ON THE SPECIFIC VALIDITY IN SPECIES PAIRS OR TRIOS OF PLANKTON ANIMALS, DISTRIBUTED RESPECTIVELY IN DIFFERENT BUT ADJOINING WATER MASSES, AS SEEN IN CHAETOGNATHS[1]

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CONTENTS

Introduction

In mentioning a great morphological change between the summer and winter generations of an enclosed form, f. *tumida* (Tokioka), of *Aidanosagitta crassa* (Tokioka), that was observed in the Lake Notoro in Hokkaido Island, I referred to the possibility that a similar morphological change might be seen between the different generations of the same stock of some eurythermal and euryhaline chaetognaths, developed respectively in different but adjoining water masses (Tokioka 1974, p. 278). This seems, however, to require more detailed explanations that are to be given on the following pages.

Generations and Intermediate Types in *Aidanosagitta crassa* f. *tumida*

One of the most striking points in the morphological change in *Aidanosagitta crassa* f. *tumida* may be the adsence of any intergrades between the summer and winter types. However, as there were eight months between the summer (August 27, 1963)

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and spring (May 9, 1964) observations, it is possible that there might be an interven-
ing generation (or generations) of an intermediate feature (or of gradually transitional
features) between the two observed generations.

The size distribution of animals was compared between the two samples respectively
hauled from the same depth (18 m to surface) at the same station (the deepest point
of the lake) in different seasons.

	<1 mm	1–1.5 mm	1.6–2.0 mm	2.1–2.5 mm	2.6–3.0 mm	3.1–3.5 mm
August sample 1963	1	78	67	66	54	64
May sample 1964	–	–	–	–	1	17

	3.6–4.0 mm	4.1–4.5 mm	4.6–5.0 mm	5.1–5.22 mm	
August sample 1963	72	50	16	3	= 471
May sample 1964	67	33	3	–	= 121

The quantity of sample decreased in May to about a quarter of that in August. There
were two modes in August, with a peak in 1–1.5 mm and 3.6–4.0 mm respectively, but
only a single in May, with a peak in 3.6–4.0 mm. As the specimens of the winter–type
caught in March 1938 had already grown up to 4.1–4.3 mm in body length at the
water temperature of -1.3 to -0.5 °C, it seems that the animal can grow at much lower
temperatures, but never mature in March to May, when the water temperature is
maintained generally below 10 °C, except in the very surface layer. The existence of
the winter type was confirmed in the middle of June 1932, when the water tempera-
ture was 8.7 °C at the bottom, but 23.8 °C at the surface. On the other side, the
summer–type specimens seemed to survive the autumn till the end of October, when
the water temperature was still 14.6 °C in the lower layer, but 11.5 °C at the surface in
1932 (Tokioka 1974, p. 276; foot note and Table 3). These seem to show that the de-
velopment and survival of the summer type are possible in the temperature range
approximately above 14 °C, and that the development and growth of the winter type are
possible at very low temperatures but the maturation is limited to the temperature
range above 10 °C.

The winter type having attained the adult state will mature in late May to early
June in lower to middle layers of a little higher salinity and of the temperature higher
than 10 °C and probably release eggs in the surface layer of slightly lower salinity and
much higher temperature. The eggs will develop in the upper layer to the summer
type at water temperatures above 14 °C. The ovary will develop to the Stages III and
IV in the size range of 4.2–4.5 mm (Tokioka 1974, p. 274). If the maturation of whole
ovarian ova is achieved in a relatively short time span, though not simultaneously, and
the animals die out shortly after the release of whole genital cells, then the individuals
larger than 4.2–4.5 mm should decrease rather sharply. Under these suppositions, the
first mode may be suggested to be continuous to the last one in the size distribution
of animals in August; in other words, the smaller individuals forming the first mode

might belong to the next generation following the larger individuals constituting the last mode. If such a simple aspect is accepted as a truth, then it is supposed that there were only two generations of the summer type till the end of August, an aged generation and a very young one just starting. Similarly, the simpler size distribution of the winter type in early May seems to imply the existance of only a single gener-ation of this type. The question seems to concern the succession from the summer type to the winter type in the two months, September and October, but the existence of another generation of the summer type is improbable in these two months when the water is being cooled rapidly.

