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Gamogenetic Forms of *Evadne tergestina* CLAUS (Branchiopoda, Cladocera) of the Inland Sea of Japan

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(Figs. 1–4, Table 1)

The cladocerans have two modes of reproduction: parthenogenesis and gamogenesis. An "explosive" population increase usually produced by these animals under optimum temperatures is the result of their high reproductive potential in parthenogenetic generation. Gamogenesis is thought to be induced by the onset of a certain condition of depression, which gives rise to the production of resting eggs. In order to acquire basic information on the life cycle of these animals, it is, therefore, necessary to make clear the population fluctuations in relation to the changes in the population structure, *i.e.*, the percentage in space and time of parthenogenetic females, gamogenetic females with resting eggs, and males. These data have not been fully elucidated until recently as regarding marine cladocerans. In some species, gamogenetic forms have neither adequately been described nor have they been known of their abundance in population especially in the waters adjacent to Japan. *Evadne tergestina* CLAUS is one of the species whose gamogenetic forms seem to have only insufficiently been observed until now.

In his original description of *Evadne tergestina*, CLAUS[1] illustrated a parthenogenetic female, a male, and an early, developing resting egg of a gamogenetic female. Since then, some authors have described and figured the gamogenetic forms of this species from widely scattered areas (cf., Monterey Bay, California, U.S.A.[2]; Black Sea[3]; coast of China[4]). During the course of the investigation into the biology and ecology of marine cladocerans of the Inland Sea of Japan,[5-10] many gamogenetic forms of *Penilia avirostris* DANA, *Evadne nordmanni* LOVÉN, *Evadne tergestina* CLAUS and *Podon polyphemoides* (LEUCKART), with much less in *Podon leuckarti* G. O. SARS, were found in plankton samples collected extensively in the Bingo- and Hiuchi-Nada regions of the central Inland Sea. The present paper deals with a brief account on the gamogenetic forms of *E. tergestina*, giving a redescription in somewhat more detail than in previous publications.

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Materials and Methods

Zooplankton was collected quantitatively with a plankton net (KITAHARA's type: 22.5 cm in mouth-diameter and 80 cm in length with bolting nylon netting of 97 μm opening) at 10 different stations in Bingo- and Hiuchi-Nada on September 11–13, 1973 (Fig. 1). Additional samplings were also made at 11 stations on September 5–6, 1974 in the same sea areas. The net was hauled vertically from near the bottom up to the surface. All the examinations and measurements were performed on specimens picked up from the plankton samples which were preserved in 5% formalin seawater. Drawings were made with the aid of camera lucida. The standard length was taken for the distance between

