short; tibiae long, about four times length of femora; tarsi longer than tibiae. Middle and hind legs white, poorly developed. *Abdomen*: Color pattern of body generally similar to that of nymphs. Penes white; lobes straight and extended laterally, about as wide as pronotum, hooked at apices; forceps four-segmented. Cerci well developed; short vestigial median filament.

Female. *Lengths*: Body 16.0–26.1 mm, forewings 14.0–20.0 mm, hind wings 5.5–8.7 mm, cerci 12.0–17.3 mm, median filament 8.0–14.0 mm. Measurements and ratios for selected population samples are presented in Table 6. *Head*: Color pattern of ocelli and eyes similar to those of male. Eyes separated laterally, MWE about as wide as MWP. *Thorax*: Color pattern of body and legs generally similar to those of male but darker. Wings more whitish than male, surfaced with a large number of short hairs (Fig. 20); wing venation similar to male except for hind wings; a vein between R1 and R2 absent. All legs poorly developed. *Abdomen*: Color pattern of body and legs generally similar to those of male but darker; three developed caudal filaments.

Egg. Length without cap 305.9–458.8 μm, width 221.8–321.2 μm (Figs. 27, 30). One polar cap with two to seven micropylar devices at capped end of egg. Sperm guide poorly defined; micropylar canal with "half-skullcap". Chorion smooth from equator to capped pole with slightly puncture-like impression near opposite pole. The base of cap without a chorionic collar.

Diagnosis. Nymphs of this species can be distinguished from those of *E. shigae* and *E. limnobium* by the relatively long mandibular tusks (Fig. 7), the blunt spine on the right mandible (Fig. 15), the semicircular frontal process, and the length of the cerci, which are longer than the median filament (male nymph, Table 5). Adult males of this species are distinguished from those of *E. shigae* and *E. limnobium* by the distinctly translucent wings (Fig. 17), and the relatively light and slender markings on the abdominal terga. Adult females of this species can be distinguished from those of *E. shigae* only by the relatively light and slender markings on the abdominal terga. Eggs of this species can be easily distinguished from those of *E. shigae* and *E. limnobium* by the large size (Figs. 27, 30).

Etymology. The species name *eophilum* is derived from the Greek *eos* meaning dawn, and *phileo* meaning like.

Type Series. HOLOTYPE. A female nymph with eggs (alcohol), CBM-ZI 33927, labeled/ Araibashi, Arakawa River, Arai, Kitamoto-shi, Saitama, Japan 27-VII-94 S. Ishiwata/ determined by S. Ishiwata and deposited in CM. PARATYPES. Two male imagoes (alcohol), CBM-ZI 33928-33929, labeled/ Araibashi, Arakawa River, Arai, Kitamoto-shi, Saitama, Japan 27-VII-94 S. Ishiwata, Light/ determined by S. Ishiwata and same deposition as holotype. PARATYPES. Three female nymphs with eggs, two male nymphs, two female adults with eggs, CBM-ZI 33930-33936, same data and deposition as holotype.

Other Material Examined. Chiba. Nodabashi, Edogawa River, Noda-shi, 8-VI-86, S. Ishiwata, 5N. Ibaraki. Ishigebashi, Kinugawa River, Ishige-machi, 6-IX-93, S. Ishiwata, Light, 10♂♂ 30♀♀, 10-IX-93, S. Ishiwata, 12N, Light, 5♂♂ 50♀♀; Tonegawabashi,

Tanaka, Koga-shi, 27-VII-94, S. Ishiwata, 1 ♂ 7N (exuviae). Saitama. Kaiheibashi, Arakawa River, Hirakata, Ageo-shi, 6-IX-93, S. Ishiwata, 101N (100 exuviae), Light, 10 ♂♂ 25 ♀♀, 27-VII-94, S. Ishiwata, 4 ♂♂ 5N (exuviae); Kamiuchimaki, Arakawa River, Asaka-shi, 6-IX-93, S. Ishiwata, Light, 2 ♂♂; Araibashi, Arakawa River, Arai, Kitamoto-shi, 10-IX-93, S. Ishiwata, Light, 1 ♂; 27-VII-94, 50N; Nukatabashi, Kounosu-shi, 17-VIII-94, S. Ishiwata, 2N, 18-VIII-94, Light, 80 ♂♂ 100 ♀♀.