Small individuals of the second generation of the summer type at the end of August will grow up in the following months, but moving down to lower layers where the salinity is a little and the temperature is considerably higher. They will mature and release eggs there, probably in (? late September to) October. The eggs will develop to the winter type in the lower layer where the water temperature drops gradually below 10°C. They will contipue to grow in the winter months in lower layer, but never attaining maturity. Thus, the data available at hand seem to suggest that there are two generations of the summer type and a single generation of the winter type alternating each other, but without producing any intermediate types between them. The complete absence of intermediate types is evidently due to the threshold effect of environmental factors on the development of the animal, as it was suggested by Murakami (1959) to explain the relation between *Aidanosagitta crassa* and its form *naikaiensis*, although at present there are no actual data available to show the temperature (and probably salinity) and developmental stage critical for respective types. Only it may be said safely that a significant temperature for the survival of the summer type might be about 14°C, and that the critical temperature for the winter type is probably lower than 10° C. Adult individuals of the summer type and juveniles of the next generation over a certain critical stage, still living at the end of October, will soon be killed by cold.

Typical Form of *Aidanosagitta crassa* and Its Form *naikaiensis*

Evidently, this kind of distinct morphological change seen alternately between the generations of the same stock of the same species developed under different conditions in the same water body is a popular phenomenon for many eurythermal limnoplankters such as some cladocerans and rotifers. As already suggested in my previous paper (Tokioka 1974, p. 278), the mechanism explaining this phenomenon seems to be appli-cable to the relation between the typical form of *Aidanosagitta crassa* and its form *naikaiensis*. The opinions of Kado (1953, 1954) and Murakami (1959) suggesting that these are nothing but only different generations of the same single species developed in different circumstances, the typical form developed in the cold winter season, while f. *naikaiensis* in the warm summer season, should be accepted. In this case, however, the different forms seem to occur separately in adjoining areas (and thus in somewhat

different water masses in a strict sense) as well as in the same water body, though generally it is rather hard to define any distinct water body in embayments open rather widely to the extensive sea area, because of the difficulties of estimating the degree of water interchange. General occurrences of f. *naikaiensis* in rather strongly protected embayments and frequent appearances of the typical form of *Crassa* in the sea areas, rather open as Mutu Bay, Ise Bay and the Yellow Sea (surface layer), seem to support this supposition, though the latter seem to be limited to the months of lower water temperatures. Further, it seems likely that the salinity in the area and at the time of occurrences of the typical form of *crassa* is slightly lower than in the protected area in the warmer season, where f. *naikaiensis* is found abundantly. There have been reported intermediate forms between the typical form of *crassa* and f. *naikaiensis*, but very rarely. This seems to justify the application of the threshold effect to the relation between these forms.

Sagitta tenuis and Sagitta friderici

Sagitta tenuis Conant had been reported in the Atlantic mainly from the coastal waters in lower latitudes, while *S. friderici* Ritter–Záhony from the Caribbean Sea, the neritic waters of Northwest to Southwest Africa and the Mediterranean Sea, before it was reported in the Pacific by Bieri (1957) under the specific name of *tenuis* from the neritic waters of Peru. Prior to this, the same chaetognath had already been described by Michael (1911), but under the name of *bipunctata*, on the specimens collected off California. The typical specimens of *S. tenuis* were reported later in the Pacific from Scammons and Manuela lagoons, Baja California (Tokioka 1959). The relation between *S. tenuis* and *S. friderici* has been discussed repeatedly by a number of specialists of Chaetognatha (for details refer to Tokioka 1961). Some researchers regard these two species as merely ecological forms of the same single species, while others admit these two as distinct species, and I had been included in the latter. However, I was forced to change my opinion by confirming a great morphological variability in f. *tumida* of *Aidanosagitta crassa* and also by suspecting a similar phenomenon between the typical form and f. *naikaiensis* of *crassa*. As suggested already in my previous paper (1974, p. 278), *tenuis* and *friderici* are very probably ecological forms of the single species *Sagitta tenuis*; *tenuis* is the typical form of the species developed limitedly in embayments in lower latitudes and of higher water temperature (and probably salinity), while *friderici* is the form developed in the open neritic waters of lower temperature (and probably salinity, too). The distributional areas of these two forms are adjoining each other. The distributional range is much more extensive in *friderici* than in *tenuis*, and this might insinuate the invasion of *friderici* into embayments. This contrasts with the case of *Aidanosagitta crassa*, in which the distributional range is more extensive in f. *naikaiensis* than in the typical form.

