THYSANOESSA EUPHAUSIIDS, COMPARATIVE MORPHOLOGY, ALLOMORPHOSIS AND ECOLOGY

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The genus *Thysanoessa* was established by Brandt for *Thysanoessa longipes*. These diagnoses were again well examined by Hansen in 1911, who gave the refined generic description (Hansen, 1911).

There have been nine or ten species of *Thysanoessa* euphausiids considered up to these days, and the morphology and ecology on those species have been contained fragmentaly in many previous papers on euphausiids (Einarsson, 1945: Boden, Johnson & Brinton, 1955: Brinton, 1962b: Ponomareva, 1962: Nemoto, 1959: 1962: etc).

This study is mainly concerned with the comparative morphology, relative growth (Allomorphosis or interspecific relative growth allometry) and discussions on the characteristic in distributions and systematic relationships of each species among the genus and other euphausiids.

In the morphological study, general external points considered as important for taxonomies and other studies are examined, and some other internal characteristics such as structures of the stomach, are also investigated. The allomorphosis among different species has been examined to consider the ecological and phylogenetic characters of each species too.

MATERIALS AND METHODS

MATERIALS

The materials of *Thysanoessa* have been collected through the following expeditions in the Antarctic and the North Pacific as shown in Table 1. They are mainly composed of two different lines of works, namely plankton net samplings and collec-

TABLE 1. EXPEDITION AND COLLECTIONS OF PLANKTONS FROM WHICH *THYSANOESSA* EUPHAUSIID SAMPLES ARE DERIVED

Cruise	Area sampled	Year	No. of sample	Remarks
North Pacific whaling expeditions	Bering and adjacent seas	1952–1964	Ca990**	Stomach contents of whales.
North Pacific whale marking	”	1955, 1958, 1959, 1960,	Ca500**	45 cm vertical haul.
KT-64-17*	South of Izu.	1964	9**	1.6 m oblique haul.
KT-65-12*	Off Wakayama	1965	5**	80 cm vertical haul.
Antarctic whaling expeditions	Antarctic	1954–1965	Ca1500**	Stomach contents of whales.
Atlantic st. M	North Atlantic		2	By courtesy of Dr. Jones.
Others	North Pacific		30**	JEDS-Cruise etc.

* Cooperative research cruise by Tansei-maru, Ocean Research Institute, University of Tokyo.

** Not all samples contained *Thysanoessa* euphausiids.

tions of euphausiids from the stomach contents of baleen whales.

MEASUREMENT OF BODY PARTS

The measuring positions are illustrated in Fig. 1, in which each indication is measured with built-in micrometer in binocular microscope. As for the length of carapace the cephalothorax length is considered as the common measureing position. But it is rather convenient to measure the edge along the lower margin of the carapace, to compare the ratios of length between anterior top and carapace denticle with the length of the carapace, and without dissection of the body. It may be called ' carapace margin length ' in this report.

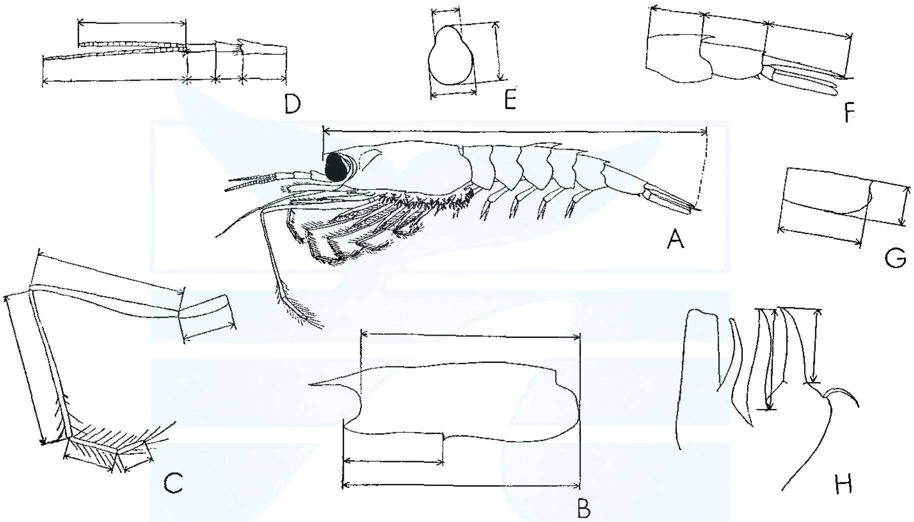

Fig. 1. Measuring positions of *Thysanoessa* euphausiid. A-Body length: B-Carapace length, carapace margin length and denticle length. C-Leg: D-First antenna: E-Eye: F-Sixth and fifth abdominal segments and telson: G-Sixth abdominal segment: H-Male copulatory organ.

The mature specimens are measured for the relative growth study. Those are males having fully developed external copulatory organs and distinct spermatophores in the reproductive organs or ducts and females with spermatophores in their thelycums or having fully developed thelycums (Einarsson, 1945).

From 5 to 15 specimens of males and females have been measured in each body length group for the allomorphosis study. About 100 specimens are selected from the mature or copulated samples, for the measurement of body length and growth, and the geographical cline examination in *T. inermis*.

KEY TO THE ADULT *THYSANOESSA* EUPHAUSIIDS

The following simple key may be applied as expressing the taxonomical characters for *Thysanoessa* euphausiids.

1a Eye has clear transverse constriction above the middle. Second pair of legs elongated.

2a Lateral margin of carapace has denticle.

3a Lateral denticle in the margin of carapace situated approximately at the middle of the carapace.

4a Strong dorsal keel and spines present at third and fourth abdominal segments.

T. longipes

3b Denticles situated considerably posterior part of the lateral margin.

5a Keels absent in the dorsal segments.

6a Sixth abdominal segment is much shorter than the sum of preceding two segments.

7a Setae on carpus and propodus of the first to third thoracic legs are as long as those of dactylus.

T. gregaria

7b Setae on carpus and propodus of the first to third legs are short and fine compared with those of dactylus.

T. parva

6b Sixth abdominal segment is longer than or as long as the sum of the two preceding abdominal segments.

8a The end of terminal process of male copulatory organ is serrated. Antennulae with the upper flagellum somewhat or considerably longer than the sum of distal peduncular joints.

T. vicina

8b The end of terminal process of male copulatory organs is not serrated. Antennulae with the upper flagellum somewhat or considerably shorter than the sum of distal two joints.

T. macrura

5b Keels present on third to fifth segments.

T. inspinata

2b Lateral margin of the carapace lacks the denticle.

T. longicaudata

1b Eye has only slight transverse constriction or without clear constriction. Second pair of legs are not so elongated or not elongated.

9a Lateral margin of carapace with lateral denticle.

T. raschii

9b Lateral margin of carapace without lateral denticle.

10a Dorsal keels present from first to fifth abdominal segments.

T. spinifera

10b Dorsal keel absent, only spines on fifth and sixth or sixth abdominal segments.

T. inermis

MORPHOLOGY AND ALLOMORPHOSIS

FIRST ANTENNAE

The first antenna, the peduncle and flagellum are often considered as sexual and taxonomical characteristics. In *Thysanoessa* euphausiids, they are rather simple

TABLE 2. RATIO AND NUMBER OF ARTICULATION OF ANTENNULAR FLAGELLUM IN *THYSANOESSA* EUPHAUSIIDS

		Example of Ratio for peduncle (%)	No. of articulation
Longer group	*T. spinifera*	Ca 90	39–50
	T. raschii	Ca 120	50–54
	T. inermis	Ca 93	27–28
Intermediate group	*T. longicaudata*	Ca 89	22–30
Shorter group	*T. vicina*	Ca 40	9–14
	T. macrura	Ca 52	9–13
	T. inspinata	Ca 56	16–18
	T. longipes	Ca 56	16–19
	T. gregaria	Ca 48	10–10

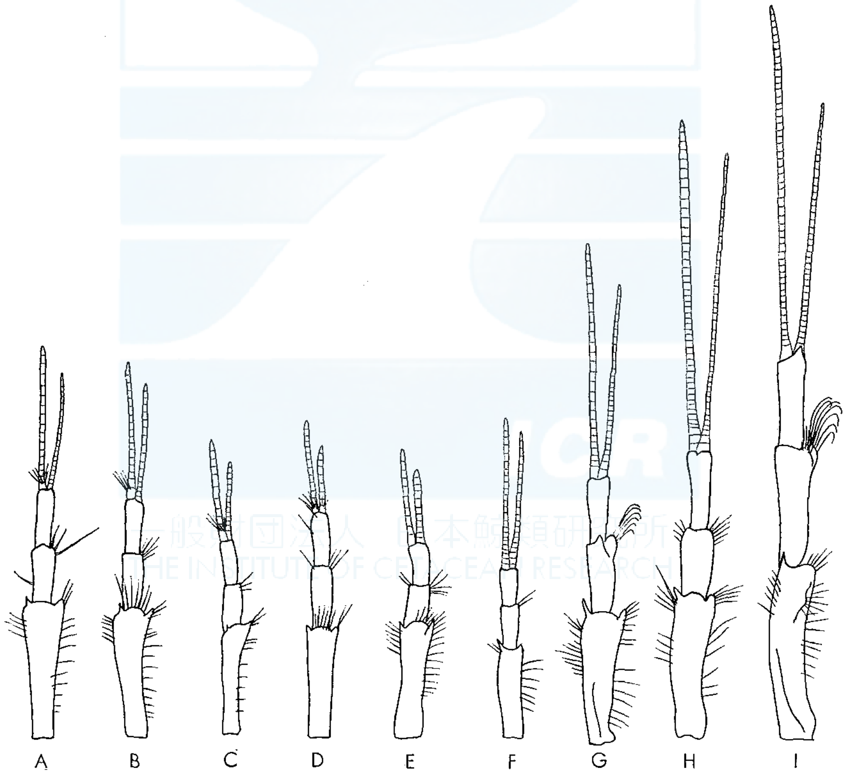

Fig. 2. Male first antenna of *Thysanoessa* euphausiids. A-*T. longipes*,B-*T. inspinata*, C-*T. vicina*, D-*T. macrura*, E-*T. gregaria*, F-*T. longicaudata*, G-*T. inermis*, H-*T. raschii*, I-*T.spinifera*, x10.

and Hansen (1911) used the length of antennule with the upper flagellum as the taxonomic character for the closely related *Thysaneossa macrura* and *T. vicina*. Three types of flagellum, longer, intermediate and shorter types are observed as shown in Fig. 2. The number of the articulations in upper and lower flagella are also divided into two or three groups.

The flagellum of longer group is rather tough in preserving, but those of shorter group are fragil especially in the intermediate species *T. longicaudata*. In the longer groups, the articulations are ranging from 20 to some 60 and lengths of longer flagellum are almost the same or longer than the peduncles. On the other hand, the shorter group has less than 20 articulations and the flagella are shorter than the peduncles. The distal fringes of flagellum are almost the same among specimens of *Thysanoessa* euphausiids. They have usually four small setae in the distal ends of the upper and lower flagella. One of the four setae has broad and tough base which sometimes two storied structure.

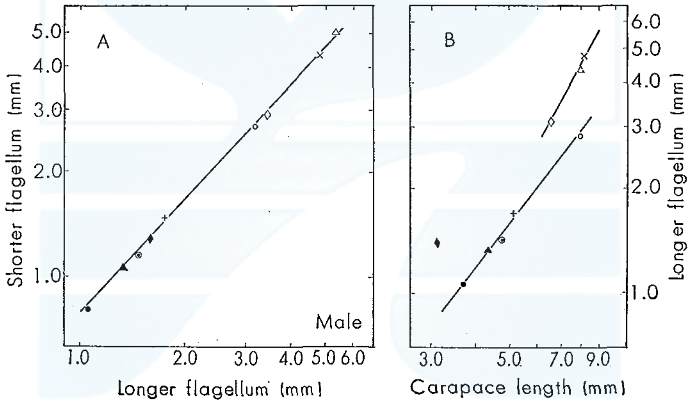

Fig. 3. Allomorphosis in *Thysanoessa* euphausiids. Relation between longer and shorter flagella, and carapace length and longer flagellum in males. Open circles-*T. longipes*, Closed circles-*T. gregaria*, Crosses-*T. inspinata*, Oblique crosses-*T. spinifera*, Open triangles-*T. raschii*, Closed triangles-*T. vicina*, Open lozenge-*T. inermis*, Closed lozenge-*T. longicaudata*, Circles with dot- *T. macrura*. Symbols are the same in following figures.

The sexual dimorphism in the peduncles of *Thysanoessa* euphausiids is typical in *T. inermis* and *T. spinifera*. Einarsson (1945) considered the possible relationships of *T. inermis* to the Pacific species *T. spinifera* which has the antennule armature of which bears close resemblance to that of *T. inermis*. The male *T. inermis* has a rounded lobe on its inner side, in the first antennular segment, bearing slightly curved spines (Einarsson, 1945).

The relation between the longer flagellum and the carapace length as allomorphosis gives three allometric tribes as shown in Fig. 3. The longer group, namely *T. inermis*, *T. spinifera* and *T. raschii* form one tribe, and *T. longicaudata* which has intermediate number of articulation between shorter and longer groups, forms another point alone. The shorter group of other species runs the same regression both in males and females. *T. longicaudata* ecologically bears the wider distribution from temperate and boreal Atlantic Ocean to the Arctic, from the atlantic by 80°N (Einarsson, 1945), than other *Thysanoessa* euphausiids belonging to the shorter group. On the other hand, it also covers the neritic and other shallow waters like the longer group.

CARAPACE

The carapace of the *Thysanoessa* group is various, but the rostrum is always well developed in every species, which is one of the generic character of the *Thysanoessa* (Hansen, 1911). All species have keels in the center of rostrum part of the carapace, longer or short, and seven species out of ten have denticles in the lateral margin of the carapace. The general outlines of each species are illustrated in Fig. 4 which do not differ from those of other euphausiids.

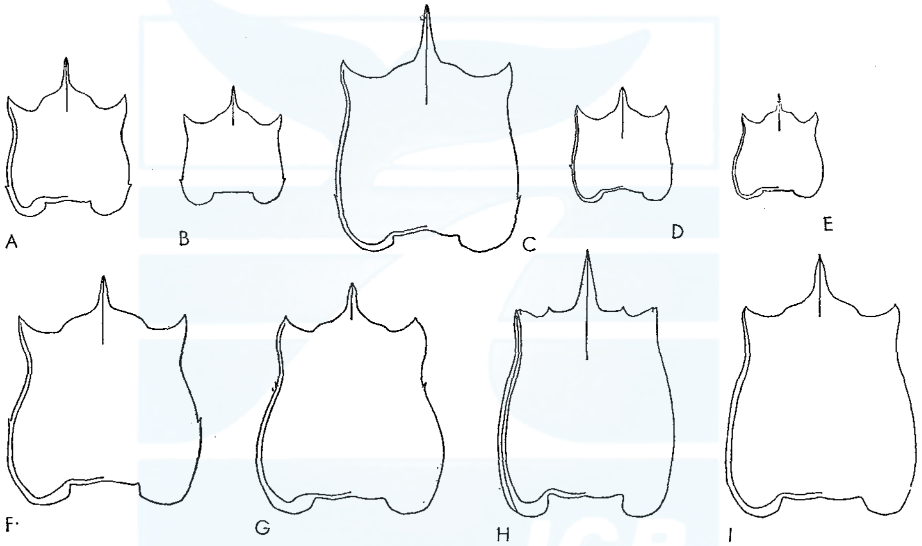

Fig. 4. Carapace of *Thysanoessa* euphausiids. A-*T. inspinata.* B-*T. vicina.* C-*T. macrura* D-*T. gregaria.* E-*T. longicaudata.* F-*T. longipes.* G-*T. raschii.* H-*T. spinifera.* I-*T inermis.*

Rostrum and keel

All *Thysanoessa* species have well developed spear pointed rostrums, but *T. gregaria*, *T. raschii* and *T. inermis* have rather broad oblong tops. Other *Thysanoessa* have acute distal ends when they are pressed on the deck glass for observations.