Distribution (Fig. 31). Japan (Honshu). This species is known only from the Kanto plain (Arakawa River, Tonegawa River, and its tributary near Tokyo).

Biology. I have collected *E. eophilum* only from the Kanto plain which has the widest open field in Japan. The nymphs of this species are found in the clay banks of large rivers; they form U-shaped burrows and are distributed in the lower courses of the rivers in an overlapping zone with *E. shigae*. Adults emerge mainly from June to October. Mass flights (mating flights) occur over the rivers only in the early morning (about 2 h before sunrise).

Discussion. *Ephoron eophilum* is similar to *E. virgo*, *E. nigridorsum*, and the Nearctic species. However, the nymphs of *E. eophilum* differ from those species listed above by the semicircular median frontal process and the presence of a blunt spine on the right mandible. The males differ from those of the Nearctic species by the convex vein running parallel to CuP (Fig. 21). The males of this species can be distinguished from those of *E. virgo* by the whitish wings. The eggs of *E. eophilum* are also distinguished from those of the other species by the larger size and the chorion. The eggs of *E. virgo* and *E. album* have a smooth chorion surface, those of *E. leukon* have large-mesh reticulation, and those of *E. nigridorsum* have two polar caps.

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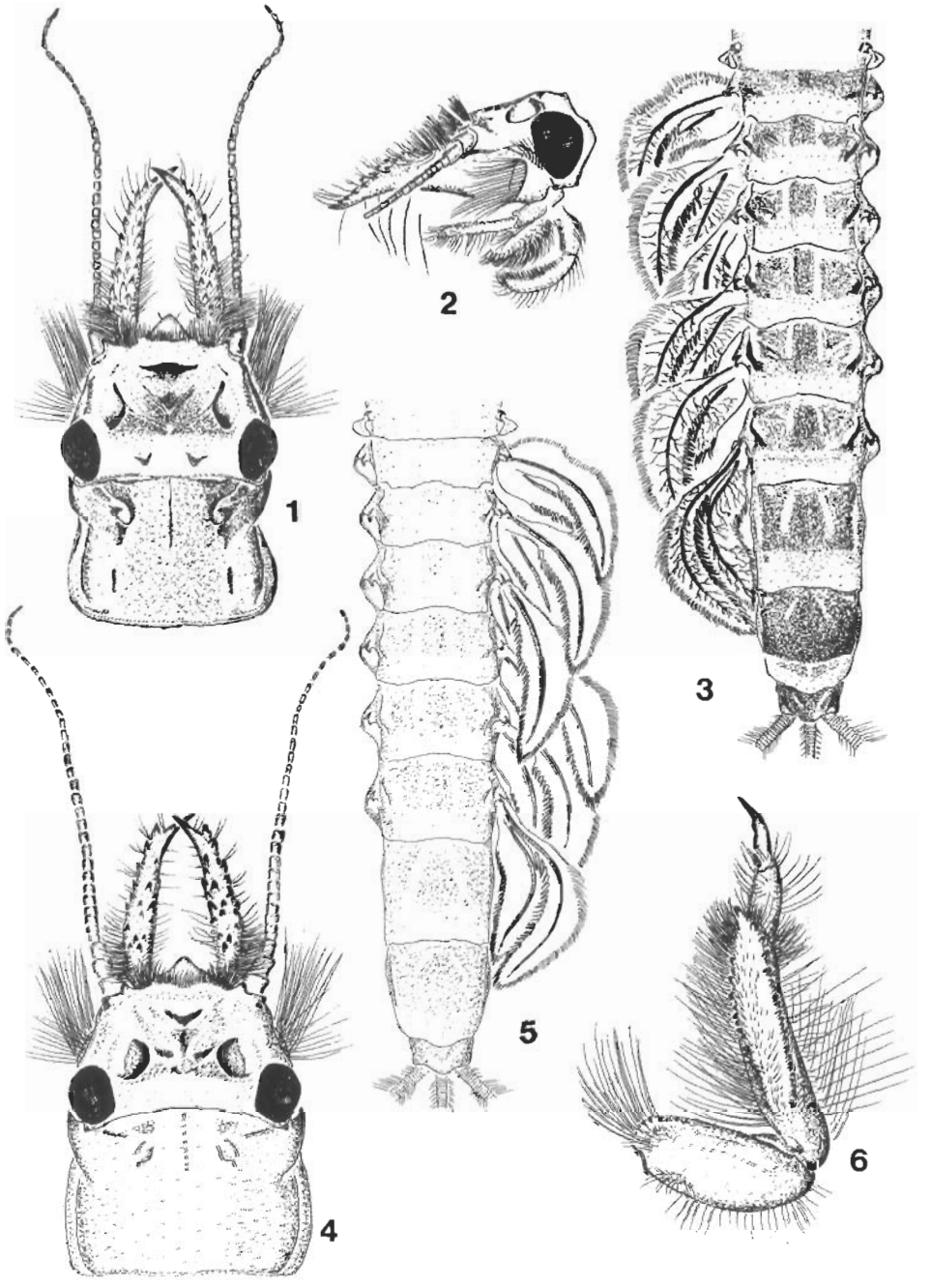
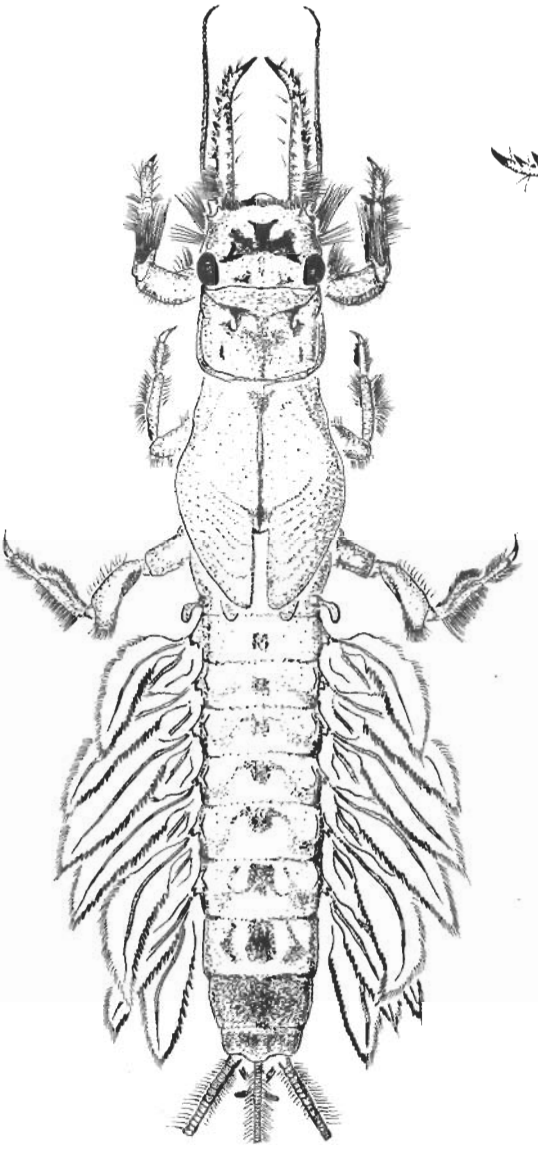
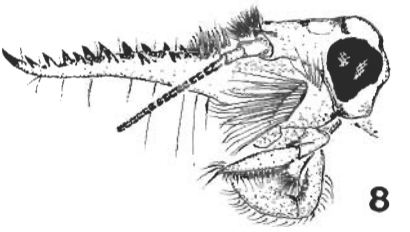
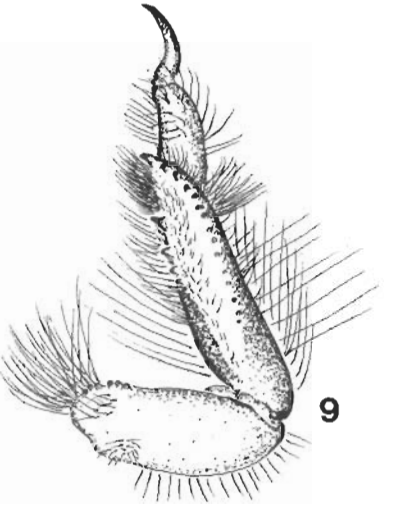