The relation between *tenuis* and *friderici* may be explained best in lower latitudes

in the eastern Pacific. So far, *tenuis* has been recorded from Scammons and Manuela lagoons in Baja California and from near the Port of Talara, Peru, under the name of *S. popovicii* Sund (Sund 1961), and is characterized in the matured state by smaller size (6 to 11 mm), a little longer tail segment (about 30 % of the total body length inclusive of the tail fin), 7 to 9 hooks, (4)5–6(7) anterior and 8 to 14 (roughly increasing with the body size) posterior teeth, and smaller ratio TC (anterior part of the posterior fin along the trunk / posterior part of the posterior fin along the tail segment x 100, 60.4–91.5). While, *friderici* has been found from the extensive neritic area from Monterey (Bigelow and Leslie 1930, as *S. bipunctata*) in the north to off Chile in the south, and is characterized in the matured state by larger size (up to 19 mm), relatively shorter tail segment (around 26 %), (5)6–9(10) hooks, 4–7 to 7–11 anterior and 8–14 to 14–25 posterior teeth, and larger ratio TC (76 to 141.7).

The larger size of matured individuals is quite general in the waters of lower temperature. The longer tail segment and the smaller ratio TC concern the rapid maturation of the ovary in embayments of higher temperature, that in turn seems to check physiologically and mechanically the growth of the trunk. In most chaetognaths, the relative length of the tail segment decreases with the animal size; this shows evidently that the growth rate of the trunk is larger than that of the tail segment. The maturation of the gonad will depress the growth of general body structures. Moreover in chaetognaths, the ovary is firmly connected by the mesenterial membrane to the body wall along the whole exterior side so that at least the posterior part of the trunk including the ovary inside will hardly be extensible after the ovary has become solid by maturation. Thus, the rapid maturation of the ovary in the circumstances of higher temperature will bring about the earlier stop of the growth of the animal, and the result will be seen in the relatively shorter trunk, especially in the shortening of the anterior part of the posterior fin along the trunk portion including the ovary within. On the other hand, the adult armature is seemingly achieved with gonadal maturation. Thus, in the same range of body size, *tenuis* in embayments shows a tendency to bear a slightly heavier teeth–armature than *friderici* in the open area. This is well contrasted with the effect of retarded maturation in the cold season, seen in the winter generation of *Aidanosagitta crassa* f. *tumida*.

There are no significant differences between *tenuis* and *friderici* in the general essential body structures such as the shape and situation of the seminal vesicle and the corona ciliata in the same range of body size.

The most noteworthy is a so prominent variability seen in the number of hooks and anterior and posterior teeth in *friderici*. Individuals of *friderici* found in the blue–green water along southern California and named by Alvariño (1961) *euneritica* are probably the largest type in the species, attaining to 19 mm in body length; they are provided with (6)7–9(10) hooks and 2–5 (rarely up to 7) anterior and 5–9 (rarely up to 14) posterior teeth. The teeth seem slightly fewer in these than in *tenuis* in the same size range. This feature, together with larger body size, is evidently due to lower tempera-