Thysanoessa spinifera have the most acute triangular, and longest rostrum, which is narrower than other *Thysanoessa* euphausiids. Three species, *T. longipes*, *T. vicina* and *T. macrura* have broader tryangular rostrums. The tip of the rostrum of *T. longipes* is somewhat slender and differes from other two species. The general shape of the rostrum of *T. macrura* is closely related to that of *T. vicina.* And it is also interesting that the rostrum of *T. raschii* is similer to *T. gregaria*, which is different conssiderably in other external points. *T. gregaria* has oblong and broader rostrum, and the shape of the keel in rostrum is different from *T. raschii.* The vertical sections of the keel in the rostrum and the carapace show also two types. The keels in the rostrum of *T. inermis* and *T. raschii* are rather gentle crest ridges, but *T. longipes*, *T. gregaria*, *T. vicina* and *T. macrura* have the sharp ridges as shown in Fig. 5. The geographical variation in rostrum of carapace in *Euphausia diomediae* is reported by Hansen (1911). Some taxonomical importance in the strech of rostrum in *Thysanopoda*, *T. aequalis* and *T. subaequalis*, is also obtained (Boden & Brinton, 1957). No geographical difference is observed in *Thysanoessa* euphausiids in rostrums in this studies.

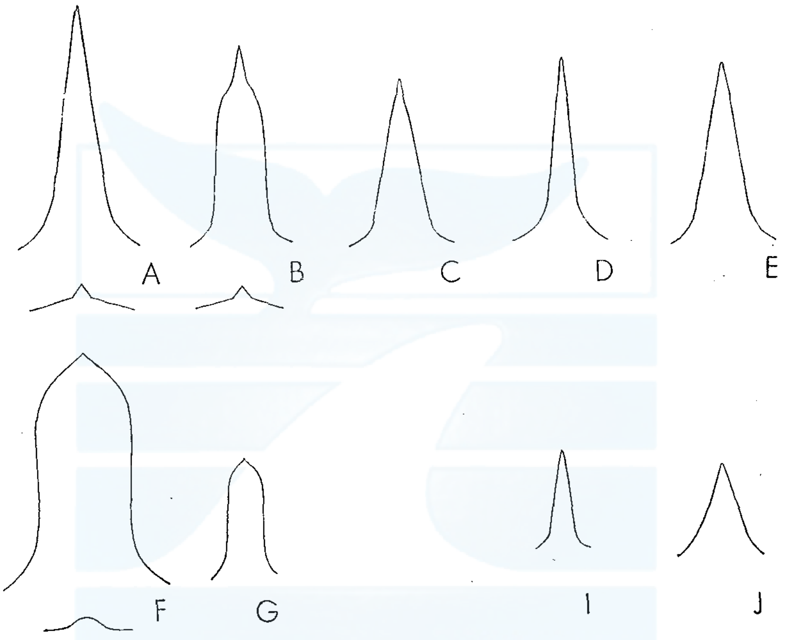

Fig. 5. Rostrums of male *Thysanoessa* euphausiids. A-*T. spinifera:* B-*T. inermis:* C-*T. longipes:* D-*T. inspinata:* E-*T. vicina:* F-*T. raschii:* G-*T. gregaria:* I-*T. longicaudata:* J-*T. macrura.*

The edge in the cove between rostrum and the anterior top of the margin of the carapace swells out in the larger *Thysanoessa*, *T. macrura*, *T. inspinata*, *T. raschii* and *T. inermis.* But it is not so clear in *T. gregaria* and *T. vicina.* *T. spinifera* has a prominent supraorbital spine in the top of the swell. The sexual dimorphism is not observed in all species but *T. raschii*, the male of which has broader rostrum than females. In the younger stages of *Thysanoessa*, the rostrums are also well developed. But their tip ends are not so pointed and they have rather blunt ends.

The anterior top of lateral margin of the carapace

Thysanoessa euphausiids have pointed ends except *T. spinifera* which has two points in the anterior top of the carapace along the supraorbital cove. As illustrated in Fig. 6, *T. gregaria*, *T. longipes* and *T. raschii* have all pointed ends, the group also includes other species but *T. spinifera*. *T. spinifera* has one keel like spine slightly upper positions of the end of the margin of the carapace. The end of the margin of the carapace also makes point, from which two streaks run along the edge of the lateral margin of the carapace.

Lateral denticle

Seven species out of ten in *Thysanoessa* have lateral denticles in the lower margin of the carapace, and other three species completely lack the denticles.

Lateral denticle present	*Thysanoessa raschii* *T. longipes*, *T. gregaria*, *T. macrura*, *T. vicina*, *T. inspinata*, *T. parva*.
Lateral denticle absent	*T. inermis*, *T. spinifera*, *T. longicaudata*.

All species are bearing only one denticle in one side margin of the carapace.

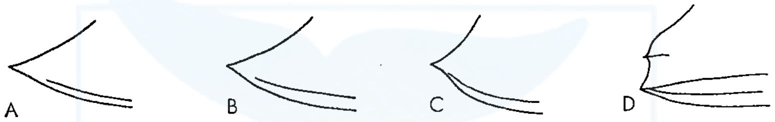

Fig. 6. The anterior top of the lateral margin of the carapace in *Thysanoessa* euphausiids. A-*T. gregaria*, B-*T. longipes* C-*T. raschii*, D-*T. spinifera*.

Fig. 7. Carapace denticles in *Thysanoessa* euphausiids. A-*Thysanoessa longipes*. B-*Thysanoessa raschii* deformed denticle. C-*Thysanoessa raschii*.

There are two types of lateral denticles of carapace. One is *Thysanoessa raschii* bearing a acute spine in the anterior part of which is also rather completely free from the margin of the carapace. On the other hand, *T. longipes* has the acute but narrower base spines which directly rise up from the margin of the carapace in the posterior position. *T. gregaria*, *T. macrura*, *T. vicina* and *T. inspinata* all show latter characteristic and *T. parva* also possibly belong to this group.

In one specimens of *T. raschii* a deformed denticle which has two character of them is observed as illustrated in Fig. 7.

T. gregaria, *T. vicina* and *T. inspinata* have sometimes very incomplete lateral denticles. Especially, *T. gregaria* sometimes completely lacks them. Samples of *T. gregaria* collected in KT-64-17 and *T. macrura* collected in the Antarctic also lack the lateral denticle in the lower margin of the carapace.

In other species of euphausiids, the local difference of the presence of this denticle is reported on *Nematoscelis tenella*. The male *Nematoscelis* has this denticle in the Atlantic, but it is absent in Pacific specimens. (Boden, Johnson & Brinton, 1955). Recently Mclaughlin (1965) described two forms, denticled and original forms of *Nematoscelis difficilis*. Mclaughlin described that the prominent lateral denticle, varying somewhat in size, occurres on the posterior third of the inferior margin of the carapace about *Nematoscelis difficilis* denticle form, (Mclaughlin, 1965), but it has another ' no-denticle ' form.

Position of lateral denticle

The position of lateral denticle is a very important taxonomic characteristic especially on *Thysanoessa longipes* and *T. inspinata* (Nemoto, 1963). Hansen also used the position of the lateral denticle for the taxonomic considerations on *Thysanoessa* groups. He (1911) stated that lateral margins of the carapace with a denticle at the middle on *Thysanoessa longipes* and denticles situated before the middle of the lateral margin of the carapace on *T. raschii*. As for *Thysanoessa gregaria* group, that the denticles is conspicuously posterior the middle of the lateral margin, is also noted as the taxonomic character by him.

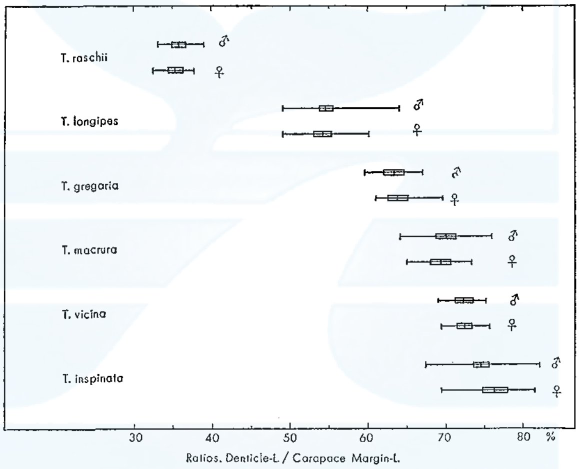

Fig. 8. Ratios, denticle length divided by carapace margin length of the carapace of *Thysanoessa* euphausiids in the world ocean. Range, mean and each standard deviations are illustrated.

The positions of lateral denticles expressed as ratios, denticle length / carapace margin length are shown in Fig. 8. There are fairly good expressions of the species range, which also confirmes the taxonomic importance of them. And there is few difference between males and females in all species.

The denticles of *T. longipes* is situated at the middle of the lateral margin, but *T. inspinata*, the closely related species of the *T. longipes*, has its denticle in far posterior position as illustrated in Fig. 8. The position of the denticles in *T. macrura* and *T. vicina* are rather similer in their positions, in which *T. vicina* shows slightly posterior position of denticles. In other closely related euphausiids species, *Euphausia pacifica* and *E. nana* established by Brinton (Brinton, 1962a) also show such tendency. The larger *E. pacifica* has the comparatively anterior lateral denticles as shown in Fig. 9, and *E. nana* from the East China sea has posterior lateral denticles. There is very clear difference between typical *E. pacifica* in the northern waters and *E. nana* in the Eastern China sea, however, some vague samples have been collected from the intermediate regions in the southern waters of the sea of Japan. These samples collected from Tsushima waters are now under examination.

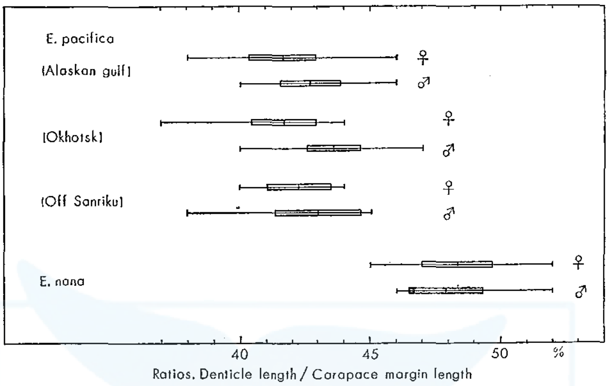

Fig. 9. Ratios, denticle length/carapace margin length of *Euphausia pacifica* and *E. nana*. Ranges, means and standard deviations are illustrated.

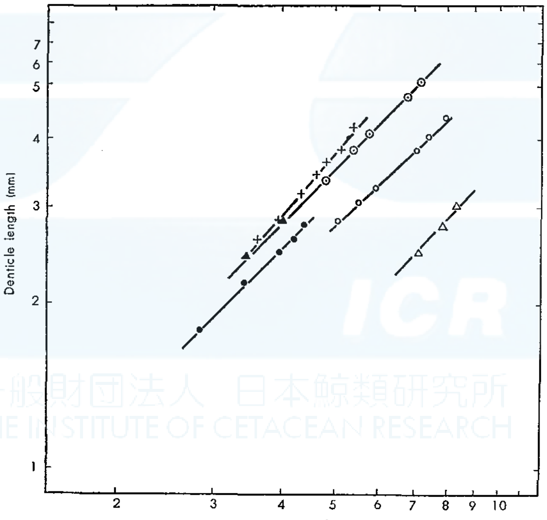

Fig. 10. Allomorphosis in carapace of *Thysanoessa* euphausiids. Relation between denticle length and carapace margin length.

Allomorphosis in the position of denticles

The allomorphosis in the relation between denticle length and carapace length for *Thysanoessa* group is given in Fig. 10. There is no difference between males and females in all species. In a previous report (Nemoto, 1963), I noticed the clear different allometry lines in *T. longipes* and *T. inspinata* which is one of the critical point for dividing those two species. The relative growth coefficient for *T. longipes* is 0.973 and *T. inspinata* 1.19. *Thysanoessa macrura* and *T. vicina* draw the same allometry line, the growth coefficient of which is 1.000.

Thysanoessa gregaria shows growth coefficient 0.925 which differs from those of other *Thysanoessa*. *Thysanoessa raschii* draw the line apart from other species as shown in Fig. 10. Those growth coefficients are as follows.

Thysanoessa raschii	1.034
longipes (adult)	0.973
macrura & vicina	1.000
gregaria	0.925

EYE

Shape and arrangement

The eye of *Thysanoessa* euphausiids are usually higher than broad with transverse constrictions or sometimes almost circular (Hansen, 1911 : Bodon, Johnson & Brinton, 1955). The ratio, lateral length/vertical length and the general shape of eyes are illustrated in Fig. 11. *Thysanoessa raschii* has almost completely circular and broad eye, and the ratio of lateral and vertical length is about 95%. But from the side view, the upper part is rather compressed as compared with *Euphausia* which is almost circular. *T. spinifera* agrees with *T. raschii* in this point showing the ratio 95%, and the upper half of the eye is also compressed. *T. inermis* has a little higher eyes showing the ratio about 87%, but no heavy constriction is observed in the fully developed specimens. The compression in the upper part in *T. inermis* is heavier than *T. raschii* and *T. spinifera.*

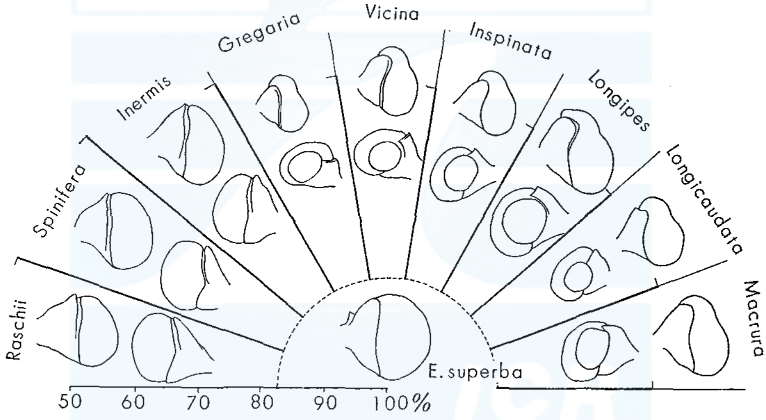

Fig. 11. Profiles and ratios of the width of the eye divided by the vertical length of bilobate eye in *Thysanoessa* euphausiids in the world ocean.

As it has been discussed by Hansen (1911), and Einarsson (1942), the younger specimens of *T. inermis* shows more higher than broad eyes. Many examples of the younger juvenile stage after the furcilia possess more typical *Thysanoessa* eyes also in *T. inermis*, but *T. longipes* of the same vertical size shows the narrower upper part of the eye and constriction. The ratio, lateral/vertical length is about 81% in *T. inermis* and 78% in *T. longipes*, latter value of which is not so different as those in adults.

TABLE 3. ARRANGEMENT OF EYES IN EUPHAUSIIDS

Species and genus	Eye	Constriction	Size Upper Lower	Crystalin cones visible	Depth of living range
Bentheuphausia	(+)	−	−	−	500–4000
Thysanopoda	+	−	−	−	0–4000
Nyctiphanes	+	−	−	−	0– 300
Meganyctiphanes	+	−	−	−	0– 300
Pseudeuphausia	+	−	−	−	0– 150
Euphausia	+	−	−	−	0– 300
Thysanoessa raschii	+	−	−	−	0– 200
„ *inermis*	+	−	−	−	0– 300
„ *spinifera*	+	−	−	−	0– 300
„ *longipes*	+	+	Upper < Lower	−	0– 500
„ *inspinata*	+	+	„ < „	−	0– 500
„ *gregaria*	+	+	„ < „	−	0–1000
„ *parva*	+	+	„ < „	−	500–2000
„ *macrura*	+	+	„ < „	−	0– 300
„ *vicina*	+	+	„ < „	−	0– 300
„ *longicaudata*	+	+	„ < „	−	0–1000
Tessarabrachion	+	+	„ < „	−	0–1000
Nematoscelis	+	+	„ ≷ „	−	0–1000
Nematobrachion	+	+	„ > „	−	100–1000
Stylocheiron	+	+	„ < „	+	0–1000

The general arrangement of the eyes in euphausiids are shown in Table 3. *Thysanoessa* euphausiids are divided into two groups. One is having the constricted eyes group and the other is round eyes group. *T. raschii* having rounded eyes is living in the shallow waters, and *T. spinifera* also is mainly living in the shallow waters although it is sometimes found in the deeper waters along the edge of coastal regions (Banner, 1954).