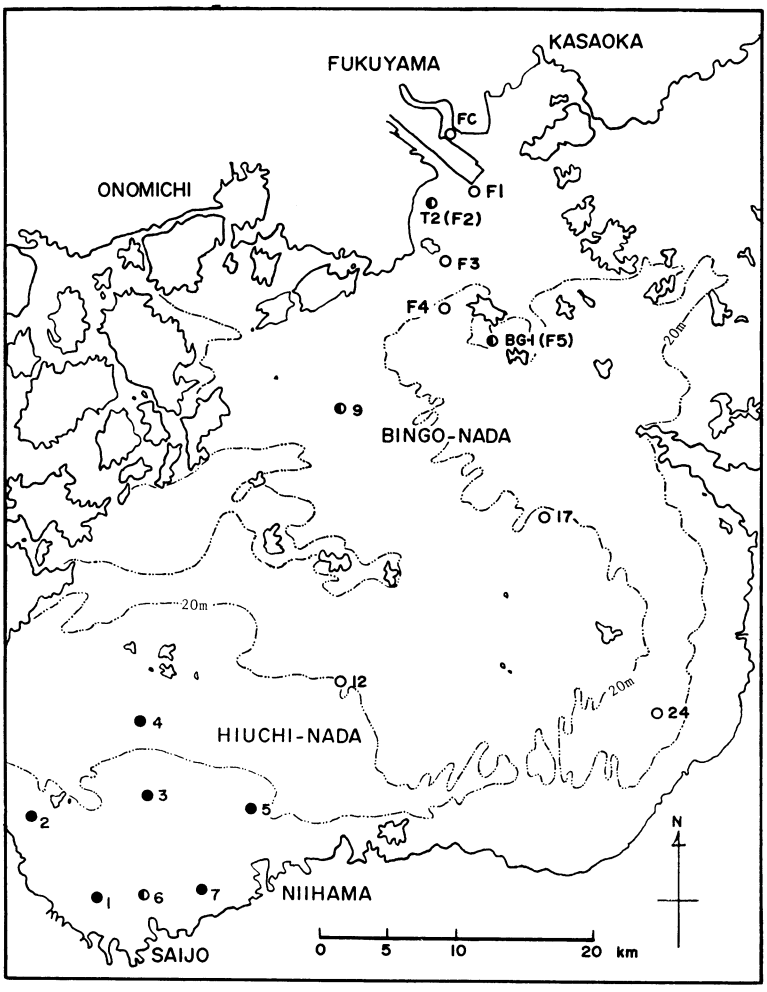

Fig. 1. Location of the sampling stations in the study area.
Solid circles: September 11–13, 1973; open circles: September 5–6, 1974; semi-solid circles: stations visited on both occasions.

the tip of the caudal furca and the notch at the base of the anterior elevator muscle of the 2nd antenna.[11]

Results

1. Parthenogenetic Females

The parthenogenetic egg is much smaller in size and poorer in yolk substances than the resting egg. Parthenogenetic females carrying eggs and embryos of various developmental stages have already been presented in a previous paper.[9] Just as in other podonid species,[11-13] advanced embryos in the brood pouch of parthenogenetic females have already their own embryos in their brood space, demonstrating a typical case of paedogenesis.[9]

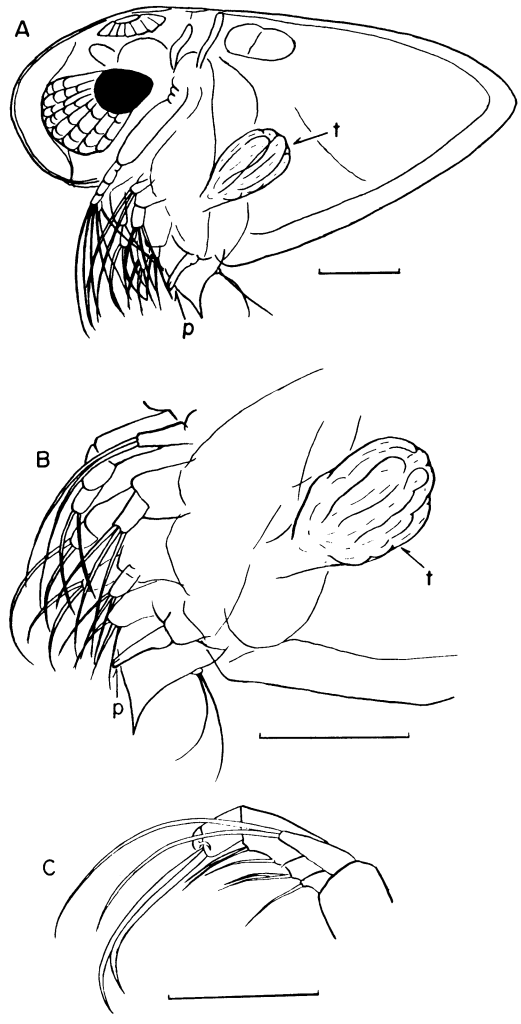

Fig. 2. *Evadne tergestina*, male.
A: side view; B: postabdomen showing the penis; C: 1st thoracic leg; t: testis; p: penis. Scale bar: 100μm.