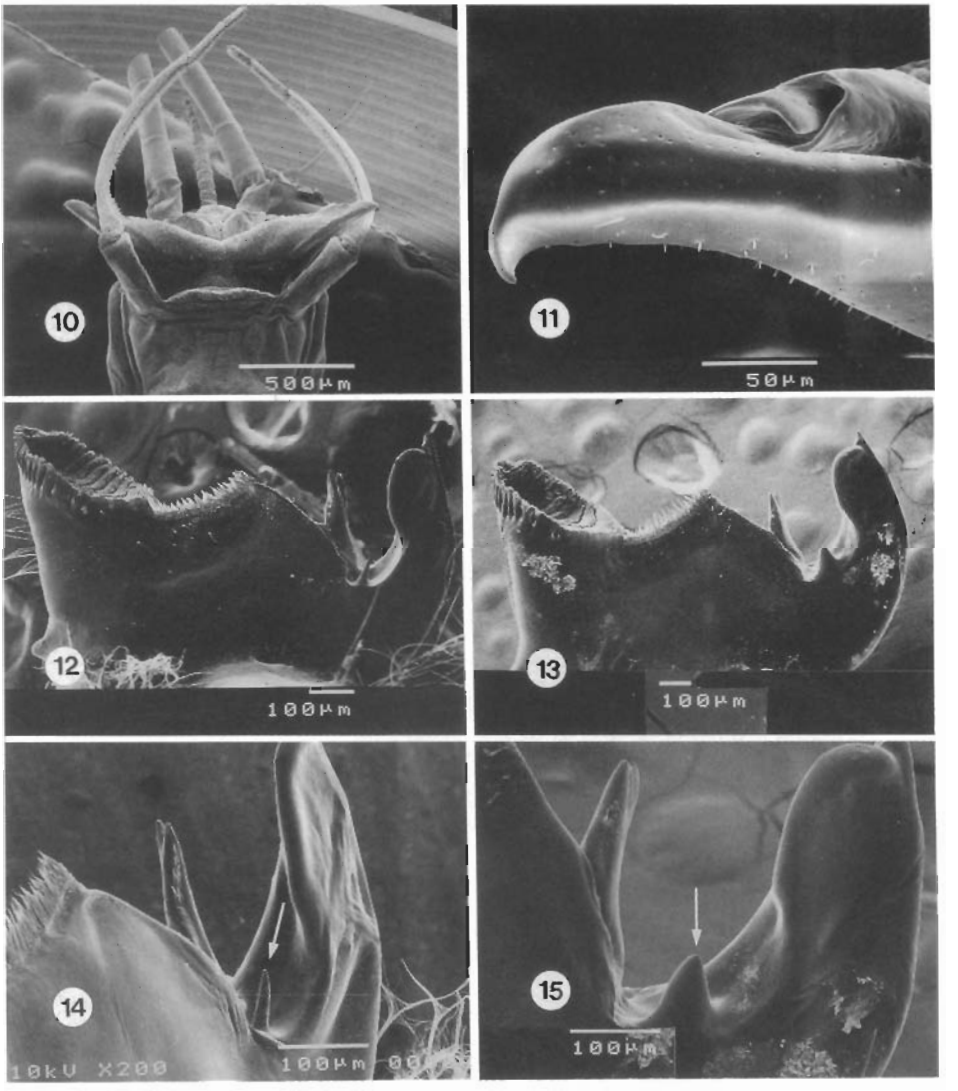
FIGS. 1–6. 1–3, *Ephoron shigae*, mature nymph: 1, head (dorsal view); 2, head (lateral view); 3, abdomen (dorsal view, gills opened, right gills removed). 4–6, *Ephoron limnobium* sp.nov., mature nymph: 4, head (dorsal view); 5, abdomen (dorsal view, gills opened, left gills removed); 6, foreleg (ventral view).