ture of the blue-green water of the California Current. However, in *friderici* collected
from the Shell Back area extending from off Baja California to off Peru, the armature
is variable. It resembles closely that of *tenuis* in some, but in others with 6 hooks the
teeth armature is relatively heavier (Tokioka 1959, pp. 360–362). Further in larger
specimens from the area and off Peru (Tokioka 1961) the anterior and posterior teeth
are more numerous than in *tenuis* and much more than in *friderici* found in the Cali-
fornia Current; these were named by Sund *peruviana* (Sund 1961). The above-men-
tioned variation in *friderici* is expressed just exactly by Bieri (1957, pp. 261–262) as
"In the 1941 Peru material a complete set of intergrades exists between S. *friderici* to
the south and S. *tenuis* to the north. The same situation has been observed by the
author in samples taken off Lower California except that there the *tenuis*-like form is
to the south and the *friderici*-like form to the north." This is quite natural, when the
water temperature in the extensive *friderici*-area in the eastern Pacific is checked; the
temperature is higher in the middle part of the area, but lower in both the California
Current in the north and the Humboldt Current in the south; and *tenuis* is the form
developed in the protected waters of higher temperature. Although the variation seems
rather gradual in the case of *tenuis* and *friderici*, the threshold effect cannot be exclud-
ed from the explanations of the relation between *tenuis* and *friderici* and further of
relations between different types of *friderici*, because the *friderici*-area includes at least
three different water masses adjoining each other in a series; the blue-green water of
the California Current, the tropical waters of Panama Bay enriched by upwelling, and
the Humboldt Current off Peru. For further details of variation in *friderici* refer to
Tokioka 1961, pp. 8–11. Bieri, who showed that S. *tenuis* and S. *friderici* were ecotypic
variants of a single interbreeding population or species and considered that the smaller
tenuis-form was a warm water form (1957), changed his opinion and admitted the
validity of S. *friderici* (1959), because larger *friderici* was distributed as far north as
the Gulf of Guayaquil in his 1952 material. He did not need to change his opinion;
his opinion and explanation of 1957 were very exact actually. The only thing he need-
ed was to add a single word "protected" to define the typical smaller form *tenuis* as a
form developed in the "protected" warm water.

Zonosagitta bedoti and Its Allies

The group of *Zonosagitta bedoti* (Béraneck) and its allies might also be included
in the present discussions. As the original description of *Sagitta bedoti* made by
Béraneck (1896) was far from complete in mentioning the details of morphology, that
are requested these days to define a species, the real image of the species is somewhat
vague. Only the reexamination of the type specimen will give a decisive conclusion.
But, when this cannot be done, it may be a way to follow the earliest exact description
which can be used to define the species in question, as in the case of *Sagitta bip-
unctata*. For *bedoti*, the description given by Ritter-Záhony (1911), largely based upon

the Fowler's data (1906) of the Siboga material, may fit this purpose. The descriptions of the anterior and posterior fins, collarette, corona ciliata, anterior end of the intestine, seminal vesicle and the armature given by Ritter-Záhony (1911, pp. 20–21), together with his text-figure (fig. 18), seem to show exactly the essential morphologies of *bedoti*, though he wholly borrowed the Fowler's data of the armature. Especially, his statement on the anterior fin and the armature formulae presented by Fowler and admitted by him are seemingly very effective in making up the image of *bedoti* probably defined in the mind of Ritter-Záhony.

No comment was made by Béraneck, and by Fowler either, as to the anterior end of the anterior fin. According to Ritter-Zahony, the anterior fin begins "etwas hinter" the anterior end of the ventral ganglion. Probably, the interpretation of the words "etwas hinter" will be one of the most essential discussions on the *bedoti*-group. As this author had noted already the taxonomical importance of the anterior reach of the anterior fin, "etwas hinter" might mean a small distance less than a *half* of the length of the ventral ganglion as it is seen in his fig. 18.

The armature formulae given by Fowler (1906, p. 7) and admitted wholly by Ritter-Zahony as the basis of *bedoti* included 16–18 mm long individuals. Fowler regarded *Sagitta bipunctata* reported by Aida from Misaki, Japan as *bedoti*. Especially, Fowler noted a single 11 mm long specimen as an individual with *abnormal* number of teeth; its armature formula was $6\text{--}7 \ \dfrac{10\text{--}11}{31\text{--}33}$.