2. Gamogenetic Forms

Gamogenesis has been found to appear in late August, when the water temperature reaches its annual maximum. The following descriptions are based on specimens collected at St. 9 on September 13, 1973. The morphological characteristics of males and gamogenetic females are in general agreement with those reported in the other podonid species.

a. Males

A male, probably adult, is shown in Fig. 2. In contrast to the female, the outline of the shell is more or less triangular, tapering to the end; the eye and the head being significantly greater than in the female. A pair of testes is situated at the hind portion of the gut, each lobe of which terminates through a seminal duct in a long, tapering, penis located just behind the last thoracic leg. The tip of the penis is slightly bifurcated. The terminal seta on the distal segment of the endopodite of the lst thoracic leg is modified into a sharp recurved hook, with 2 ventral setae also differentiating into very strong, falciform bristles.

b. Gamogenetic Females

The gamogenetic female has a large resting egg, which looks dark in transmitted light due to its possession of rich yolk substances. Fig. 3A shows a female having an early, developing, resting egg with 3 accompanying nurse cells. A more advanced resting egg is illustrated in Fig. 3B. At this stage, the egg becomes more rounded in shape with much yolk deposition, and is provided with a thick membrane. A female carrying a fully-developed resting egg is shown in Fig. 3C. The resting eggs liberated from gamogenetic females in the laboratory have already been presented elsewhere.[8,9] The resting egg of *Evadne tergestina* is spherical in shape, 170–240 μm in diameter with a mean of 200 μm, and brownish in color, with a thick, transparent, outer membrane. Another characteristic feature of the gamogenetic female is the possession of an opening in the postero-dorsal part of the brood pouch and the shell, called the vagina by some authors,[17] as shown in Fig. 3A, B, C.

3. Population Structure Containing Gamogenetic Forms

Fig. 4 shows the size-frequency distributions of two populations of *Evadne tergestina* containing gamogenetic forms, collected respectively at St. 9 on September 13, 1973 and at several stations on September 6, 1974. Individuals were classified into 4 categories: females with parthenogenetic eggs, females without eggs, gamogenetic females with resting eggs and males. Females having parthenogenetic eggs are represented by all size groups ranging from 320 to 600 μm in standard length. Males appear in a wide range between 340 and 500μm in length. On the contrary, gamogenetic females are found only in individuals larger than 480 μm in both cases of collection. There is, therefore, a clear tendency for resting eggs to be formed in larger females.

4. Differences in the Percentage of the Gamogenetic Forms at Different Stations

The intensity of gamogenesis of *Evadne tergestina* has not adequately been described in previous publications. It may, therefore, be worthwhile to mention here the result of