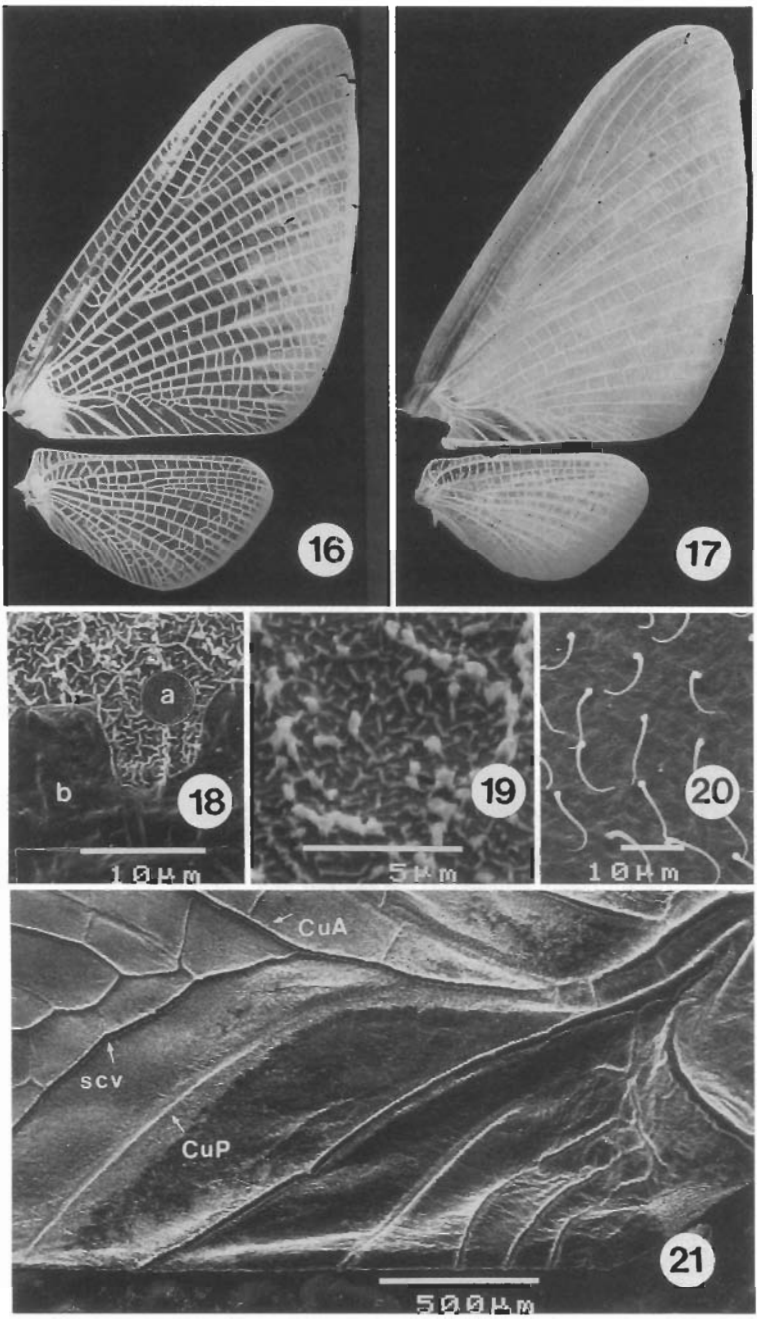




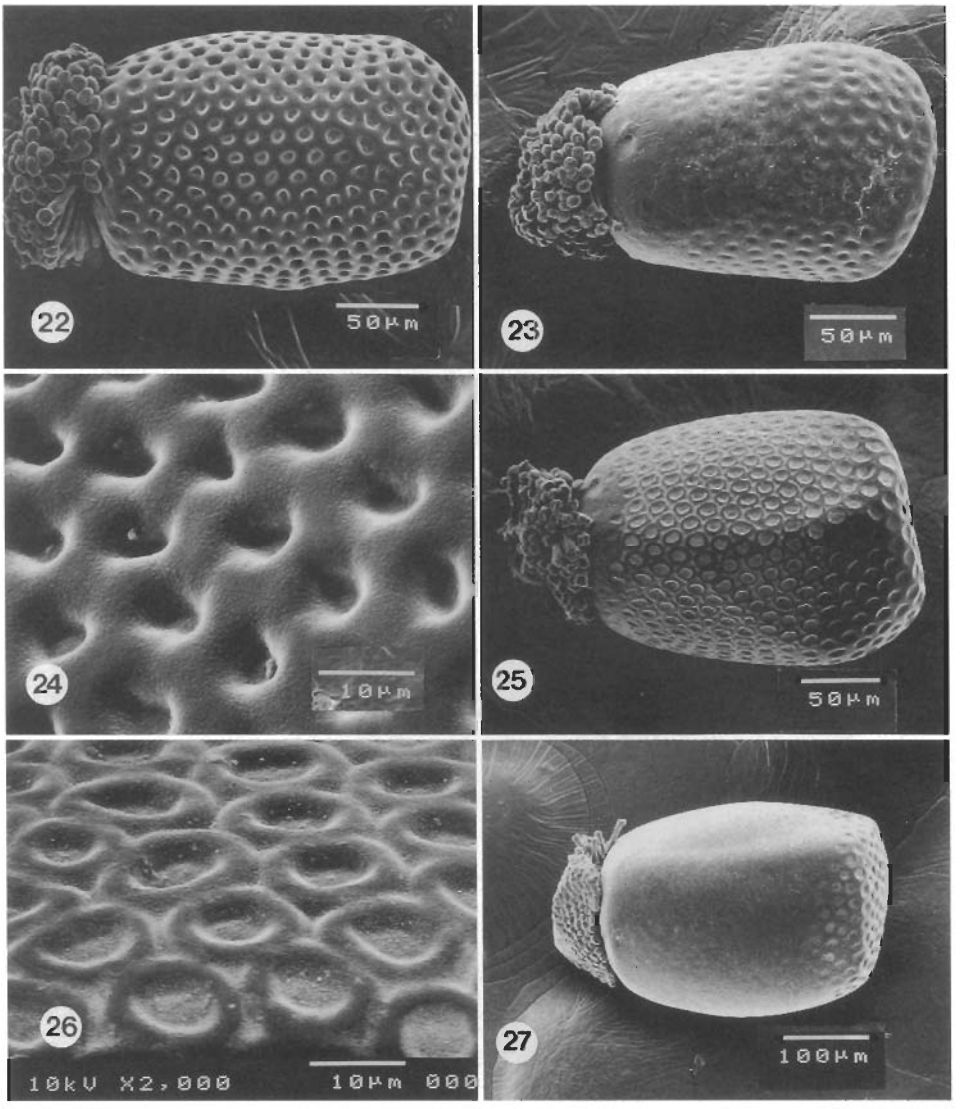
FIGS. 7–9. *Ephoron cophilum* sp.nov., mature nymph: 7, nymph (gills opened); 8, head (lateral view); 9, foreleg (ventral view).