	Body length	Tail segment	Hooks	Anterior teeth	Posterior teeth
	5 mm	35%	6–7	5	10
A	6	33	7	6	12
	7	28	6–7	7–8	16–20
	8	29	6	7	21
	11	27	5–7	9–11	18–27
B	13	23–30	6–7	10–13	20–32
	14	21–28	6–7	9–10	24–29
	15	26	6–7	10	27
	16	28	6	10	21
C	17	23	6	10–11	17–21
	18	22	6	9	21

(After Fowler 1906, Siboga specimens)

The formula presented by Béraneck $(7 \ \dfrac{8\text{--}10}{18\text{--}22}$ in 13 mm long individual, with 25 % tail segment) merges wholly in the formulae shown above. The Fowler's formulae themselves might include some other specimens of the type regarded by him as abnormal, as seen in (B) in the formulae.

The distribution of the form which is provided with the anterior fin reaching more anteriorly over the middle of the ventral ganglion and with the armature formula like (A) and (C) in the Fowler's formulae, covers nearly the whole neritic waters of temperate Japan. In the waters of lower temperature, such as the Yellow Sea, specimens much larger than 18 mm are met with abundantly, but their armature formulae (D)

are quite continuous to (C) in the Fowler's formulae.

	Body length	Tail segment	Hooks	Anterior teeth	Posterior teeth
C′	14.5–16.2 mm	22.8–23.5%	6–7	9–11	17–20
	16.5–17.0	23.0–25.3	6–7	8–11	16–24
	17.5–17.7	22.9–23.2	6–7	10–13	20 24
	18.0–18.5	21.6–25.0	6–7	11–13	19–24
D	25.0–26.9	24.8–26.4	6–7	10–13	24–24
	27.6–28.1	24.2–25.4	6–7	12–12	22–25
	28.5–29.8	23 8–24.2	6–7	12–13	23–24

(After Tokioka 1940, p. 40 ; Japanese specimens)

A few individuals somewhat like the unusual specimen noted by Fowler had been collected in Sagami and Suruga Bays, the neighbouring waters of Seto, and the western waters off Kyusyu Island, but left undescribed till an enough number of specimens were found in the plankton samples hauled in the waters surrounding the Palao Islands (Tokioka 1942, p. 543). These individuals are characterized by much smaller size of matured specimens, 11 mm at the maximum in the Palao material; the smallest mature specimen was 7.69 mm in the Arafura material. The anterior fin begins behind the middle of the ventral ganglion and the posterior teeth are more abundant as compared with *bedoti* in the same range of body size, especially those living in the Japanese waters. These were named f. *minor* of *bedoti* (Tokioka 1942, pp. 541–543).

Body length	Tail segment	Hooks	Anterior teeth	Posterior teeth
4.74–4.91 mm	29.5–31.0%	6–7(+1)	5–6	9–10
5.0 –5.53	28.0–28.6	7–7(+1)	6–7	12–13
6.3 –6.6	27.0–28.0	7–7	7–8	13–20
7.0 –7.45	23.6–26.8	7–7(+1)	8–10	18–20
7.51–7.52	28.2–28.9	7–7	7–9	15–19
8.5(2)	25.3–29.4	7–7(+1)	11–11	24–26
10.8(2)	25.9–25.9	6–7	11–13	25–32

(After Tokioka 1942, p. 543 ; Palao specimens)

Body length	Tail segment	Hooks	Anterior teeth	Posterior teeth
5.6 –5.67 mm	29.1–29.5%	7–7(+1)	5–7	9–13
5.92–6.35	29.9–30.1	6–7(+1)	7–9	17–17(+1)
7.26–7.32	29.6–29.9	(+1)6–7(+1)	7–9	15–17
7.69–7.73	29.2–29.6	(+1)6–7(+1)	10–10(+1)	20–21
8.3 –8.5	28.7–29.3	(+1)6–7	9–11	20–22
8.5 –8.69	28.2–29.0	(+1)5–7	9–10	20–22
8.7(2)	27.7–29.2	7–7	10–11	20–21
8.78–9.0	27.7–28.9	6–7	10–10	20–22
9.2 –9.28	26.6–27.4	(+1)6–7	10–10	21–22
9.45–9.83	27.3–28.6	7–7	9–10	22–23