Other euphausiids bearing constricted eyes live in broader range in vertical distribution in the sea. *Thysanoessa*, *Tessarabrachion*, *Nematoscelis*, *Nematobrachion*, and *Stylocheiron* have the constricted eyes. Those species have rather bigger eyes and the range of the vertical distributions attain deeper waters in the sea except some Antarctic and Arctic species of *Thysanoessa*. The upper and lower part of the constricted eyes are sometimes about same size and sometimes different. In *Thysanoessa*, the lower part is generally bigger than the upper part. In *Stylocheiron* and *Tessarabrachion*, the lower parts are also larger than the upper parts. The lower parts of some species are larger than the upper but smaller in other *Nematoscelis*. The upper parts are generally larger in *Nematobrachion* euphausiids.

The size of the eye

The male has larger eyes than females in general comparing with the body size. The series of the relative size indicates that the smaller the body length is, the larger the eye is among the gregaria group, which has constricted eyes in adults. And this is not the same in *T. spinifera*, *T. inermis* and *T. raschii.*

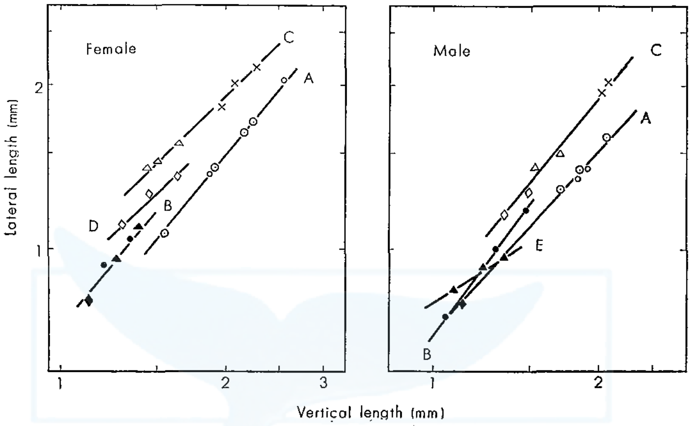

Fig. 12. Allomorphosis in eye of *Thysanoessa* euphausiids in the world ocean. Relations between lateral and vertical length. A-*longipes, macrura:* B-*gregaria, vicina, longicaudata:* C-*raschii, spinifera:* D-*inermis*

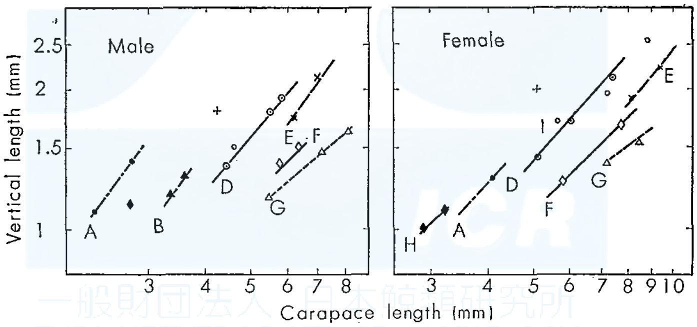

Fig. 13. Allomorphosis in eye of *Thysanoessa* euphausiids. Relation between vertical length of eye and carapace margin length.

Allomorphosis in eyes

The relation between vertical and lateral lengths of eyes in adult specimens are plotted in chart as shown in Fig. 12. There are three or four allometry groups both in males and females group.

T. macrura and *T. longipes* form the same line, the coefficient of relative allomorphosis of which is about 1.2. But *T. gregaria* and *T. vicina* shift the line, although the constriction in the upper part of eyes is positive, and the growth coefficient of the allometry is ranging 1.33–1.57. *T. spinifera*, *T. inermis* and *T. raschii* also form one allometry group, but *T. raschii* shifts to a little high initial growth index in females as illustrated in Fig. 12.

The relative growth between the vertical length of the eye and carapace length is very various as illustrated in Fig. 13. There are many allometry lines in males. Only *T. macrura* and *T. longipes* take the same line, but *T. gregaria*, *T. vicina*, *T. raschii*, *T. inermis* and *T. spinifera* occupy different allometry lines respectively. That *T. gregaria*, *T. vicina*, and *T. macrura* differ considerably in the relative growth indices between carapace length and the vertical length of eyes is possibly due to two reasons. The relative growth for the carapace in *T. longipes* is the same as *T. macrura*. The body length of *T. longipes* is about the same as *T. macrura*, and they are both living in cold pelagic waters. They are considered to be surface living euphausiids shallower than 500 meter and the ecological position in the sea may be related with each other both in northern and southern hemisphere.

TABLE 4. RELATIVE GROWTH COEFFICIENT IN ALLOMORPHOSIS BETWEEN VERTICAL AND LATERAL LENGTH IN EYES OF *THYSANOESSA* EUPHAUSIIDS

Species	Coefficient	
	Male	Female
T. macrura, *T. vicina*	1.16	1.19
T. gregaria	1.33	1.57
T. spinifera, *T. inermis*	1.17	1.17
T. raschii	(1.17)	(1.17)

On the other hand, *T. gregaria* group, *T. gregaria*, *T. macrura* *T. vicina* are different considerably in males. in *Thysanoessa* euphausiids, the sexual difference in the body length of males and females is very clear in *T. gregaria* and other species which have bilobate eyes. The type of eyes of females in those species are that of younger stages of the same species eyes of males especially in *T. gregaria* and *T. vicina*.

The upper part of bilobate eye of males swells like horse bean but guiter-shaped in females. This character is not so clear in *T. macrura*, *T. longipes* and *T. longicaudata*. In the younger stages of some *Thysanoessa* euphausiids, eyes are rather related to each other even in the *T. inermis*. The eye of *T. inermis* in about 5 mm specimen is nearly the same with that of *T. longipes* in the same body length as illustrated in Fig. 14 and former discussions. This shape is that of females in adults in *T. gregaria* group as illustrated also in Fig. 14. The female type is becoming to the younger type is already pointed out as for many other species as the evolution in speciations. This sexual difference may be firstly connected to the step of the development of variations in the body parts (Eimer, 1890).

Brinton (1962b) considered the evolution and local forms of *Stylocheiron affine* and *S. longicorne* in the Pacific areas according to the combinations of the variations in the ratios, length of sixth abdominal segment divided by depth and width of lower section of eye divided by width of upper section. This combination is also checked for *Thysanoessa* euphausiids in which possible relationship among species is also suggested. The inter specific differences in the ratios in those points nearly coincide with other characters.

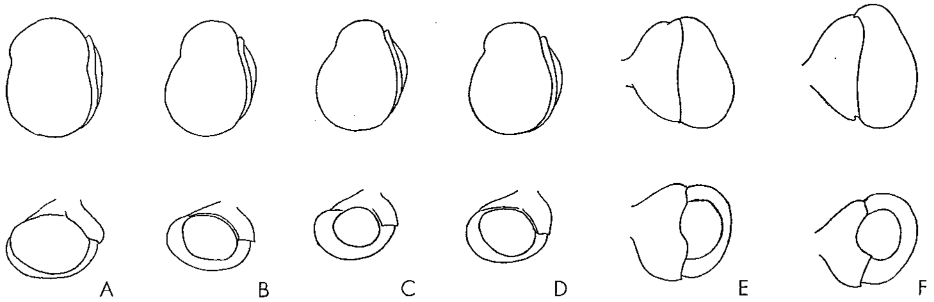

Fig. 14. Eyes of *Thysanoessa* euphausiids. A-Male *T. gregaria*, B-Female *T. gregaria*, C-Female *T. vicina*, D-Male *T. vicina*, E-Young *T. inermis* in juvenile stage 5 mm, F-Young *T. longipes* in juvenile stage 5 mm.

Among *Thysanoessa* euphausiids, *T. inermis*, *T. raschii* and *T. inermis* make group apart from other species, although species contained show sexual dimorphism. Except *T. gregaria*, other four species form group of high ratio in the upper and lower parts of eye and fifth and sixth abdominal segments. The former group scarcely show the differences in two points, but *T. gregaria* and *T. vicina* show the sexual dimorphism in the ratio of abdominal segments. *T. longicaudata* and *T. longipes* show little difference in the ratio of eyes. On the other hand, *T. gregaria* shows heavy sexual dimorphism in the ratio of eyes.

ABDOMINAL SEGMENTS

Keel and abdominal spines

The arrangement of keels and abdominal spines are given in Table 5. Among nine species of *Thysanoessa* euphausiids treated here, three species have

TABLE 5. ARRANGEMENT OF KEELS AND ABDOMINAL SPINES ON THE ABDOMINAL SEGMENTS IN *THYSANOESSA* EUPHAUSIIDS

	Abdominal segments					
Species	1	2	3	4	5	6
T. raschii	—	—	—	—	—	—
T. inermis	—	—	—	(ksp)	(k)sp	SP
T. spinifera	K	K	K	KSP	KSP	SP
T. longipes	—	—	KSP	KSP	KSP	SP
T. inspinata	—	—	K	K	K	SP
T. longicaudata	—	—	—	(k)	(k)	—
T. gregaria	—	—	—	—	—	(sp)
T. parva	—	—	—	—	—	—
T. vicina	—	—	—	—	—	—
T. macrura	—	—	—	—	—	—

K: Well developed dorsal keel. SP: Well developed dorsal spine. Smalls show the presence of keel or spines, but they are not well developed. Extraordinary ones are in bracket.

dorsal keels and four species have abdominal spines. Dorsal keels are well developed in *T. spinifera*, *T. longipes* and *T. inspinata*. *Thysanoessa raschii*, *T. gregaria*, *T. parva*, *T. vicina* and *T. macrura* have no developed keel and no spine. *T. inermis* has only abdominal spines on fifth and sixth segments or sixth segment only, but some extraordinary specimens have also keels and spines on fourth segment. Two closely related species, *T. longipes* and *T. inspinata* have keels on third, fourth, fifth segments, and spines on sixth segments. But well developed abdominal spines are present on third, fourth and fifth segments of *T. longipes* alone. *Thysanoessa longicaudata* has no clear keel and spine but it is considered to belong to *T. longipes* group. In some younger furcilia stage 5, slight keels are described on third and fourth abdominal segments by Einarsson (1945) and some present specimens from the station M also bear keels on fourth and fifth segments.

Thysanoessa gregaria and three other *gregaria* type euphausiids are without any keels and abdominal spines.

Thysanoessa spinifera has keels on the first, second, third, fourth and fifth segments and abdominal spines of fourth, fifth and sixth segments. The presence of clear keels on first and second segments is only found in *T. spinifera*.

Two and one spine forms of Thysanoessa inermis

In a previous report, (Nemoto, 1959), I described the possible difference beween one and two spine forms of *Thysanoessa inermis* in the Atlantic and the Pacific.

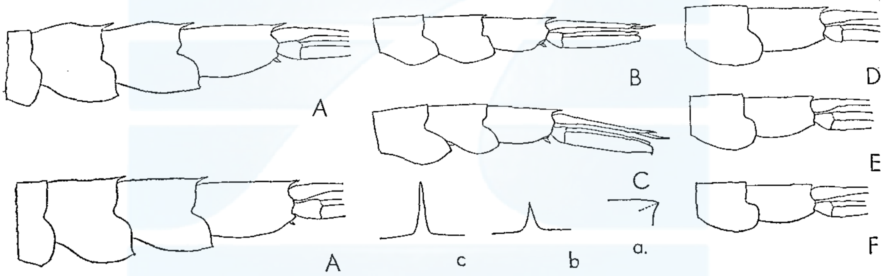

Fig. 15. Three spine, two spine and one spine forms of *Thysanoessa inermis*. A-Three spine form *T. inermis*: B-Two spine form: C-One spine form: D-10.5 mm larva: E-9.4 mm larva: F-8.2 mm larva. a-fifth dorsal segment in one spine form: b-fifth dorsal segment in two spine form: c-sixth dorsal segment in two spine form.

According to Hansen (1911), the majority of specimens taken in the Pacific has a dorsal spine which semetimes proportionaly long, sometimes rather short, and sometimes nearly or completely rudimentary, in the fifth abdominal segment and in rare case wanting. On the other hand, Einarsson (1945) stated none of the numerous specimens examined by him had shown even the slightest sign of a spine on the fifth segment in the Atlantic. Hansen (1911) also saw some specimens, taken off Cape Cod, with a conspicuous spine, while in another it was rudimentary I found none of the two spine form in the sample of Okhotsk Sea in my previous investigation, (Nemoto, 1959). I have examined many specimens of *Thysanoessa inermis* in the Okhotsk Sea after then, and the average values 16.7% in females and 11.1% in males are obtained by present examination as the percentage occurrence of two spine form. Further the occurrences of two and one spine forms of *Thysanoessa inermis* are examined on the materials collected from the Bering Sea to the waters of the Gulf of Alaska in the North Pacific. The occurrences of one and two spine form of *Thysanoessa inermis* are shown in Fig. 16. The two spine form is about 50 to 60 percent of the total in the waters off Kamtchatka, and about 60 to 70 percent in the eastern waters of the Bering Sea. The two spine form occupies about 75 or more percent in the waters of the Gulf of Alaska. This geographical cline is more appreciable when we consider the lower occurrences of two spine form in the Okhotsk Sea.

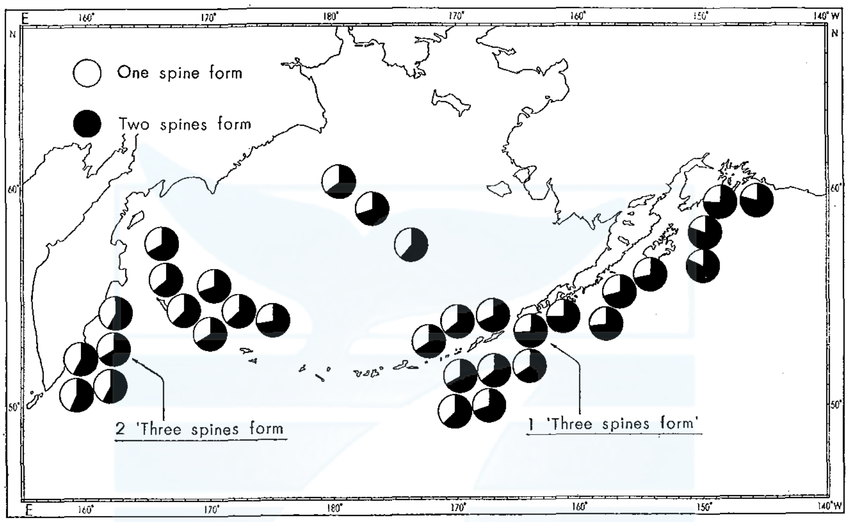

Fig. 16. The occurrences of one and two spine forms of *Thysanoessa inermis* in the northern part of the North Pacific. Black-Percentage occurrence of two spine form. White-One spine form.

This type of geographical cline, specific cline (Huxley, 1940) is also found in a plaice *Platichys stellatus* (Pallas) in the North Pacific. *Platichys stellatus* has the eyes in the right side of the body. But it has eyes in the left side from the specimens in the western Pacific and Japan. The percentage occurrence of left side eyes is about 70% from the specimens collected from Alaskan Peninsula and about 50% in the California. The occurrence of the two spine form of *T. inermis* is somewhat or considerably lower than those reported in the former report, (Nemoto, 1957), and this is attributable to the number of specimens examined and the selection of samples.

The younger *T. inermis* lacks completely abdominal spines of fifth and sixth segments. As a example, small size specimens collected at 53–40N, 165–20W, are examined. The average length is 8.2 mm in which both abdominal spines are undeveloped. Slight protrusion is observed on sixth abdominal segment at the average body length of 9.4 mm. The well developed abdominal spine is observed in samples of 10.5 mm long. So, it is desirable to treat the adults or well developed specimens to compare the occurrences of two and one spine forms of *T. inermis* as it is done here.

Three spine form of T. inermis

The three spine form of *Thysanoessa inermis* is reported in 1962 (Nemoto, 1962). Two new female specimens are found among samples collected at 52–53N and 162–12E, which also bear the abdominal denticles on the fourth segments. One specimen has strong spines on fourth, fifth and sixth abdominal segments with well developed keel on fourth and fifth abdominal segments. The another one is without keels but has spines on fourth, fifth and sixth segments too. The body length are 21 and 18 mm respectively and copulated.

Einarsson (1945) stated that " I will here confine myself to pointing out the possible relationship of this species to the Pacific species *Thysanoessa spinifera* Holmes, which has dorsal spines on the three last abdominal segments and the antennal armature of which bears close resemblance to that of *T. inermis* ". It is very interesting to note that one keel on the fourth abdominal segment is higher in the middle position and resembles rather to that of *T. spinifera* than to *T. longipes.*

Allomorphosis in length of abdominal segments

The sixth abdominal segment has been generally used as a taxonomical character to some extent for the species of euphausiids. It has been used as the combined or direct comparison with fifth or fifth and fourth abdominal segments. Here the length of sixth abdominal segments is plotted against the carapace margin length in logarithmic chart in Fig. 17. *T. macrura* and *T. vicina* form one allometric tribe and *T. longipes*, *T. inspinata* and *T. raschii* form another tribe. *T. longicaudata* belongs to *T. macrura* tribe in males but it shifts in females slightly.