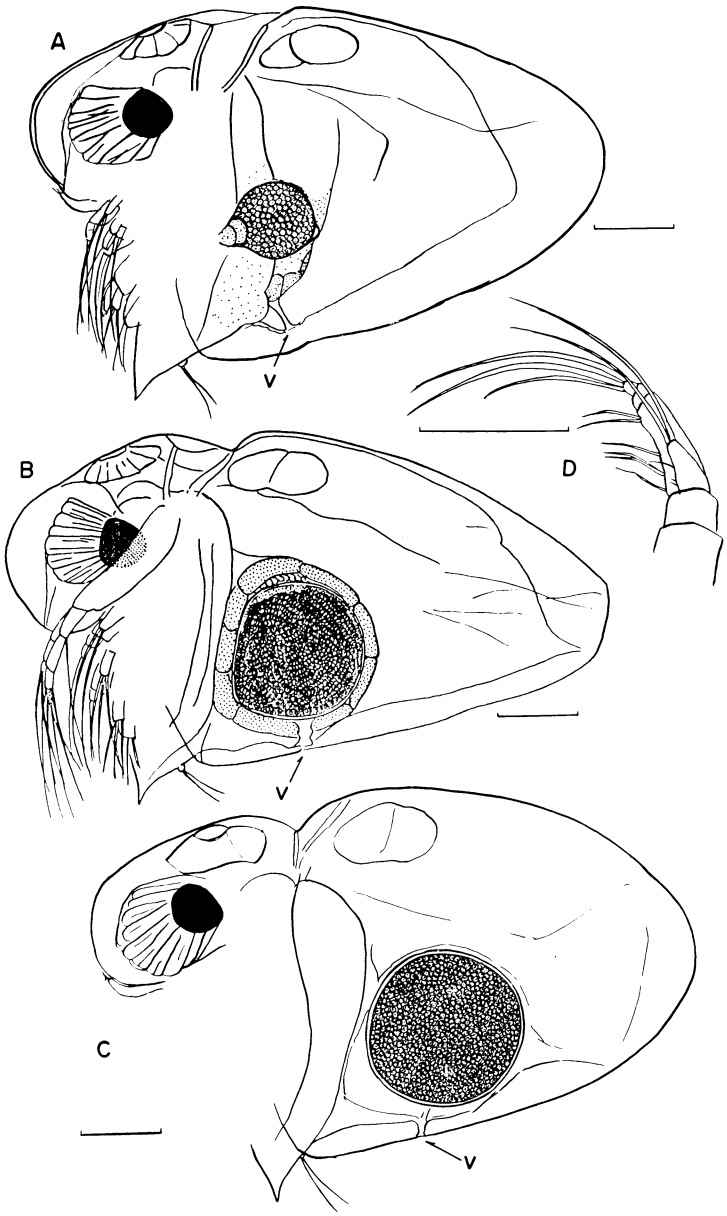

Fig. 3. *Evadne tergestina*, gamogenetic females.
A: gamogenetic female with an early, developing resting egg and 3 accompanying nurse cells; B: gamogenetic female with a well-developed resting egg; C: gamogenetic female with a fully-developed resting egg; D: 1st thoracic leg; v: vagina. Scale bar: 100μm.

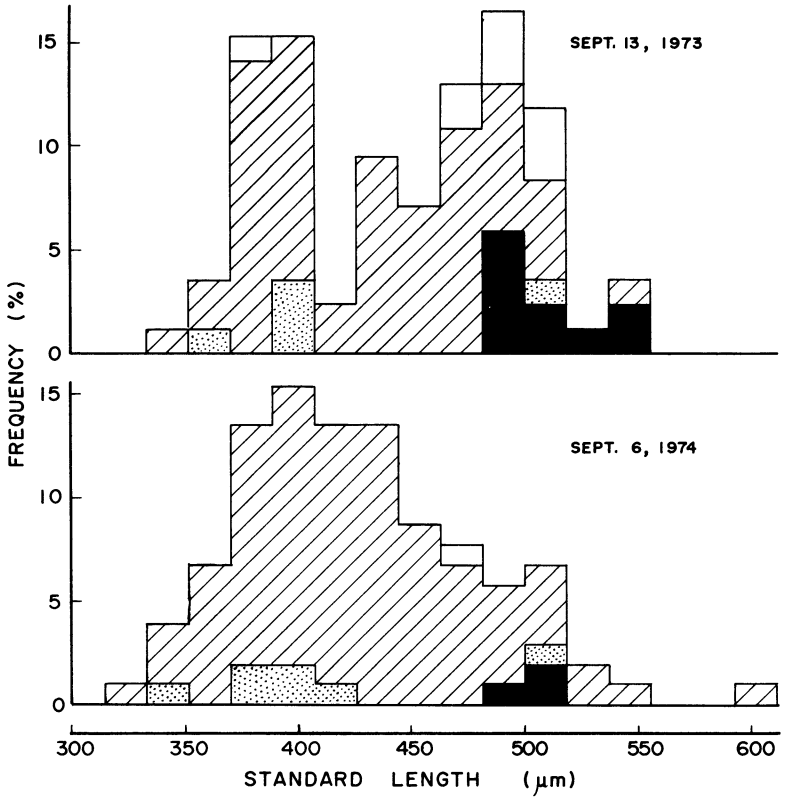

Fig. 4. Size-frequency distributions of two populations of *Evadne tergestina* containing gamogenetic forms (St. 9, September 13, 1973 and several stations, September 5–6, 1974).
Open column: females without eggs; hatched column: females with parthenogenetic eggs; solid column: gamogenetic females with resting eggs; dotted column: males.