(After Tokioka 1942, p. 546 ; Arafura specimens)

In 1965, a form further smaller than f. *minor*, less than 8.5 mm in adult size and attaining the maturity at only 6.1 mm, was found in the very inshore water of the salinity 23.0 to 27.0 ‰ and named f. *littoralis* (Tokioka and Pathansali 1965). This is separable very clearly from f. *minor* by rather distinct collarette developed around the

neck and slightly more hooks (8-9), although the general body appearance and the teeth formula are quite the same as in the latter; the anterior fin begins on the ventral ganglion but near its posterior end and the rayless-zone is narrower in both lateral fins.

The typical form of *bedoti*, f. *minor* and f. *littoralis* are clearly inhabitants of the neritic waters or the waters of a nature somewhat neritic, as none of these forms has ever been found in the vast central area of the oceans. Excepting the records of a few individuals drifted out into the marginal area of the oceanic regions, the typical form is distributed limitedly to the temperate to tropical neritic waters of the West Pacific and Indian Oceans along the continents and big islands of Japan and the Malay Archi pelagoes, while f. *minor* is seemingly confined to the tropical waters neritic or rather oceanic but somewhat enriched and adjoining the neritic waters. The salinity is very probably slightly higher in the waters inhabited by f. *minor* than in the neritic waters inhabited by typical *bedoti*. Forma *littoralis* is clearly a special form confined to the waters of markedly lower salinity (and protected) in the tropical region of the "*bedoti*-area" of the Indo-Pacific. All these waters are adjoining one another, and the species *bedoti* seems eurythermal and euryhaline. It is very possible that the individuals developed in the usual neritic waters will bear the feature of the typical form described by Ritter-Záhony and mature at the body length over 10 mm, while those developed in the tropical waters adjoining the neritic waters and of slightly higher salinity will bear the appearance of f. *minor* and mature at 8-10 mm, and the individuals developed probably in the protected waters of much lower salinity, so far known from around Peninsular Malay, will show the feature of f. *littoralis*. And further, there may be a significant variation in body length and a little less variation in the armature within the range defined for respective forms, according to the environmental differences. For example, typical *bedoti* is generally much larger in the Yellow Sea of lower temperature than in the tropical neritic waters and specimens of f. *minor* sparsely occurring in the waters of the Izu District, Middle Japan are significantly larger than those collected from the neighbouring waters of the Palao Islands and the Arafura Sea.

The problems as to the *bedoti*-group have been made somewhat complicated by establishment of *nagae* and *bruuni*. Alvariño (1967) regarded f. *minor* as the type of the species *bedoti* and treated the above-mentioned typical form of *bedoti*, definable on the description and text-figure given by Ritter-Záhony and the (most part of) armature formulae given by Fowler, and seemingly inclusive of the individual described by Béraneck, as a new species and named it *nagae*. Her *bruuni* resembles f. *littoralis*. If it is acceptable that the single neritic species *bedtoi* can bear different features in different water masses adjoining one another, without producing any intermediate forms between them, the *bedoti*-group should be composed as follows:

   Zonosagitta bedoti typical form (= *nagae*)
       f. *minor* (= *bedoti* of Alvariño)
       f. *littoralis* (? = *bruuni*).