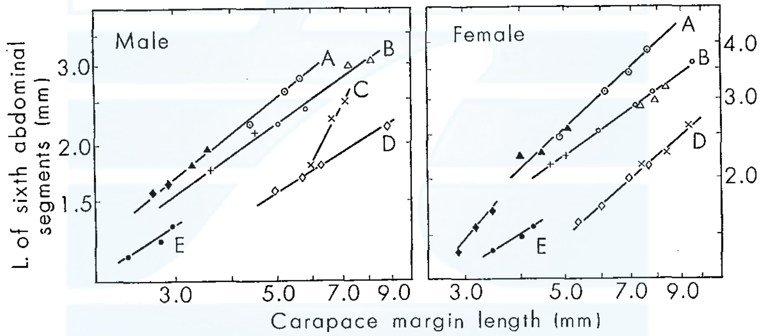

Fig. 17. Allomorphosis in abdominal segment of *Thysanoessa* euphausiids. Relation between carapace margin length and length of sixth abdominal segment.

T. spinifera and *T. inermis* occupy the same allometric tribe in females but they take different lines in males respectively.

T. gregaria is one species which forms allometric tribe by itself. The growth constant values are about the same for every groups except male *T. spinifera.*

It is very interesting to see that the *T. raschii* which differs consideraly from *T. longipes* group in other external characters form the same allometric tribe with *T. longipes* in sixth abdominal segment for carapace.

As the next step, the length of sixth abdominal segments are plotted against the length of fifth abdominal segments as shown in Fig. 18. Like above case, *T. macrura* and *T. vicina* form the same allometric tribe, but *T. longipes*, *T. inspinata* and *T. longicaudata* make another tribe. Other *T. gregaria*, *T. inermis*, *T. raschii* and *T. spinifera* draw respective allometric tribe by themselves. There is no difference between males and females of each species.

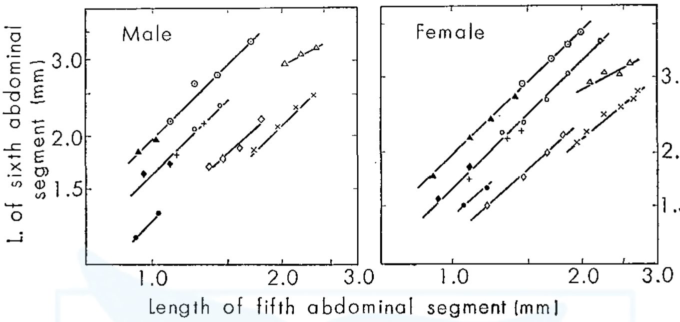

Fig. 18. Allomorphosis in abdominal segments of *Thysanoessa* euphausiids. Relation between length of fifth abdominal segment and length of sixth abdominal segment.

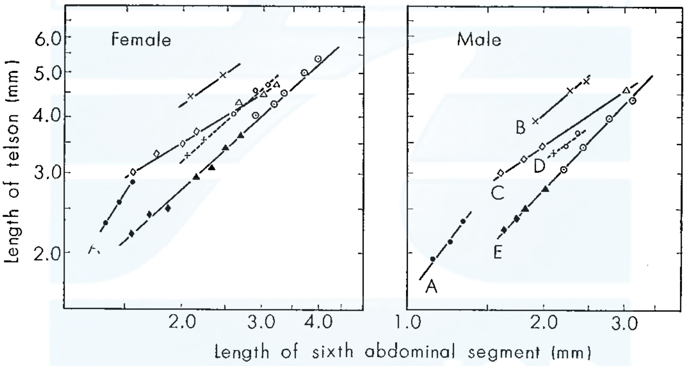

Fig. 19. Allomorphosis in telson of *Thysanoessa* euphausiids. Relation between length of telson and length of sixth abdominal segment.

The telson attached to the sixth abdominal segment is considered as one swimming apparatus. The length of telson against sixth abdominal segment in logarithmic chart is given in Fig. 19.

T. macrura, *T. vicina* and *T. longicaudata* form the same allometric tribe and growth constant. *T. longipes* and *T. inspinata* make the same tribe and *T. inermis* and *T. raschii* make another one. *T. gregaria* and *T. spinifera* make respective allometric tribe by themselves.

PREANAL SPINES

The preanal spines of euphausiids sometimes have been considered as a taxonomic character. The illustrations of them in *Thysanoessa* have been drawn for *Thy-*

sanoessa longipes and *T. gregaria.* (Boden, Johnson & Brinton, 1955) and *T. macrura* (Nemoto & Nasu, 1958). The latter is also drawn for the sexual dimorphism from the young stages. The preanal spines of available species of *Thysanoessa* group are

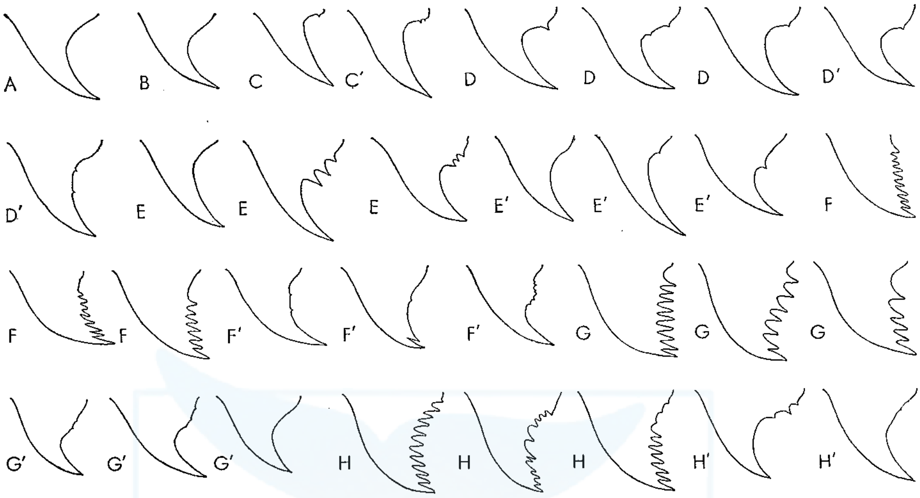

Fig. 20. Preanal spines of *Thysanoessa* euphausiids. A-*T. longipes:* B-*T. inspinata:* C-*T. spinifera:* D-*T. raschii:* E-*T. inermis:* F-*T. gregaria:* G-*T. vicina:* H-*T. macrura.* Males are illustrated with dots.

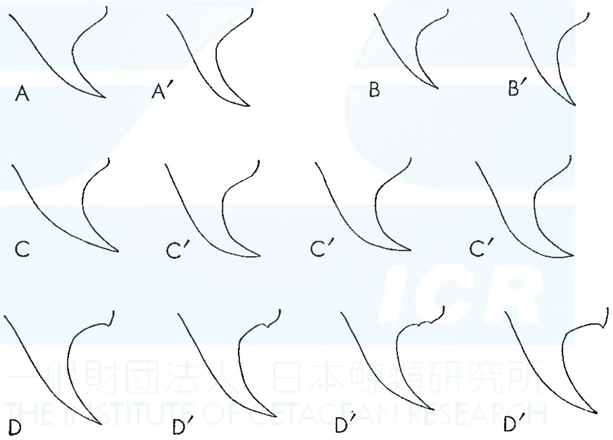

Fig. 21. Preanal spines of *Thysanoessa* euphausiids. A-*Thysanoessa longipes:* B-*T. inspinata:* C-*T. longicaudata:* D-*T. spinifera.* Males are illustrated with dots.

illustrated in Fig. 20. These spines are divided into following three groups.

Typical sexual dimorphism present	*T. macrura*, *T. gregaria*, *T. vicina*
Slight sexual dimorphism present	*T. inermis*, *T. raschii*, *T. spinifera*
Sexual dimorphism nearly absent	*T. longipes*, *T. inspinata*, *T. longicaudata*

In a strict sence, the sexual dimorphism is existing also in the third group. As it is illustrated in Fig. 21, the male *Thysanoessa longipes* has rather acute and thick spine. On the other hand, females have rather long and curved spines.

In all species in which the sexual dimorphism is observed, females have the deep denticulations in the concave part of the edge of preanal spines. Males have rather simple spines with a few small denticles along the same part.

This group includes *T. gregaria*, *T. macrura* and *T. vicina* possibly including *T. parva*.

Thysanoessa raschii and *T. inermis* show slight sexual dimorphism, but *T. inermis* shows more distinct differences.

In other euphausiids, these sexual dimorphism is also observed. *Euphausia vallentini* in the southern hemisphere has heavy denticulated preanal spines in females and small denticles along the inner margin of the preanal spines in males. Another example is given by Boden, Johnson & Brinton (1955) on *Nematobrachion flexipes*. They stated the preanal spine is simple in males and bifid in females, and the male preanal spine is also simple in *Nematoscelis difficilis* (Mclaughlin, 1965).

THORACIC LEGS

The general arrangement of *Thysanoessa* is illustrated in Table 6. Three species of *Thysanoessa*, have non-elongated second legs and thoracic legs are similar in structure of setae and spine as the skimming apparatus for foods. Other seven species have elongated second legs, and rather degenerated fifth and sixth thoracic legs. The former group may be connected to genus *Euphausia* and the latter may resemble to the other groups in the thoracic legs, such as *Tessarabrachion*, *Nematoscelis*, *Nematobrachion* and *Stylocheiron* species. Of course, there is not enough data for the feeding mechanism of euphausiids, it seems that euphausiids which have elongated thoracic legs are carnivorous more or less or polyhagous as *Thysanoessa* species. Especially *Nematobrachion* species are considered as typical carnivorous euphausiids mainly feeding on copepods in the deeper layer of the sea. The possible relation between the eyes and feeding apparatus for the living environment is now under

TABLE 6. ARRANGEMENT OF THORACIC LEGS IN *THYSANOESSA*

Species	Number of functional legs	Similarity		Elongated legs	Reduced legs	
		even	uneven		Male	Female
Thysanoessa raschii	6	+		—	7, 8th	8th*
,, *inermis*	6	+		—	,,	,,
,, *spinifera*	6		(+)	(2nd)	,,	,,
,, *longipes*	6		+	2nd	,,	,,
,, *inspinata*	6		+	2nd	,,	,,
,, *gregaria*	6		+	2nd	,,	,,
,, *parva*	6		+	2nd	,,	,,
,, *macrura*	6		+	2nd	,,	,,
,, *vicina*	6		+	2nd	,,	,,
,, *longicaudata*	6		+	2nd	,,	,,

* Distal three or four segments are lacking in 7th leg.

examination, and here the allomorphosis in *Thysanoessa* euphausiids in thoracic legs and morphology of dactylus of first and second legs which have special feeding character are investigated.

Allomorphosis in the total length of legs

The first legs show three allometric tribes when they are plotted against carapace margin length. *T. macrura*, *T. longipes*, *T. inspinata*, *T. vicina*, *T. longicaudata*

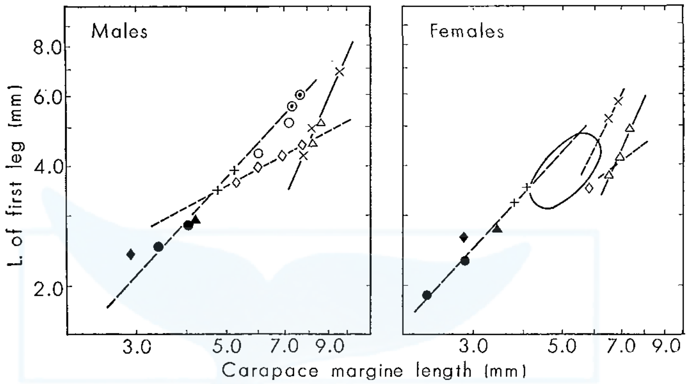

Fig. 22. Allomorphosis in leg of *Thysanoessa* euphausiids. Relation between length of total first leg and carapace margin length.

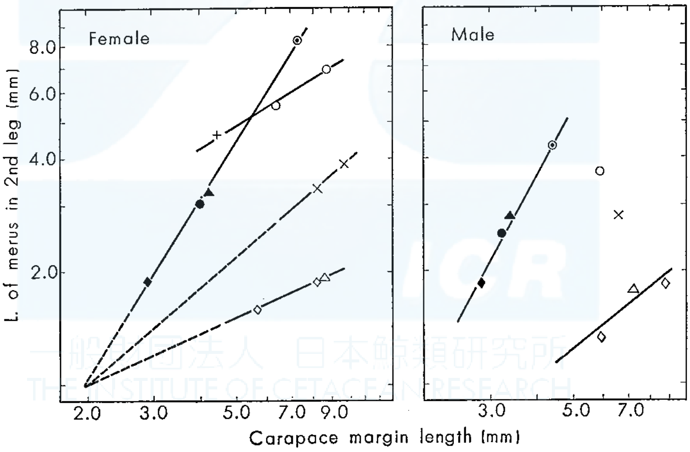

Fig. 23. Allomorphosis in merus in second leg of *Thysanoessa* euphausiids. Relation between length of merus of second leg and carapace margin length.

and *T. gregaria* are making one allometric tribe, which closely corresponds to the shorter spine group in the dactylus of the first logs.

The next group is *T. spinifera* which form the tribe by itself both in males and females. *T. raschii* and *T. inermis* are considered to form the same allometric tribe although *T. raschii* shows some vague points in females.

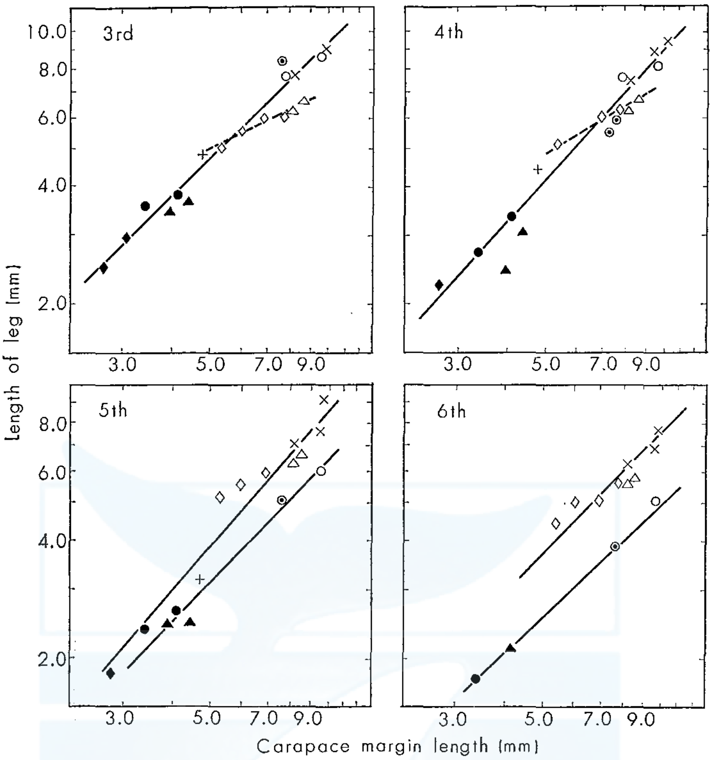

Fig. 24. Allomorphosis of leg in *Thysanoessa* euphausiids. Relation between length of carapace margin length and total length of thoracic legs.

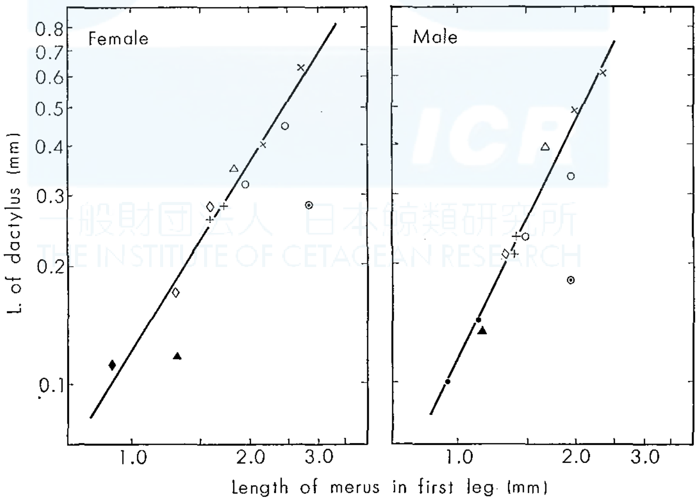

Fig. 25. Allomorphosis in *Thysanoessa* euphausiids. Relation between the length of merus in first leg and length of dactylus.