Table 1. Variations in the abundance and the composition of reproductive types of *Evadne tergestina* at different stations in Hiuchi- and Bingo-Nada, central Inland Sea of Japan (September 11–13, 1973)

Region	Station	Abundance (Number/m^3)	Number of specimens examined	Females without eggs	Females with parthenogenetic eggs	Gamogenetic forms		
						Females with resting eggs	Males	Total
Hiuchi-Nada	1	3,560	313	4 (1.3)%	276 (88.2)%	4 (1.3)%	29 (9.3)%	33 (10.5)%
	2	0	0	–	–	–	–	–
	3	40	0	–	–	–	–	–
	4	40	20	0 (0.0)	18 (90.0)	0 (0.0)	2 (10.0)	2 (10.0)
	5	2,100	96	0 (0.0)	80 (83.3)	4 (4.2)	12 (12.5)	16 (16.7)
	6	1,530	68	0 (0.0)	62 (91.2)	4 (5.9)	2 (2.9)	6 (8.8)
	7	1,060	58	0 (0.0)	51 (87.9)	4 (6.9)	3 (5.2)	7 (12.1)
Bingo-Nada	9	1,440	129	4 (3.1)	95 (73.6)	16 (12.4)	14 (10.9)	30 (23.3)
	BG1	2.090	187	17 (9.1)	137 (73.3)	17 (9.1)	16 (8.6)	33 (17.7)
	T2	26,430	598	3 (0.5)	579 (96.8)	3 (0.5)	13 (2.2)	16 (2.7)

the observations made on the present materials because of scarcity of available data on this problem. The abundance and the composition of each reproductive type of *E. tergestina* examined at 10 different stations within a period of 3 days are presented in Table 1. While a marked variation in abundance of *E. tergestina* can be noted, there also exists a significant difference in the percentage of gamogenetic individuals in the total population between stations. The percentage of gemogenetic forms attained a maximum of 23.3% of the total population at St. 9, of which females with resting eggs constituted 12.4% and males, 10.9%. At St. T2, where abundant specimens were caught, the population was composed almost entirely of parthenogenetic generations, while the gamogenetic forms represented only 2.7%.

Discussion

Evadne tergestina is a warm-water species, which makes its first appearance in this area in June under a temperature of approximately 18°C and disappears in October. The population usually attains its greatest abundance in August under the annual maximum temperature (27°–28°C). Then, the gamogenesis is found to become intense as in the case of the same species in the Gulf of Trieste, North Adriatic Sea.[14]

CLAUS,[1] DOLGOPOLSKAYA[3] and CHENG and CHEN[4] figured the male of *Evadne tergestina,* but there are some points which were somewhat different from our present observation. The 2 terminal setae of the endopodite of the 1st thoracic leg figured out by them are just like those of the female (Fig. 3D), and not modified into thick, falciform ones as in our present study here (Fig. 2C). In *E. nordmanni,* BAKER[2] illustrated these setae as "differentiated into fairly robust structures with gently recurved, blunt distal ends." However, in *E. tergestina,* the tip is not blunt but sharply pointed. It may well be that these setae, along with the recurved terminal hook, are used to seize the female during mating. Regarding the penis, BAKER[2] reported in *E. nordmanni* that "the distal 0.50–0.66 composed of 2 elongated, subcylindrical parts, endopodite and exopodite, of subuniform width," yet in the present specimens of *E. tergestina* only a slight bifurcation at the tip of the organ could be observed.

The formation of resting eggs of Polyphemoidea has previously been described in the following marine species: *Evadne nordmanni,*[12, 16] *Podon intermedius,*[16] and *P. leuckarti,*[13] as well as in several Caspian species: *Podonevadne camptonyx typica,*[17] *P. angusta,*[18] and *Cercopagis pengoi.*[18] In the gamogenetic female, the ovarium has a group of 4 large germ cells (tetrad), of which only the 3rd cell (in Podonidae) or the 2nd cell (in Cercopagidae[18]) is fertilized and grows up to become the resting egg. The residual 3 cells serve as nurse cells for this resting egg. Such a process is also clearly seen in *E. tergestina* (Fig. 3A). The fact that the resting eggs tend to be formed in larger females implies that more than one parthenogenetic brood may be produced by a female before gamogenesis occurs.