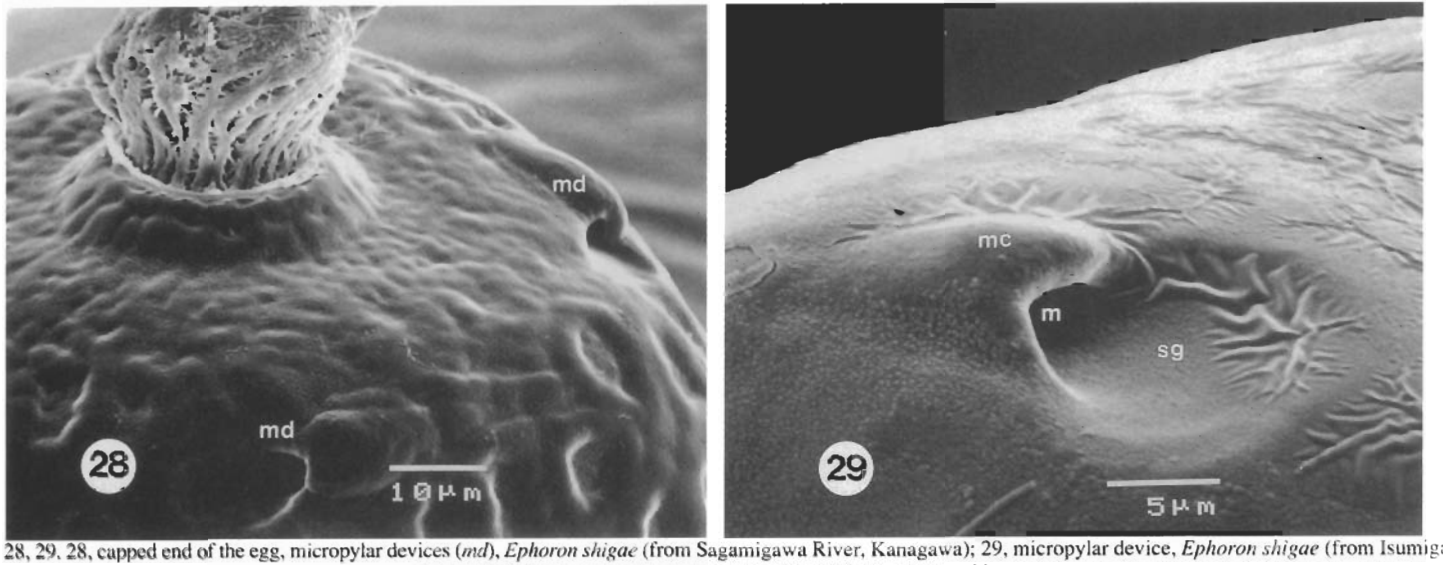
FIGS. 10–15. 10, 11, male genitalia (ventral view): 10, *Ephoron shigae*; 11, penis lobe, *Ephoron limnobium* sp.nov. 12, 13, right mandible (anteroventral view): 12, *Ephoron limnobium* sp.nov.; 13, *Ephoron eophilum* sp.nov. 14, 15, a spine (arrow) between outer and inner incisors of right mandible: 14, *Ephoron shigae*; 15, *Ephoron eophilum* sp.nov.



FIGS. 16–21. Wings. 16, 17, forewing and hind wing (male): 16, *Ephoron limnobium* sp.nov.; 17, *Ephoron eophilum* sp.nov. 18, 19, male forewing (ventral view): 18, *Ephoron limnobium* sp.nov., (*a*) whitish area, (*b*) hyaline area; 19, *Ephoron eophilum* sp.nov., showing a network of tubercles in whitish area. 20, female wing surfaced with a large number of short hairs, *Ephoron eophilum* sp.nov. 21, strong convex vein (*scv*) running parallel to CuP, forewing, *Ephoron eophilum* sp.nov.



FIGS. 22–27. Eggs. 22–24, *Ephoron shigae*: 22, from Kotogawa River, Kagawa; 23, from Isumigawa River, Chiba; 24, chorion. 25, 26, *Ephoron limnobium* sp.nov.: 25, from Lake Biwa, Shiga; 26, chorion. 27, *Ephoron eophilum* sp.nov.



FIGS. 28, 29. 28, capped end of the egg, micropylar devices (*md*), *Ephoron shigae* (from Sagamigawa River, Kanagawa); 29, micropylar device, *Ephoron shigae* (from Isumigawa River, Chiba) (*m*, micropylar; *mc*, micropylar canal; *sg*, sperm guide).