In second legs, the allometric tribes are given for the length of merus. Although *T. longipes* stands a little apart from the main line of the shorter group of the dactylus in the first leg, they fairly well coincide with the allomorphosis in the first dactylus.

In third and fourth legs, the wide band includes all species of *Thysanoessa* as illustrated in Fig. 24. In these figures, *T. inermis* and *T. raschii* form the oblique line which cross the main line. This is the same tendency in the first leg, and *T. inermis* and *T. raschii* form the distinct allometric tribes in fifth and sixth legs by themselves. But *T. spinifera* shift the tribe in fifth and sixth legs as illustrated in Fig. 24. It makes allometric line with *T. inermis* and *T. raschii* in sixth and fifth legs. These are confirmed by the skimming structure with well developed setae in those legs. On the other hand, *T. macrura T. longipes*, *T. gregaria* and *T. vicina* have shorter and poorly developed setae in those legs.

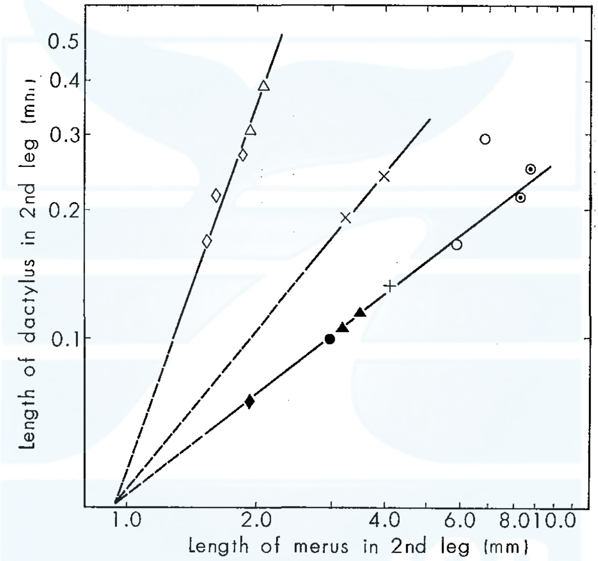

Fig. 26. Allomorphosis in legs of *Thysanoessa* euphausiids. Relation between length of merus and dactylus in 2nd leg.

The allomorphosis in thoracic leg joints in *Thysanoessa* euphausiids are also very characteristic. The length of dactylus of the first legs are plotted against the length of merus of the first legs in logarithmic chart. They form only one allometric tribe except *T. macrura*. The structure of dactylus of those species bearing somewhat peculiar characters as discussed. The position of *T. vicina* may shift from the main group if more data were obtained as it is basing rather small number of data.

The length of dactylus of other legs are also plotted against for the length of merus. They are shown in Fig. 26, and 27. In second leg, three allometric tribes are observed. *T. inermis* and *T. raschii* form the same tribe as the first leg, but *T. spinifera* differs considerably from the group. The oceanic group, *T. macrura*, *T. inspinata*, *T. vicina*, *T. gregaria* and *T. longicaudata* form one tribe and position of

T. longipes is somewhat vague as shown in Fig. 26. *T. longipes* also show some shift from those species in the relation between length of merus in second leg and carapace margin length. The length of dactylus is very variable in second legs of *Thysanoessa* euphausiids, and its variation in length is closely connected with the length of other joints of legs. *T. inermis* and *T. raschii* has shorter merus and longer dactylus. *T. spinifera* has somewhat longer merus and shorter dactylus than the former two species. It should be noted that *T. spinifera* differs in this point because it belongs to the *T. inermis* group in many other characters.

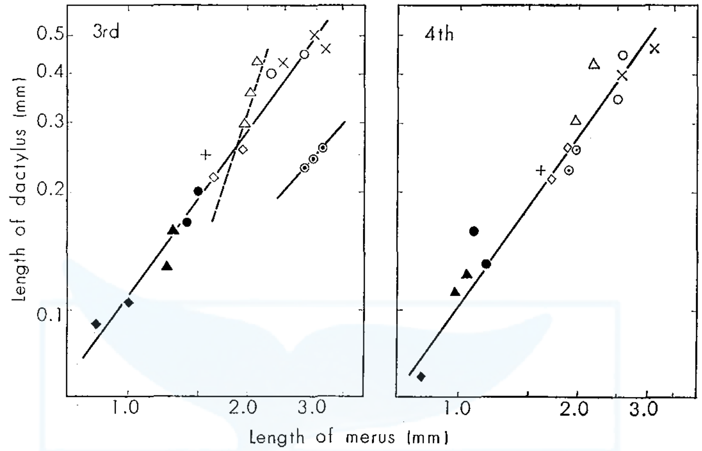

Fig. 27. Allomorphosis of leg in *Thysanoessa* euphausiids. Relation between length of merus and length of dactylus in 3rd and 4th legs.

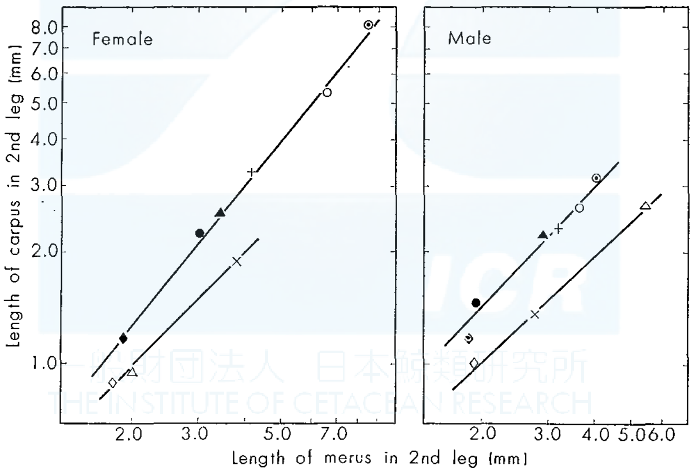

Fig. 28. Allomorphosis in legs of *Thysanoessa* euphausiids. Relations between length of merus and carpus in 2nd leg.

In the third legs of *Thysanoessa* euphausiids, the dactylus length against the length of the merus of the same legs form one allometric tribe except *T. macrura* which has rather shorter dactylus still in the third leg.

From fourth legs to sixth legs, all *Thysanoessa* euphausiids run the same line in allometric tribe in the relation between length of merus and length of dactylus. And setae in merus and carpus are developed in *T. inermis*, *T. spinifera* and *T. raschii*. The setae of *T. longipes*, *T. gregaria* and other pelagic species have rather rigid spines and number of setae are small.

The characteristic position of *T. macrura* in the allomorphosis in the dactylus of first and third legs may suggest the relation to the related species *Tessarabrachion oculatus* which has elongated second and third legs and shorter dactylus in those legs. The allomorphosis in the relation between length of carapace margin length and total second legs, *Tessarabrachion oculatus* stands the same line with *T. longipes*, *T. gregaria*, and *T. macrura* (Nemoto, 1962). In the allomorphosis in the relation between dactylus and merus of third legs, it shifts from the group of *T. longipes* with *T. macrura*.

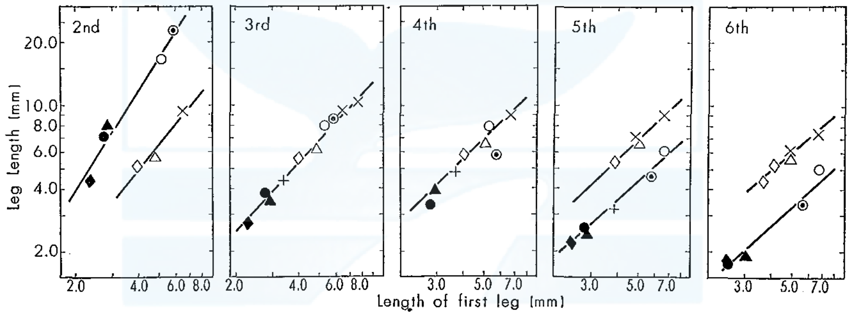

Fig. 29. Allomorphosis in legs of *Thysanoessa* euphausiids in the world ocean. Relation between first leg and other legs.

The relation between carpus and merus in second legs in *Thysanoessa* euphausiids is as follows. Both in males and females, there are two allometric tribes in *Thysanoessa*. *T. inermis*, *T. raschii* and *T. spinifera* form one line and other six species form another one. It clearly seems that *T. spinifera* belongs to the same tribe with *T. inermis* and *T. raschii*, although it belongs to the different tribe alone in dactylus.

The total leg length of each species are plotted against the length of the first leg. In the second legs, *T. spinifera*, *T. raschii* and *T. inermis* form one allometric tribe and other *Thysanoessa* species having longer second legs form another group. The third and fourth legs show no difference between above two groups in the total leg length, but *T. macrura* shifts slightly in fourth leg. In fifth and sixth legs, the general degeneration is observed in *T. macrura* group which has elongated second legs. The degeneration is heavy in sixth legs as illustrated in Fig. 29.

Dactylus of the first legs

The shapes of the dactylus of the first legs are very various in each species. *Thysanoessa inermis* and *T. raschii* have rather long dactylus and shorter top spines. The spines along the inner margin of the dactylus are ranging 5–8 in *inermis* and

8–12 in *raschii*. *T. spinifera* has also long dactylus and the spines of inner margins are ranging 8–14 and has shorter top spines.

T. longipes has somewhat shorter dactylus and longer top spines, but it has many spines in the inner margin of the dactylus. It should be noted *T. longipes* often has a half size spine along the inner margin at the most basic position as illustrated in Fig. 30.

The fringes in the spines are different in *T. spinifera* and *T. gregaria* groups. *T. spinifera* and *T. inermis* have fringes of the same length even in the top of the spines although they curve to the acute point. In *T. gregaria* and related speciees, the fringe are uneven in length and the top fringes are comparatively short as illustrated. The fringe of *T. macrura* has small number of spines along the inner side, but type of the fringes is seemed to be *inermis* type. The closely related species, *T. vicina* is gregaria type dactylus which has few spines in the inner margin of the dactylus. But it has short and pecurial fringes differing from those of *T. inermis* and *T. gregaria*.

TABLE 7. NUMBER OF SHORT SPINES IN INNER MARGIN OF DACTYLUS OF THE FIRST LEG IN *THYSANOESSA* EUPHAUSIIDS

Species	Male	Female	Type of fringe
T. spinifera	8～14	8～14	Inermis
T. raschii	8～12	8～12	”
T. inermis	5 or 6	6～ 8	”
T. longipes	5～ 7	7～ 9	Gregaria
T. inspinata	4～ 6	5 or 6	”
T. longicaudata	3～ 5	3～ 5	”
T. gregaria	1	1 or 2	”
T. macrura	2 or 3	2 or 3	(Inermis)
T. vicina	1	1	Vicina

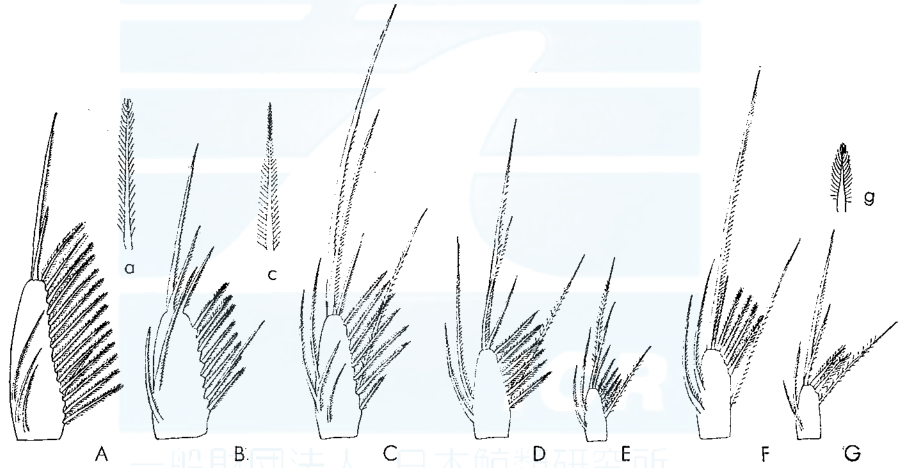

Fig. 30. Dactylus of first leg of *Thysanoessa* euphausiids. A-*T. spinifera:* B-*T. raschii:* C-*T. longipes:* D-*T. inspinata:* E-*T. longicaudata:* E-*T. macrura:* G-*T. vicina.*
a- spine of dactylus in *T. spinifera:* c- spine of *T. longipes:* g- spine of *T. vicina.*

Shape of the dactylus in the second legs

T. inermis and *T. raschii* have slender dactylus which bears the long spines along the margin of the dactylus. The number of the side spines in *T. raschii* are ranging 4 to 6 in one row, and *T. inermis* has 2 to 4 spines. These two species are considered as the same group also in the allometric tribe. *T. spinifera*, however, is considered to belong to another group. The dactylus is not so slender, rather short and the side row of spines is not observed. Those spines are growing in the distal edge of the top as illustrated. Other *Thysanoessa* have also shorter dactylus, but the arrangement of spines are the same with *T. spinifera*. There are two rows of small setae in the spines.

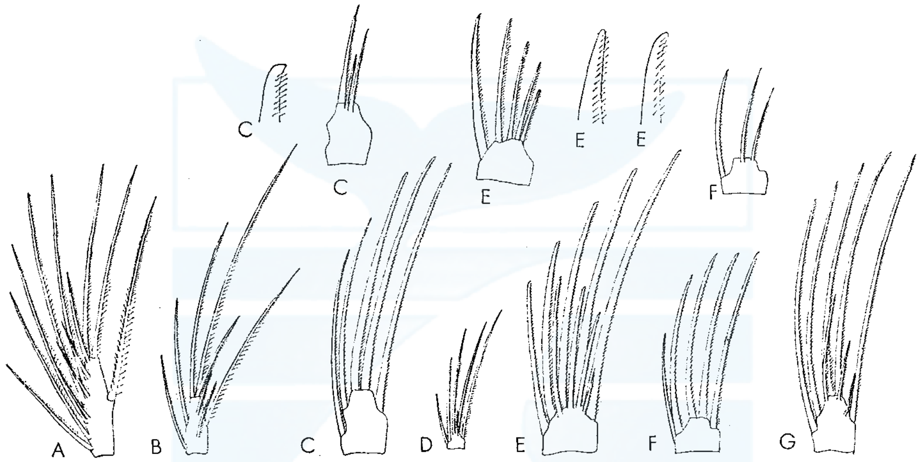

Fig. 31. Dactylus of second, and third legs in *Thysanoessa* euphausiids. A-*T. raschii;* B-*T. inermis;* C-*T. spinifera;* D-*T. longicaudata;* E-*T. macrura;* F-*T. inspinata;* G-*T. macrura*, third leg. Upper figures show the shorter spines.

These shapes of the dactylus are closely connected with the relative growth, allomorphosis of dactylus against the merus and carpus in the elongated second legs.

The shape of dactylus in second legs are discussed on *Euphausia superba* by Barkley (1940) and pecurial spines (Putzborsten according to Zimmer, 1927) are found in the inner side of the dactylus. These spines are yellowish or red in the living condition, and easily observed in their activity. But the sweeping or cleaning for their legs or setae is not observed by Barkley (1940).

None of this peculiar spines is found in *Thysanoessa* euphausiids. In *T. gregaria* group, the dactylus is shorter and the corresponding series of spines or setae become strong spines in the margin or inner edge of the dactylus.

It is very interesting that not only hervivorous *Euphausia* species but it is also found in the carnivorous euphausiids such as *Nematobrachion* species, although the second leg of *Nematobrachion* species is not elongated.

MOUTH APPARATUS

Here *T. gregaria* and *T. inermis* are mainly examined which are belonging to different type respectively comparing with other *Euphausia* and *Nematobrachion* species according to structures of thoracic legs.

Upper lip

The general shape and function of the upper lip in *T. gregaria* is almost the same with *Euphausia superba* and *T. inermis* which have also nearly the same shape of upper lip.

Lower lip

The lower lip of *T. gregaria* and *T. inermis* are also nearly the same with that of *E. superba* but having edge spines in the outer margins of the false jaws. These spines are characteristic denticles in *Thysanoessa* euphausiids but they may not have special mechanism in feeding.