The differences in the intensity of gamogenesis at the different stations as seen in Table 1 may be correlated with the possible regional differences in the cumulative effect of

environmental conditions on the reproduction of this species. However, the environmental factors which have been responsible for the induction of gamogenesis cannot be specified here at present. A similar case has also been reported for *Penilia avirostris* in the present study-area.[9] In connection with this problem, GIESKES [15] states that the number of males and sexual females in a (cladoceran) population, together with body size and number of young in the brood pouch, may be used as "ecological indicators."

From Table 1, we can calculate the number of resting eggs of *Evadne tergestina* that are to be released into the water within a reasonably short period. For example, at St. BG1 having a depth of 20 m, at least approximately 3,800 eggs (2,090×0.091×20) will sink to the bottom of 1 square meter. Since the production of the resting eggs usually lasts for a certain period until the population disappears, an accumulation of eggs onto the bottom will be expected. A recent investigation made in November, 1977 (ONBÉ, ARIYOSHI and YAMAMOTO, unpublished) revealed the existence of abundant resting eggs of marine cladocerans in the bottom sediment of the same study-area. As to the eggs of *E. tergestina*, a maximum density of 7,940/m^2 was recorded near St. 12 (Fig. 1). In this warm-temperate sea, *E. tergestina* is considered to overwinter in the form of resting eggs in sea-bottom sediment during the period from November to May.

Summary

A redescription is given of the gamogenetic forms of *Evadne tergestina* CLAUS (Branchiopoda, Cladocera) in somewhat more detail than in previous publications, based on the specimens collected on September 11–13, 1973 at several stations in the central Inland Sea of Japan. The adult male is provided with a pair of testes, each lobe of which terminates through a seminal duct in a long, tapering penis situated just behind the last thoracic leg. The terminal seta on the endopodite of the 1st thoracic leg is modified into a sharp, recurved hook, with 2 ventral setae also differentiating into very strong, falciform bristles. The gamogenetic female has a large resting egg, which looks dark in transmitted light, and an opening, the vagina, on the shell surface behind the caudal furca. These characteristics are similar to those in other podonid species. The number of gamogenetic forms in the total population on these dates varied considerably according to the stations, ranging from 2.7% to 23.3%, of which males comprised 2.2–12.5% and females with resting eggs, 0–12.4%. There seems to be a clear tendency for resting eggs to be formed in larger individuals.

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瀬戸内海産枝角類トゲナシエボシミジンコの有性生殖個体について

遠　部　　卓

瀬戸内海中央部，備後灘・燧灘における海産枝角類トゲナシエボシミジンコ(*Evadne tergestina* CLAUS)の有性生殖個体について，従来の報告よりもやや詳しく再記載した。成体オスには1対の精巣があり，輸精管を経て1対の陰茎に終る。第1胸脚内枝末端の刺毛は鋭く反曲した小鉤に変形し，その腹側にある2本の刺毛も強い鎌状剛毛に変形している。有性生殖メスは1個の大きい球形の耐久卵（休眠卵）をもち，尾爪背後方に育房に通ずる生殖孔（膣）の開口がある。これらの特徴は Podonidae に属する他種について従来記載された点とほぼ類似しているが，若干の差も認められる。1973年9月本水域の数定点における本種の個

体群全体中に占める有性生殖個体の出現率は2.7 － 23.3 %の範囲にあり，そのうちオスが 2.2 － 12.5 %，耐久卵保有メスは0 － 12.4 %であって，場所によりその出現率にかなりの差のあることが見出された。なお耐久卵の生産は大型のメスによって行なわれる傾向が認められる。