If it is confirmed that f. *minor* has already been fixed as a distinct species, this form
may have a new name or may be better called *polyodon* Doncaster as suggested already
(Tokioka 1942, p. 543), because the posterior teeth (26) of Doncaster's species seem
rather numerous for its body length (12 mm)

Flaccisagitta lyra and Its Allies

Although *Flaccisagitta lyra* is an oceanic species but not a neritic one, it is eury-
thermal as seen from its wide horizontal and vertical distributions. Especially, the idea
of Furnestin (1962) suggesting two successive vertical migrations from the surface to
2000 m or more and two spawning stages in 600 to > 2000 m layer in the life history
of the same individual seems to concern this nature. There had been found a number
of individuals of *lyra*, with less connecting band between the lateral fins and without
a remarkable protrusion of the shaft edge of hooks at the basal portion covered by the
ventral column, and these were treated as *gazellae*-form of the species *lyra* by research-
ers who considered *gazellae* Ritter-Záhony was synonymous with *lyra* Krohn, because
no definite relation was confirmed between the above-mentioned two features (Tokioka
1939). However, David (1955) showed that the situation of the seminal vesicle differed
clearly between *lyra* and *gazellae* and further that *gazellae* was distributed limitedly in
the Subantarctic and Antarctic waters, but leaving the treatment of *gazellae*-type of
lyra unsettled. Further, Alvariño (1962) established *scrippsae* for the individuals of *lyra*,
occurring in the mixing waters of the Kurosio and Oyasio Currents, in their confluent
extension, or in the adjoining waters of lower temperatures; the most characteristic
feature for this new species seemed to be the existence of the collarette.

The exact situation of the anterior end of the anterior fin has been known to be
considerably variable in many species, for instance as confirmed in the different gen-
erations of the same population in the same water body in *Aidanosagitta crassa* f.
tumida, and the reach of the *long* ovary will naturally be related with the time needed
for the maturation of this organ in different environments. The existence of distinct
collarette cannot be a specific feature in *some* species, as seen in *Aidanosagitta crassa*
and its form *tumida*. Then, it is very probable that *scrippsae* separated (at least partly)
for the differences in those features represents merely the generation of *lyra* having
developed in the mixing waters of Kurosio and Oyasio Currents and of temperatures
lower than in the adjoining subtropical region much affected by the Kurosio Current
on the west side of the North Pacific, while the typical form of *lyra* is the generation
having developed in the subtropical to tropical regions and thus experienced higher
temperatures at least at some critical developmental stage.

The similar interpretation seems to be applicable to the relation between *lyra* and
gazellae in the southern hemisphere. The Subantarctic region where *gazellae* is dis-
tributed is adjoining the subtropical region in the southern hemisphere and the Ant-
arctic region is adjoining the Subantarctic, but these are separated from one another

rather sharply by convergences and divergences; moreover the difference in the situation of the seminal vesicle has been noted between *lyra* and *gazellae*. At present, I hesitate to merge *gazellae* into *lyra* for these two reasons, especially for the latter. If it had been shown in some species that the situation of the seminal vesicle is significantly variable with the environmental conditions, then I would like to include *gazellae* within *lyra*.

The *gazellae*-type of *lyra* is problematical. It has been suggested by some researchers that the *gazellae*-type of *lyra* is only a young stage of *lyra* (Alvariño 1962, p. 14). Rather, it is suggestible that the thickness of the connecting band between the lateral fins and the special structure of the ventral column of hooks are reflecting some factors of the circumstances in which respective individuals have passed their certain developmental stages. It is very desirable to gather the data of the vertical distribution of the *gazellae*-type of *lyra* in the subtropical to tropical regions. If this type is limited to deeper layers, for instance, in the Japanese waters, then it might be possible that this is a young stage of f. *scrippsae* carried there by the submerged Oyasio Current at least in the middle to southern waters of Japan as suggested by Alvariño (1962, p. 15). Further, it is very desirable, too, to see whether or not sexually matured individuals exist in the *gazellae*-type of *lyra* and to confirm the situation of the seminal vesicle if they really exist.