Mandible

The general shape of mandible of *Thysanoessa* seems not to be so different from other euphausiids, however, the number of furrows in the mill-like process are not so much as *Euphausia superba* (Barkley, 1940).

First maxilla

The first maxilla has very strong processes along the edge of basis. *T. gregaria* has about seven tough processes. *Euphausia vallentini* and *E. superba* (Barkley, 1940) have much more processes along the basis of the first maxilla. These processes are accompaied with other small spines. The coxa has also processes and many spines. But these processes and spines reduced in carnivorous euphausiids, *Nematobrachion boopis*. Other euphausiids, *Euphausia superba*, *E. vallentini* have considerably many spines and processes. It is considered *Thysanoessa* euphausiids stand the intermediate position between carnivorous and hervivorous euphausiids from the structure of those maxilla.

Second maxilla

The second maxilla is long and covers the first maxilla. The general shape of the second maxilla is different between *T. inermis* and *T. gregaria*. *T. inermis* has longer segment in the last endopodite which corresponds to *Euphausia* species. (*E. superba*, 1940 Barkley: *E. vallentini*, Nemoto). But the shape of the last segment of *T. gregaria* is rather short and rounded. The carnivorous *Nematobrachion boopis* has also rather short and rounded segment, and setae are long but fragile and sparsely scattered. The mechanism of those second maxilla is considered to collect and move the odds which congregated in front of the mouth from the outer side to the opening of lower and upper lip and then to the mandible. The spines and setae of the coxa and the first ishium of the endopodite are the most important for the action, but the long spines and setae in the last segment of the endopodite are also usefull for the collection and not to miss the food. The carnivorous animals use the long sparse spines bearing special structure which is very effective to seize those food such as copepods and other active animals.

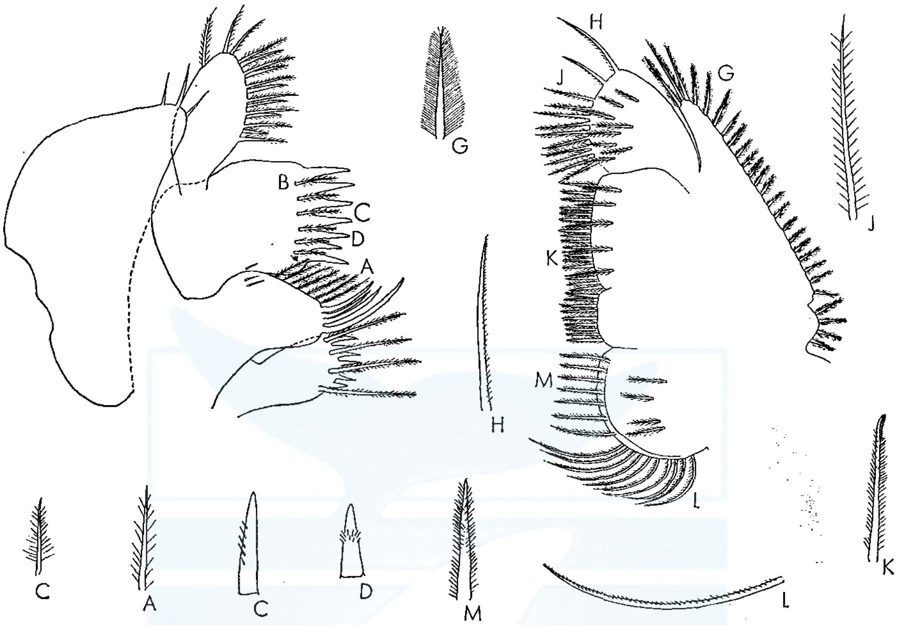

Fig. 32. First (Left) and second (Right) maxilla of *Thysanoessa gregaria* and spines of maxilla.

INNER STRUCTURE OF STOMACH

The inner wall of euphausiids are constructed to crash the foods of them such as diatoms, foraminfera, other zoo-planktons and phyto-planktons. The preliminary figures are given in the previous book on foods of whales and another paper (Nemoto, 1965). The food organisms are described by Ponomareva (1955). According to her list, *Thysanoessa* generally feeds on zooplanktons especially in *T. longipes* as well as phytoplanktons.

The stomach structure of *T. inermis* is given in Fig. 33. The general pattern of structure is the same with other euphauiids. It has, however, peculier bunch of spines in the middle of the lower margin of the side plate of the stomach wall. They may be called ' cluster spine ' of the euphausiids. This type of the cluster spine is characteristic in *Thysanoessa* euphausiids and related species *Tessarabrachion.* Every species of *Thysanoessa* euphausiids have row of cluster spines ranging from 10 to 40 in the middle of the side plates. The number of the cluster spines is small in *T. vicina* and *T. macrura*, and other *Thysanoessa* have 20 or more number of spines. The general shape of spines are not different among each species. *T. raschii* and *T. inermis* have about 20–25 cluster spines, *T. longipes* and *T. inspinata* have about 30 spines, and *T. spinifera* has about 40 cluster spines. *Thysanoessa* euphausiids have other spines to crash in the anterior part of the side plates as illustrated in Fig. 33. Especially *T. inermis*, *T. longipes* and *T. inspinata* and *T. vicina* have strong spines in the anterior edge parts of the side plates. These spines have some taxonomical characters as given in *T. longipes* and *T. spinifera*. In *Euphausia* genus, these spines congregate and form the circle bunch of spines as illustrated in a former report (Nemoto, 1965, Fig. 8). This type of cluster spines are characteristic in *Euphausia*, but they lack the row of cluster spines in the low or middle part of the side plate of the stomachs. The cluster spines in circles and isolated spines in *Thysanoessa* euphausiids are made to crash foods with the spines in upper side plates in the stomach walls. The circle cluster spines are fit for the porpose to crash hard wall cell of diatoms and related organisms. So *Thysanoessa* euphausiids lacking this circle cluster spines show good adoptation to catch zooplankton or other animals without hard shells. In the central part of the side plates, there are many isolated spines as illustrated in Fig. 32. These spines are also considered to crash their foods, and are most dominant in the central part of the side plates in the *Thysanoessa* and *Euphausia* species. In some species in the deep sea living *Thysanopoda* such as *Thysanopoda monacantha* has this type of spine, but other *Thysanopoda*, *T. tricuspidata* has one row of spines in the middle of the side plates. And *Nematobrachion boopis* completely lacks those spines in the side plates. All *Thysanoessa* euphausiids have central row of spines in the bottom plates. This row of spines is clear in *Thysanoessa longicaudata*, and *T. inermis*, but it is not so strong in other *Thysanoessa*.

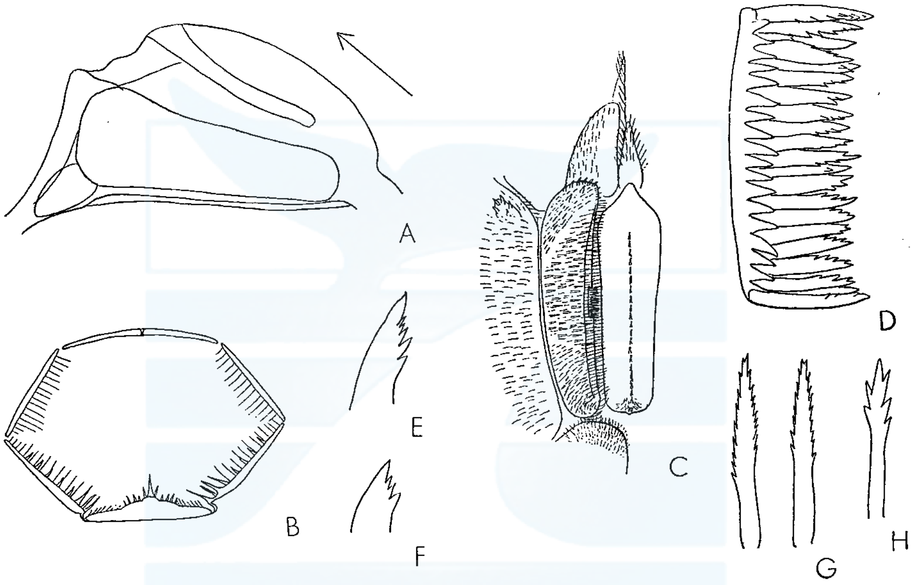

Fig. 33. Stomach of *Thysanoessa inermis*. A-Lateral view: B-Cross section at middle: C-Base part of the stomach: D-spine cluster in side plate of stomach: E,F,G,H,-Chewing spines in the stomach.

This central row of spines is also typical in *Thysanopoda monachantha*, *Nematobrachion* *boopis*, (Nemoto, 1965 Fig. 9.) and *Euphausia* species. But *Nematoscelis* has two branch rows and *Stylocheiron longicorne* and *S. abbreviatum* have only slight or no row of these spines.

The stomach of *Thysanoessa* is considered as a polyphagus type from the arrangement of cluster spines and isolated spines in the side plates. The side view of the stomachs of *Thysanoessa* shows no swell of the posterior portion of the stomach just above the pyloric region of the intestine. *N. boopis* has very swollen stomach in the posterior part (Nemoto, 1965 Fig. 9) which fit to take vast quantity of undigested foods such as copepods and other living zooplanktons at one occasion.

COPULATORY ORGANS

The male copulatory organs of euphausiids are considered one of the best specific characteristics and the female copulatory organs, namely thelycum, are also pointed out as one of the best character for taxonomy by Einarsson (1942). In some closely related euphausiids, *Thysanopoda aequalis* and *T. subaequalis* (Boden & Brinton, 1956), *Euphausia nana* and *Euphausia pacifica* (Brinton, 1962a), the copulatory organs do not exhibit so well their specific characters. In a former report, (Nemoto, 1963) I also discussed the possible difference in the relative growth of the length of the process and spines in the male copulatory organs in closely related *T. longipes* and formarly spineless form, *T. inspinata*. On *Euphausia nana* and *E. pacifica*, the microstructure of the male copulatory organs are considered as the taxonomic characters, however, the body length, horizontal distribution are also main discriminating points about two species (Brinton, 1962a).

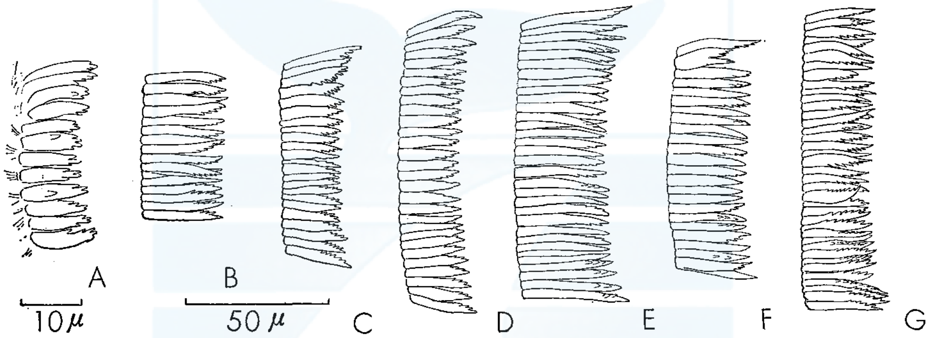

Fig. 34. Spine clusters of stomachs of *Thysanoessa* euphausiids. A-*Thysanoessa vicina:* B-*T. macrura:* C-*T. gregaria:* D-*T. longipes:* E-*T. inspinata:* F-*T. raschii:* G-*T. spinifera.*

The copulatory organs in *T. gregaria* group in males has terminal process distally expanded, but in the younger stages it is not so expanded as discussed in the previous report on *T. macrura* (Nemoto, 1958). The young *Thysanoessa macrura* has also broader base of terminal process but the tip is pointed.

The copulatory organs of *Thysanoessa* euphausiids are divided into four or five groups. *T. gregaria*, *T. macrura*, *T. vicina* and *T. parva* have rather related male copulatory organs as illustrated in Fig. 35.

The edge of the tip in terminal process of *T. gregaria* and *T. vicina* are serrated, and no clear serration is observed in *T. macrura* and *T. parva.*

T. raschii and *T. inermis* have similar male copulatory organs. Both species have two long menbranous wings or expansions from the tip almost to the bases. (Boden, Johnson & Brinton, 1955). The proximal and lateral processes are well developed but not expanded in the ends. *T. spinifera* has not the broad terminal spine. It has, however, the terminal spine of broad base and both proximal and lateral spines have acute ends. The broad base of a terminal spine is identical with *T. inermis* and *T. raschii* and it is considered as the original type of the copulatory organs of *Thysanoessa* euphausiids of *inermis* group.

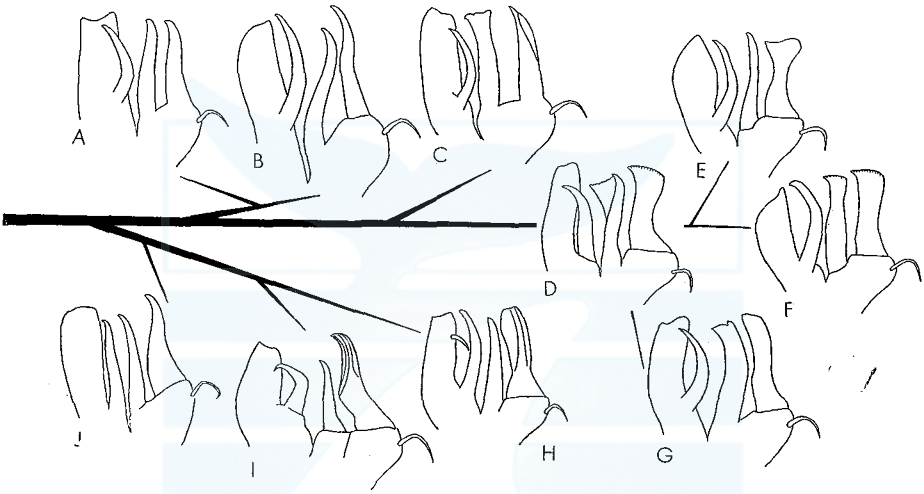

Fig. 35. Male copulatory organs and possible relationships in dendrogram in *Thysanoessa* euphausiids. A-*T. inspinata*, B-*T. longipes*, C-*T. longicaudata*, D-*T. gregaria*, E-*T. macrura*, F-*T. vicina*, G-*T. parva*, H-*T. inermis*, I-*T. raschii*, J-*T. spinifera*.

T. longipes and *T. inspinata* have three main processes which are not expanded in the tapered ends. But those are slender and the base is not broad as *T. spinifera.*

T. inspinata has short and robust processes and main characters are the same with those of *T. longipes.* The base of terminal process is not so broad as *T. spinifera.*

T. longicaudata has pointed terminal process, it has thin keel on the outer side. The proximal process flattens out considerably above the middle and forms somewhat spoon-shaped plate with an uneven upper edge. The terminal end of the proximal process is not serrated. This character is bearing a resemblance to *T. parva* or *T. gregaria,* but its base of terminal process is rather narrow and pointed end is quite different from those of *T. gregaria* group.

DISTRIBUTION

Three main distributions in the World Ocean contain following species listed in

Table 8 and 9. Two Arctic and boreal species *T. inermis* and *T. raschii*, are common in the Atlantic and the Pacific.

T. longicaudata is only found in the Atlantic and *T. longipes* and *T. inspinata*, *T. spinifera* are only distributing in the boreal region of the Pacific. Other two species *T. macrura* and *T. vicina* are Antarctic species, and two species *T. gregaria* and *T. parva* are distributing both in southern and northern temperate water regions.

T. spinifera is distributing only along the American side, the eastern part of the Pacific and *T. inspinata* and *T. longipes* are abundant throughout the boreal regions of the Pacific. The latter two species are rather rare in the shallow Arctic Sea. (Johnson, 1956) and the occurrence of *T. inspinata* in the sea of Japan is somewhat uncertain still in recent studies (Komaki & Matsue, 1958), although Ponomareva considered it also distributed in the Sea of Japan.