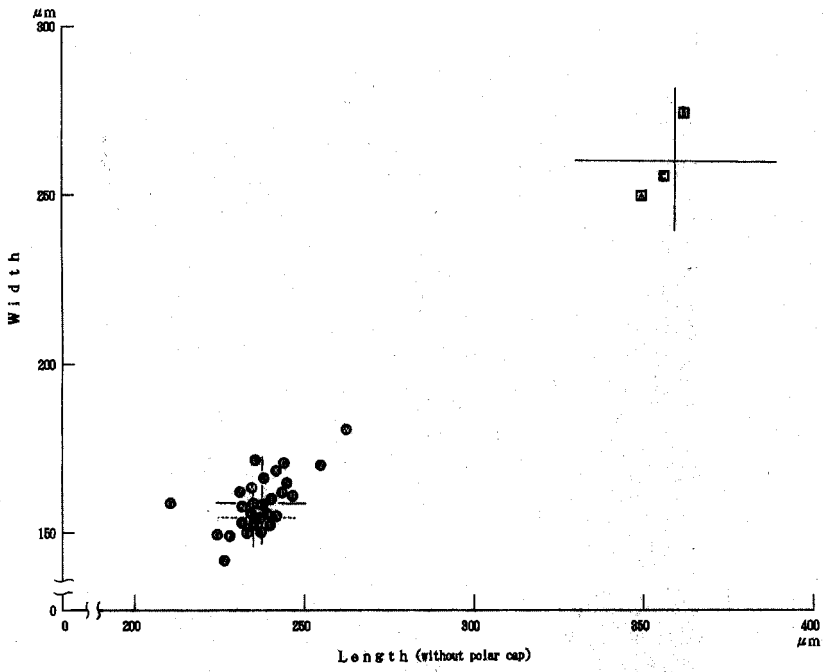


FIG. 30. Egg size of *Ephoron shigae* (●), *E. limnobium* sp.nov. (○), and *E. eophilum* sp.nov. (□). Letters correspond to those in Figure 31. Each value is a mean of 30 eggs from a female subimago or a mature female nymph. Bars near the symbols show standard deviations of the values of each species (broken lines: *E. limnobium*).

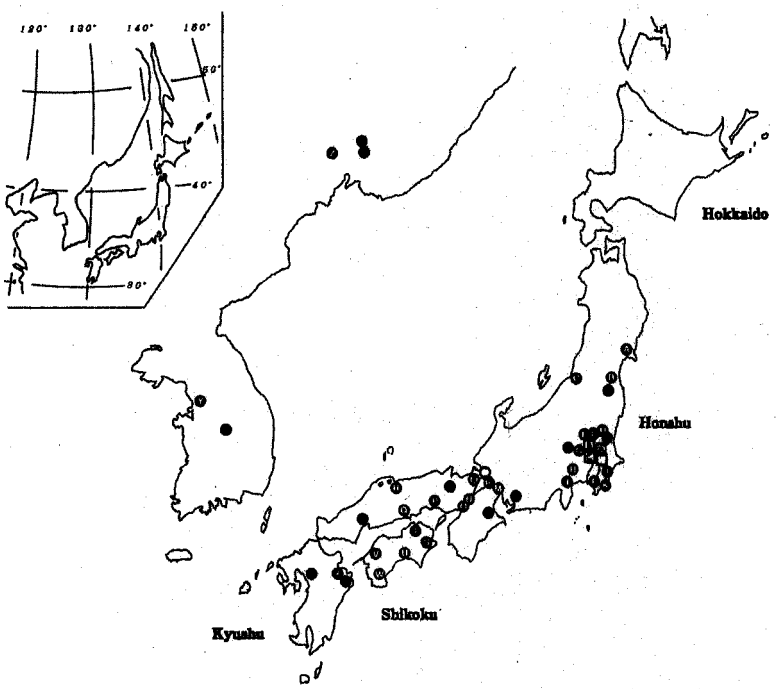


FIG. 31. Distribution of *Ephoron shigae* (●), *E. limnobium* sp.nov. (○), and *E. eophilum* sp.nov. (□). Marks without letters lack in egg data; letters correspond to those in Figure 30.