TABLE 8. OCCURRENCES OF *THYSANOESSA* EUPHAUSIIDS IN THE WORLD OCEAN

Species	North Atlantic	North Pacific	Southern Hemisphere
Thysanoessa raschii	+	+	−
,, *inermis*	+	+	−
,, *longipes*	−	+	−
,, *inspinata*	−	+	−
,, *longicaudata*	+	−	−
,, *spinifera*	−	+	−
,, *gregaria*	+	+	+
,, *parva*	+	+	+
,, *macrura*	−	−	+
,, *vicina*	−	−	+

TABLE 9. OCCURRENCES OF *THYSANOESSA* EUPHAUSIIDS IN THE NORTH PACIFIC

	Arctic Sea	Bering Sea West	Bering East	Okhotsk Sea	Japan Sea	North-west Pacific	Alaskan Gulf	American Coast
Thysanoessa raschii	+	+	+	+	+	+	+	±
,, *inermis*	±	+	+	+	+	+	+	−
,, *longipes*	±	+	+	+	+	+	+	+
,, *inspinata*	−	+	−	−	− ?	+	+	+
,, *spinifera*	−	−	+	−	−	−	+	+
,, *gregaria*	−	−	−	−	− ?	−	−	+
,, *parva*	−	−	−	−	−	−	−	−

T. spinifera shows pecurial distribution in the eastern part of the North Pacific. (Nemoto, 1962: Brinton, 1962b). It has not been recorded from the Arctic Ocean, north Bering Sea, Okhotsk Sea and the Sea of Japan. It is only distributing in the shallow neritic waters of the east coast of the North America. It is found dominantly in the stomachs of baleen whales in the coastal waters of the east Aleutian Is. (Banner, 1954: Nemoto, 1959). The most northern record is given in a former report (Nemoto, 1962) and the most western record is given by Hansen, (1915). The concentration of this species is also observed along the continental shelf of the Gulf of Alaska from the observation of the stomach contents of baleen whales. The southern range of the distribution is given by Banner (1949) and Brinton (1962b) along the California coast of North America.

The range of water temperature and salinity is considered slightly different from other neritic *T. raschii* and *T. inermis*. *T. spinifera* occurres in a little wamer temperature and lower salinity and T-S diagram chart for *T. spinifera* is different from those euphausiids. (Nemoto, 1962).

Thysanoessa inermis is distributing in the boreal Arctic water in the Atlantic and the Pacific. In the Atlantic, general distribution is observed between the February ice limit and the surface isotherm for 10°C (Einarsson, 1945). And the Pacific distribution is also limited within the February surface isotherm 10°C (Brinton, 1962b: Nemoto, 1962) and the main distribution is found within 15°C in summer isotherm (Nemoto, 1962). *T. inermis* is considered to spawn in the shallow waters along the continental shelf, and Glover (1952) described *T. inermis* as the shallow water species. In one former report, I reported that *T. inermis* occurres in the stomachs of baleen whales as their foods very often in the coastal waters of Kamchatka peninsula and along the continental shelf of the Alaskan peninsula in the Bering Sea (Nemoto, 1962). *T. inermis* also found in the Okhotsk Sea and Japan Sea. But latter occurrence is restricted in the northern half waters (Komaki & Matsue, 1958: Ponomareva, 1957). The concentration of *T. inermis* is also observed in the southern edge of the shelf along the Alaskan peninsula and the Gulf of Alaska, and it goes down to the waters off Vancouver (Brinton, 1962b).

The possible relation between *T. inermis* in the Atlantic and the occurrence of it in the western part of the Pacific is expressed in the two and one spine forms of *T. inermis*. In recent investigations, Johnson (1956) reported it from the Chukchi Sea but only few specimens. The main range of the *T. inermis* distribution is limited the line of continental shelf of the Bering Sea, and the ice limit in summer in the shallower Atlantic north waters. Thus the interchanging of Atlantic and Pacific stocks in recent age may not occur to effect the main distribution and of two and one spine forms as shown in percentage occurrence of them.

T. raschii is uaully distributing along the shallow continental shelf or the neritic shore waters in the Arctic boreal regions. It plays the role of foods of balleen whales in the off waters of Anadyle Gulf, Bristol Bay and main occurrences are also observed along the Kamtchatka peninsula, Anadyl Gulf, and the shelf of the Gulf of Alaska. Other investigations prove that it also occurres in the Japanese coast of Okhotsk Sea (Nemoto, 1959), north shallow waters of Okhotsk Sea and northern part of the Sea of Japan (Ponomareva, 1955).

The main stocks of *T. raschii* in the Pacific and the Atlantic are living within ice covered waters in winter seasons. It is also more common in the North pole sea than other euphausiids (Johnson, 1956). The interrelation between the Pacific and Atlantic stocks may be closer than other euphausiids, and possible continuity of distribution through the north pole waters is considered.

The southern range of *T. raschii* is restricted to the cold current and summer concentration of this species is found even in the low salinity (Einarsson, 1945: Nemoto, 1962). This position may be compared with the Antarctic *Euphausia* *cristallorophias* along the Antarctic continental shelf.

T. longipes is differeing from other neritic *Thysanoessa spinifera*, *T. inermis* and *T. raschii*, considered as pelagic form. Its main distribution is given by Brinton (1962b) and Nemoto (1962) in the northern part of the North Pacific. *T. longipes* is transported to the north American secter of the Arctic sea (Johnson, 1956), which coincides with the flow of the Arctic water current from the southern waters through Bering strait (Johnson, 1956). Considering from the occurrences in the stomach contents of baleen whales (Nemoto, 1959: 1962) and plankton net investigations (Banner, 1949: Brinton, 1962b), *T. longipes* concentrations are observed in the eastern Bering Sea (Nemoto, 1962: Brinton: 1962b) in the off waters of Alaskan continental shelf and mid waters along the Bowers Bank. The former occurrences are found in company with *T. inermis* and dominant occurrences are found in a little more off waters in the north waters of Unimak Is. The heavy concentrations are also observed in the southern waters of Aleutian Is. along the latitudinal belt of 50°N (Brinton, 1962b) by plankton investigations.

The closely related species *T. inspinata* (Nemoto, 1963) or the spineless form of *T. longipes* (Banner, 1949) is found in more southern waters. It consitutes the smaller part of the food of baleen whales in the southern Bergin Sea (Nemoto, 1959) which is possibly the northern limit of this species. The general distribution of *T. inspinata* is given by Brinton (1962b) as the unspined form of *T. longipes*. The southern limit of this species is considered in the western side of the Pacific coincide with the range of cold current Oyashio. Brinton gave the most southern record 34–17N, 156–11E, where the submergence at the southern margin of the range is observed (Brinton, 1962b). The present data collected by Tansei-maru in KT-64–17 cruise, *T. inspinata* occurred from 33°–50N and 138–30E as the more western waters in the southern waters of Japan.

T. macrura and *T. vicina* are only distributing in the southern hemisphere. Those two Antarctic species have been found in the circumpoler belts from the subantarctic to the Antarctic. From the external characteristics, they are considered to come from *gregaria-parva* relatives not *longipes* or *inermis*, and its distribution suggests also phylogenetic speciations like the relation between *T. longipes* and *T. inspinata*.

The distribution of *T. gregaria* is well discussed by Brinton (1962b) with some phylogenetic consideration in view of biantitropical panoceanic distribution of this species in southern and northern hemispheres.

The vertical and latitudinal distribution of *Thysanoessa* euphausiids is given in Fig. 36. In both Arctic and Antarctic seas, *Thysanoessa* euphausiids extend to the deeper waters following to the equator. *Thysanoessa raschii*, the most northern species is living in shallow water usually upper than 200 metre, and *T. inermis* upper than 300 metre in the North Pacific. The southern waters species, *T. macrura* and *T. vicina* are also living in the layers upper than 300 metre (Hardy & Gunther, 1935). *T. longipes* is generally considered to live in the layers upper than 500 metre, and deeper waters in the southern waters near 40N latitudes. The closely related species *T. inspinata* which is living more southern waters (Brinton, 1962) is considered to distribute into deeper waters (Nemoto, 1962). The deep water species *T. parva* is usually found from 750 to 2000 metre depth in the waters. The vertical zones of euphausiids distribution are illustrated by Brinton (1962b) as the mid Pacific profile in the North Pacific. The Arctic and subarctic species of euphausiids found in the surface layers often found in the middle layers of temperate waters of lower latitudes.

The deep sea living *T. parva* has far reduced spine and setae in the thoracic legs, although *T. gregaria* and other species have also reduced setae in thoracic legs especially in second legs.

This tendency is also observed in carnivorous euphausiids *Nematobrachion* species. But the remarkable point in *T. parva* is the lack of strong fringes in setae as well as the reduction of setae. As a taxonomic character in *T. parva*, these fine fringes in setae in legs are described. These fine fringes may be also adoptation to the deep sea living where the small food organisms such as diatoms are comparatively scarce as compared with surface layers.

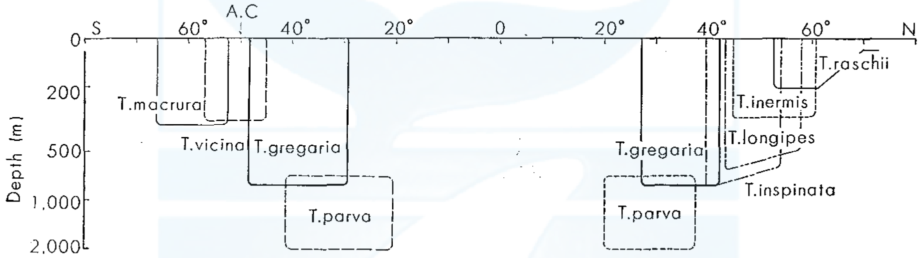

Fig. 36. Profile of the vertical and latitudinal distribution of *Thysanoessa* euphausiids along the section approximately 160E.

Among *Thysanoessa* euphausiids, *T. inspinata* is found by KT-64–17 cruise from the south waters of Japan by deep oblique haul, where *T. gregaria* possibly distributes from the surface to about 1000 m deep. The Pacific boreal species *Tessarabrachion oculatus* is also collected by this cruise in the same position. This submargence of boreal species in temperate waters is observed in other groups of plankton such as chaetognata *Sagitta elegans* in the south waters of Honshu (Marumo, 1965).

Brinton considered the biantitoropical panoceanic distribution of *Thysanoessa gregaria* may be explained by Pleistocene cold waters distribution. The 7°C and 11°C isotherms at 200 m are associated with the limitation of the recent range of *T. gregaria.* and *T. gregaria* crossed the equater by this cooling of 2 1/2° to 3°C at 200 m in Pleistocene age.

At this circumstance, the North Pacific subarctic species, *T. longipes* may still occupy the coastal fauna in the region 20–30N where the colder California current runs and it never has the chance of transgressing the equator.

From above explanations for the distribution of *Thysanoessa* euphausiids two hypotheses may be derived.

One is the trespass of *T. vicina* and *T. macrura* or their ancestor in the Antarctic waters is earlier than the transgression of the equator by *T. gregaria,* and speciation of *T. inspinata* from *T. longipes* or its relatives is possibly later than that age.

The second hypothesis is that *T. parva* is also specialized into southern and northern hemisphere at about the same age of *T. gregaria* or a little later age, and it also transgressed the equator after the specialization as *T. parva*, not the age of the original type of *T. parva* in the older ages.

DISCUSSION

The allometric study and comparative morphology explain fairly well the taxonomic and ecological positions of each species in *Thysanoessa* euphausiids.

TABLE 10. CHARACTERISTICS IN COMPARATIVE MORPHOLOGY AND ECOLOGY IN *THYSANOESSA* EUPHAUSIIDS

	EYE		ANTENNULE		CARAPACE			ABDOMINAL SEGMENTS		LEGS			PREANAL SPINE	COPULATORY ORGAN			STOMACH		LIVING DEPTH			
	constriction	sexual dimorphism	flagellum	sexual dimorphism	rostrum	denticle	eye hole spine	keel present	spine present	1st dactylus	2nd dactylus	3rd dactylus	sexual dimorphism	inermis type	longipes type	gregaria type	cluster spine	central spine	0–300	300–500	500–1000	1000–2000
T. inermis	−	−	◇	+	◇	−	−	−	+	◇	◇	◇	±	+			+	±	+	−	−	−
T. raschii	−	−	◇	−	△	+	−	−	−	◇	◇	◇	±	+			+	±	+	−	−	−
T. spinifera	−	−	◇	+	×	−	+	+	+	◇	×	◇	±	±	±		+	±	+	±	−	−
T. gregaria	+	+	●	−	△	+	−	−	−	●	●	◇	+			+	+	(±)	+	+	±	−
T. macrura	+	±	●	−	⊙	+	−	−	−	●?	●	⊙	+			+	+	(±)	+	+	−	−
T. vicina	+	+	●	−	⊙	+	−	−	−	●?	●	◇	+			+	+	(±)	+	+	−	−
T. longicaudata	+	±	◆	−	◇?	−	−	±	−	○	●	◇	−		±	±	+	+	+	+	+	−
T. longipes	+	±	●	−	◇?	+	−	+	+	○	●	◇	−		+		+	(±)	+	+	±	−
T. inspinata	+	±	●	−	◇?	+	−	+	−	○	●	◇	−		+		+	(±)	+	+	±	−
T. parva	+		?			+	−	−	−		?		?			+	?		−	−	+	+

The similarity in morphological characters of *Thysanoessa* euphausiids is listed in Table 10. In general consideration *T. inermis* and *T. raschii* resemble each other. *T. inermis* differs in the sexual dimorphism in the first antenna, presence of spines in the posterior abdominal segments, shape of the rostrum and the absence of the carapace denticle in the lower margins. But other main characteristics are the same with *T. raschii*. The arrangement of thoracic legs resembles to *Euphausia* species.

T. spinifera shows the first characteristic point in the sexual dimorphism in the first antenna. The rostrum of the carapace has also specific difference among these three species. The most peculiar point is that the eye hole spine along the carapace margin is present in *T. spinifera*. None of other *Thysanoessa* has this spine. The shape of dactylus in thoracic legs approximately the same among those *T. inermis*, *T. raschii* and *T. spinifera*. Only the dactylus of *T. spinifera* in the second leg differs from other two species. It bears the intermediate characteristics between *T.*

raschii group and *T. gregaria* and other species which have elongated second legs. Third dactylus does not differ among every species except *T. macrura* as it is discussed in the former part. And no special difference is given in other dactylus in posterior legs.

Preanal spines in those Inermis species show slight sexual dimorphism, and other two groups also divide themselves from those species as fairly clear dicisions. The group of *T. parva* is still unknown, but it may possibly belong to *T. gregaria* group. The Atlantic *T. longicaudata* has non-sexual different preanal spines in denticulation and belongs to *T. longipes* group. Longipes group species have the same character in the dactylus of the first legs and shape of the rostrums, but *T. longicaudata* lacks the lateral denticle of the carapace. The second leg of *T. spinifera* stands peculiar intermediate position between *T. inermis* group and *T. gregaria* group. And this tendency is also observed in the relation between merus and dactylus in the second leg. These characters show that the second leg of *T. spinifera* becomes elongating and the dactylus shortening which is more relating to *T. gregaria* group. *T. gregaria* group is considered off shore living species and they are now developing to more carnivorous feeder in selection of the food. The short and bearing tough spines in the dactylus of the elongated legs are also often observed in other carnivorous euphausiids. And a little elongated second leg in some younger forms of *T. inermis* (Hansen, 1911, Einarsson, 1945) is noted already, especially in *T. neglecta* form in the Atlantic. According to the Einarsson's consideration, *T. neglecta* is only a transitory form in the developmental history of *T. inermis*. It has longer second legs and shorter dactylus from the figures by Einarsson, (1945 Fig. 19) and constricted eye. The illustrated specimens stand clearly in the *gregaria* group from the length of each joint. The larval forms of *T. inermis* usually have eyes longer vertically, which is almost the same as *T. longipes* eyes in those stages. Thus *T. inermis* sometimes shows in its developmental stages the different pattern of allomorphosis in second leg, and it is considered as the one explanation for the different group of allomorphosis in *Thysanoessa* euphausiids is originated from the above different developmental stages.

Another neritic species *T. raschii* has non-elongated second leg, and non-constricted eye in adults, and it has no clear form of elongated second leg in furcilia stages like *neglecta* form of *T. inermis*. But it has lateral denticles in the anterior part of the margin of the carapace, although the denticle is situated far posterior part of the lateral margin of the carapace in the furcilia stages of *T. raschii*. This would suggests full development in this character if the speciation is attributable to excessive growth. There are three main types are observed in *Thysanoessa* euphausiids in male copulatory organs. One is *inermis* type which includes *T. raschii* and *T. inermis*. *T. spinifera* has this character, but it bears also *longipes* type as discussed in the former part. *T. gregaria* is considered to belong the same group with *T. macrura*, *T. vicina* and *T. parva*. *T. longicaudata* is standing in the intermediate position between *T. longipes* and *T. gregaria*. This is also one of the expression of the phylogenetic position of *T. longicaudata* that it does not belong to the *gregaria* group. The position of *T. longicaudata* is also confirmed by the presence of central spines in the base plate of the stomach structure. This central spine is clear also in some other euphausiids. *Thysanopoda*, *Nyctiphanes*, and *Nematobrachion* species have well developed central spines in the base plate. Only *T. longicaudata* among *Thysanoessa* has well developed central spines and *T. inermis* group has vague spines. *T. longipes* and *T. gregaria* have trace of central spines but sometimes they have spines like *T. inermis*. The type of cluster spines in the anterior part of the side plate of the stomachs are nearly the same in *Thysanoessa* species, but some difference in related species such as *T. longipes* and *T. inspinata* is observed.

The bilobate eye of seven *Thysanoessa* euphausiids in adult may directly be connected to the broader living range in the depth of the sea at present or their ancestors (Brinton, 1962b).

TABLE 11. LIST OF SIMILARITY IN ALLOMORPHOSIS IN *THYSANOESSA* EUPHAUSIIDS

	CARAPACE M. L.	CARAPACE M. L.						TOTAL 1ST LEG					MERUS : dactylus					MERUS	CARAPACE M. L.		SIX ABD. SEGMENT	
	: Denticle l.	: 1st leg	: 2nd merus	: 3rd leg	: 4th ,,	: 5th ,,	: 6th ,,	: 2nd	: 3rd	: 4th	: 5th	: 6th	: 2nd	: 3rd	: 4th	: 5th	: 6th	: 2nd carpus	: Antennule	: 6th abd. segment	: 5th segment	: Telson
T. inermis	–	◇?	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇
T. raschii	△	◇?	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	△	△	◇
T. spinifera	–	×	×	◇	◇	◇	◇	◇	◇	◇	◇	◇	×	◇	◇	◇	◇	◇	◇	◇?	×	×
T. gregaria	●	●	●	◇	◇	●	●	●	◇	◇?	●	●	●	◇	◇	◇	◇	●	●	●	●	●
T. macrura	⊙	●	●	◇	◇	●	●	●	◇	◇?	●	●	●	⊙	◇	◇	◇	●	●	⊙	⊙	⊙
T. vicina	⊙	●	●	◇	◇	●	●	●	◇	◇	●	●	●	◇	◇	◇	◇	●	●	⊙	⊙	⊙
T. longicaudata	–	●	●	◇	◇	●	●	●	◇	◇	●	●	●	◇	◇	◇	◇	●	◆	⊙?	◆	⊙
T. longipes	○	●	●	◇	◇	●	●	●	◇	◇	●	●	●	◇	◇	◇	◇	●	●	△	◆	○
T. inspinata	+	●	●	◇	◇	●	?	●	◇	◇	●	●	●	◇	◇	◇	◇	●	●	△	◆	○

The similarity in allometric tribes are illustrated symbolically in the Table 11. As the general aspects of the list, those tribes are also divided into two main groups. In the relative growth of the lateral denticle and carapace length, however, each species demonstrates respective tribe except *T. vicina* and *T. macrura*.

It is suggested the same allometric tribe of *T. macrura* and *T. vicina* in the position of lateral denticle means they closely related each other and position of *T. vicina* is larval stage of *T. macrura* in this relation. Because the position of lateral denticle of the carapace is situated in the posterior part and goes up to forward with the body development especially in the furcilia stages. The body size of *T. vicina* is smaller than *T. macrura* and lateral denticle is situated a little posterior position. These characters are the larval characteristics. The general distribution of those species show that the adult form, namely the lateral denticle of the carapace situating in the anterior position, of each group is found in the colder waters. The body size of *T. inspinata* is smaller than *T. longipes*, and *T. vicina* is smaller than *T. macrura*. Thus those specific differences are connected with the body development in those species. The wamer water type may be the larval type, which has the posterior carapace denticles, and having smaller body length. The phenomena like this have been found on American fresh water fish as a consideration of the evolution of those fish (Hubbs, 1940).

The legs of euphausiids are generally considered as the feeding and swimming apparatus and legs vary very much among euphausiid species.

The general allomorphosis in legs of *Thysanoessa* euphausiids shows also two main groups. The total leg length against carapace margin length and total first leg are both the same in third and fourth legs, but it differs in first, second, fifth and sixth legs. As for the relation of total length of the first legs for carapace length, *T. inermis*, *T. raschii* and *T. spinifera* form one allometry group and other six and possibly *T. parva* form another group.

T. spinifera stands itself in the second leg aparting from *T. inermis* but it forms the same allometric tribes in fifth and sixth legs with *T. inermis* and *T. raschii.*

The allometric group of second legs are also divided into two groups. These groups coincide with also groups of fifth and sixth legs. From the observations on structure of legs, the reduction in the posterior thoracic legs is considered as the steps to the carnivorous feeding type. *Thysaneossa* euphausiids have even in the *gregaria* group, rather long and skimming setae in sixth and fifth legs. But other carnivorous *Nematobrachion* species have none functional setae and reduced fifth and sixth legs. The surface feeding and hervivorous euphausiids, such as *Euphausia*, have functional and long sixth and fifth legs in general. Thus it may be considered some of *Thysanoessa* euphausiids bear both types of feeding and omnivorous feeding type. Among them, *T. inermis*, *T. raschii* are surface feeder type. The general features of setae in thoracic legs as the feeding apparatus are discussed by Barkley (1940). *T. inermis*, *T. raschii* and *T. spinifera* resemble to *E. superba* in the arrangement of those setae in ishium and merus and in the allomorphosis relationship of every leg length.

In the allomorphosis in the relation between merus and dactylus of each legs shows also two main allometric tribes as in the relation between merus and carpus in second legs. But *T. macrura* shows peculiar position in first and third legs which occupys the independent allometric tribe. *T. spinifera* occupys also the tribe itself in second leg.

Although the different allometric tribes are observed in second legs, no difference is found in the allomorphosis from fourth to sixth legs in the relation between merus and dactylus. Thus the speed in the development in each joints from small and oceanic species to large neritic species is the same for each species. Only second legs, and first and third legs partly, show the significant allomorphosis difference, which also have special means for ecological and morphological structures. The allomorphosis in the relation between carapace margin length and abdominal segments varies considerably in each species. It is very interesting that *T. raschii* forms the same tribe with *T. longipes* and *T. inspinata*. *T. macrura*, *T. vicina* and *T. longicaudata* form one tribe and *T. gregaria* forms itself one tribe. In the relation between the length of sixth and fifth abdominal segment, *T. gregaria* also forms tribe only itself. *T. gregaria* is only one species living in the tempeate surface waters, and posterior parts of the abdominal segments are considered as the swimming apparatus of euphausiids. If it is true, *T. raschii* takes somewhat curious position to form the same allometry line with other two oceanic species. *T. vicina* and *T. macrura* form the same tribes not only in the denticle length but also the legs and abdominal segments relationship in general. The former relation in lateral denticles is considered as the close interspecific relation and the latter are partly the similarity in ecological characteristics such as feeding and swimming in the sea.

The preliminary phylogenetic development in *Thysanoessa* euphausiids is in considered as follows. The original form of *Thysanoessa* is possibly belonging to the group of *Nematoscelis* and *Tessarabrachion* relatives.

From the ancestor of *Thysanoessa*, two branches are considered which comparatively earlier times developed to the different directions. Those are *T. longipes* and *T. gregaria* group, and *T. inermis* and *T. spinifera* group. The former stem is developing along the *Thysanoessa* line, that is oceanic and wider vertical range of distribution. The later stem is developing to the different neritic inhabitance such as *T. inermis*, *T. raschii* and *T. spinifera.*

In the Antarctic, *Euphausia crystallorophias* is living as the real neritic species. Its colonization of Antarctic waters is considered by John (1936) as the series of *E. lucens—E. vallentini—E. frigida* and this series is divided into two branchs, those are *E. superba* and *E. crystallorophias.* And the transgression of the ancestor of *E. frigida* series from the south as the *E. pacifica* series is possibly at the same time that the genus *Thysanoessa* become antitropical (Brinton, 1962b). At these time, the later stem became developing as neritic and surface living species.

T. longipes or its ancestor is considered coming from the stem different *T. inermis*-ancestors and *T. gregaria*-ancestors as it bears the male copulatory organs and preanal spines of different forms. Further the distribution of *T. longipes* and *T. inspinata* is fixed in only North Pacific. This shows the transgression of equator of these *T. longipes* group did not occur at the age of transgression of *T. gregaria* group. They possibly occupy the northern colder waters already at that times, and they shift the postulated distributions of transgression of equator at the cooling age discussed by Brinton (1962b).

Thysanoessa inermis and *T. raschii* are common in the north Atlantic and Pacific, and they had possibly contact through North pole sea still in later ages. This may be endorced by the distribution of one and two spine forms of *T. inermis* and neritic species *T. raschii.* Before the differenciation between *T. inermis* and *T. raschii*, *T. spinifera* or its ancestor is fixed as the neritic and shallow water species from the consideration on the structure of male copulatory organs and the allomorphosis of body parts. The restricted distribution of *T. spinifera* along the west coast of North America may contradict this assumption. But it is generally accepted that it is closed in Aleutian and California current, and the cold North Bering Sea and general water transport from the west to the east in the North Pacific drift may be the barriers for the extension of *T. spinifera* to the west Pacifiic (Nemoto, 1962). The position of Atlantic *T. longicaudata* is very characteristic. It is considered it comes from the way between *T. longipes* stem to the ancestors of *T. gregaria* or directly from ancestor of *T. longipes*. *T. longicaudata* completely lacks the carapace denticle but it is sometimes absent in many species which usually have carapace denticles and some species have two forms which have denticles and none (*Nematoscelis difficilis*, Mclaughlin, 1965). It is apparent that the external characters such as male copulatory organs and carapace denticles and preanal spines, the *T. gregaria* ancestor has four other present *Thysanoessa* species, *T. macrura T. vicina*, *T. parva* and *T. gregaria* at least.

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SUMMARY

Thysanoessa euphausiids are investigated under the comparative morphology and allomorphosis studies, to get general considerations on morphological and taxonomical characters as well as ecological peculiarities. The main results are summarized as follows.

1. Modified and simple key for the taxonomy of *Thysanoessa* genus is given.

2. Three main groups, namely longer, intermediate and shorter forms are found on the first antenna. *T. inermis*, *T. spinifera* and *T. raschii* form the longer group, and they run also the same allometric tribe in allomorphosis in the relation between carapace length and length of the flagellum. *T. vicina*, *T. macrura*, *T. inspinata*, *T. longipes* and *T. gregaria* form the shorter group and also the same allometric tribe. *T. longicaudata* forms different tribe apart from those two groups.

3. The shape of the rostrums, lateral denticles are examined. The position of the lateral denticle have very important taxonomical characters especially in closely related species under the evolution of the neoteny-like speciation.

4. Shape of eyes of *Thysanoessa* are very various. Neritic and shallow water

species have round and none constricted small eyes which show no sexual dimorphism. The allometric tribes in eyes are very various among each species and sex, which is possibly due to the reflection of the complex ecological characteristics.

5. Arrangement of dorsal keels and abdominal spines are examined. One and two spine forms of *Thysanoessa inermis* show the geographical cline in the North Pacific in occurrences of each form. One spine form occurrence is high in western Pacific especially in the sea of Okhotsk, in which it is ranging about 80 to 90 percent like the Atlantic specimens. But it decreases following to the east and only about 25 percent in the waters of the Gulf of Alaska. Three spine form of *T. inermis* is again described from the North Pacific.

6. *T. gregaria* stands in peculiar position among *Thysanoessa* species in the allomorphosis in telson, fifth, and sixth abdominal segments. It is possibly due to the wamer water habitat in the transition zone apart from other *Thysanoessa. T. macrura* and *T. vicina* have close relations also in those points, which shows the ecological and phylogenetic similarities are very close also in these body parts.

7. In *T. spinifera* and *T. longicaudata*, the allomorphosis in each sex is different in the relation of abdominal segments and other body parts. The dalay in the development of the carapace in males may bring this variation, and these sexual differences among allometric tribes are considered as one of speciation of the direction from the female type to the male type.

8. Preanal spines of *Thysanoessa* euphausiids are divided into three groups, according to the sexual dimorphism. It is present in *T. macrura*, *T. gregaria*, *T. vicina* and possibly in *T. parva*. Only slight dimorphism is observed in *T. inermis* and *T. raschii*, and nearly absent in *T. longipes*, *T. inspinata* and *T. longicaudata.* These sexual dimorphisms are already found still in younger adlescents.

9. Allomorphosis and structures of thoracic legs especially dactylus of them are examined. In the relation between carapace length and second thoracic legs, three allometric tribes are observed. *T. inermis* and *T. raschii* run the same line, and *T. longipes*, *T. inspinata*, *T. gregaria*, *T. macrura*, *T. vicina* and *T. longicaudata* form another tribe. *T. spinifera* forms one tribe itself. These tribes are nearly the same with the first legs, and *T. longipes* group is corresponding to the shorter dactylus group. There is no difference in the allomorphosis in third and fourth legs, but *T. inermis*, *T. raschii* and *T. spinifera* form another tribe apart from *T. gregaria* group which has shorter and poorly developed setae in those legs.

The characteristic positions of the dactylus in the first and third legs of *T. macrura* are observed.

10. The structures of the dactylus of first and second legs are investigated. The number of the spines along the inner margin of the dactylus of the first leg varies in each species, and corresponding to the shorter and longer groups of the dactylus. *T. spinifera* and *T. raschii*, the longer group, have 8 to 14 spines and *T. inermis* has 5 to 8 spines. The shorter group has less than 9 and *T. gregaria*, *T. macrura* and *T. vicina* have only 1 to 3 inner spines.

The dactylus of second legs is long in *T. inermis* and *T. raschii,* and *T. spinifera* has rather shorter dactylus. Other *Thysanoessa* euphausiids have shorter dactylus and elongated merus and carpus, which may be the simpton of carnivorous habit.

11. The first and second maxilla of *Thysanoessa* species show the carnivorous and hervivorous characters, which stand the intermediate position between the carnivorous euphausiid, *Nematobrachion* and the mainly hervivorous euphausiids *Euphausia* and other species.

12. The inner structure of the stomachs of *Thysanoessa* euphausiids has special row of spines which is named as ' Cluster spines '. This row of cluster spines is found along the base part of the side plate of inner wall of the stomach. The isolated tough spines are also found along the anterior part of the side plate, which also very effective for the crashing their foods such as diatomes and other hard shell organisms. But *Thysanoessa* euphausiids have no circle ' cluster spines ' in the anterior part of the side plate.

13. Male copulatory organs of *Thysanoessa* prove also *T. macrura T. vicina* and possibly *T. parva* are belonging to the relative of *T. gregaria. T. longicaudata* stands peculiar position, and *T. inspinata* shows close similarity to *T. longipes.*

14. The similarity and difference in allomorphosis and morphological study are compared to get characteristics and phylogenetic considerations.

From the morphological observations, three main types are found. *T. longipes, T. inspinata* and *T. longicaudata* form one group, *T. raschii, T. inermis* and *T. spinifera* second group, and *T. gregaria, T. vicina* and *T. macrura* (possibly *T. parva* is included in this group) third group. The most typical difference among those three groups is the sexual dimorphism in preanal spines. The characteristics expressed in preanal spine and male copulatory organs of *T. longicaudata* suggest that it comes from the *T. longipes* ancestors rather than *T. gregaria* group.

15. General distribution of each species shows the possible correlation between the evolution and present distributions, suggesting that *T. vicina* and *T. macrura* are fixed in the Antarctic before the transgression of the equator by *T. gregaria*, and the speciation of *T. inspinata* from *T. longipes* is possibly later than that age in the North Pacific.

16. The preliminary consideration of the phylogeny of *Thysanoessa* is stated. *T. longipes* and *T. gregaria* groups are developing along the *Thysanoessa* line, which is oceanic and wider vertical range of distribution, in which *T. longipes* and *T. inspinata* or their ancestor is coming not through the *T. gregaria* or *gregaria* ancestor, although some morphological characters are related to it. *T. longicaudata* also comes from the way between *T. longipes* and the ancestors of *T. gregaria* or directly *T. longipes* group but possibly not from *T. gregaria* group. The close relations between two groups, *T. longipes* and *T. inspinata*, *T. macrura* and *T. vicina* may be explained as the neoteny type evolution.

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