Other Species Pairs in Chaetognatha

In addition, there are some other species groups to which the above-mentioned explanation might be applicable. One of these is the group of *Aidanosagitta neglecta* (Aida) and its allies such as *oceania* (Gray) that is limited to the lagoon waters (and some embayments) of the tropical Pacific. To clarify the relation between these two species, it will need further materials from the tropical regions of the Indo–Pacific, though at present I *feel* that these two are already separated as distinct species, as *neglecta* is a stenothermal species limited to the surface layer of the tropical to subtropical oceanic waters of the Indo-Pacific. The relations between *Eukrohnia hamata* (Möbius) and its allies, especially *E. bathypelagica* Alvariño, *Sagitta setosa* Müller and its allies, and between *Parasagitta elegans* (Verrill) and its allies, especially *arctica* Aurivillius, might be explained in a similar way, but in this paper I want to refrain myself from the discussions concerning these, as I have not enough data of these deep-sea, European, or Arctic species at hand to make any comments on actual bases.

Stable and Variable Structures in Chaetognatha

Throughout the above-mentioned species pairs or groups, it may be seen that in spite of a very remarkable variability, there are still existing some essentially specific morphologies in Chaetognatha. It is very important to learn what kind of morphologies

are changed with environmental factors or remain unchanged. In chaetognaths, at least discussed in the present paper, a significant variability can be seen in the following structures.

(1) Size of mature individuals: Mature individuals will become larger with the prolongation of time needed for growth and maturation at lower temperatures.

(2) Relative length of the anterior fin: In the development of fins, the anterior fin appears at last and generally it is elongated with the growth. Further, the elongation of this fin can seemingly be divided into two vectors, one is the growing rate of the fin itself and the other is the effect of maturation. Generally, the growth of invertebrates will be ceased when the maturation is achieved, although the completion of adult features may be accelerated in some parts of the maturing process. The anterior reach of the anterior fin may be slightly less in the generation developed at lower temperatures, as seen in the winter type of *Aidanosagitta crassa* f. *tumida* and f. *scrippsae* of *Flaccisagitta lyra*, but also in the generation matured too rapidly in the waters of higher temperatures, as seen in f. *minor* and *littoralis* of *Zonosagitta bedoti*.

(3) The ratio TC: This seems to be related to the rate of maturation as mentioned already in detail as to *Sagitta tenuis* (see p. 397).

(4) Development of fin rays: The formation of rays is seemingly much accelerated by maturation, as seen in f. *minor* and *littoralis* of *Zonosagitta bedoti*.

(5) Tail fin: Refer to the spatulate tail fin of the winter type of *Aidanosagitta crassa* f. *tumida*.

(6) Collarette: This tissue seems to develop only at lower temperatures or at lower salinity in such species as the typical form of *Aidanosagitta crassa* and the winter type of its f. *tumida*, f. *scrippsae* of *Flaccisagitta lyra* and f. *littoralis* of *Zonosagitta bedoti*. This never means that the formation of the collarette may be an adaptation for the life in the said circumstances, because a very prominent tissue is seen in such tropical oceanic species as *Aidanosagitta regularis* and *Pterosagitta draco*.

(7) Hooks: The completion of adult structures of the hook itself may be accelerated by the maturing process as seen in *Flaccisagitta lyra*, but the variation of hooks in number seems rather complicated. Generally speaking, the hook increases in number till a certain developmental (or growing) stage, but then decreases by wearing out. There are two problems about this, one concerns the time of appearance of the peak number of hooks in life history and the other is the time of maturation. Usually, the peak comes early, and retardation of growth will generally bring about retaining of a little more hooks in individuals developed at lower temperature. But, when the increase of the hook is retarded at lower temperatures in the species in which the peak comes late, the animals might mature before the peak and then bear somewhat fewer hooks.

(8) Anterior and posterior teeth: The teeth, however, increase steadily with age and maturation in most species so that the individuals grown up rapidly at higher temperatures may bear slightly larger number of teeth than those of the same size grown slowly at lower temperatures.

(9) Length of the ovary: In the species which are provided with the ovary limited to a short posterior part of the trunk, the anterior reach of the ovary is nearly fixed. But, in those with longer ovaries, the anterior reach of the organ fluctuates somewhat. Generally, in rapid maturation at higher temperatures, therefore in smaller matured specimens, the ovary tends to be shortened, sometimes markedly, and of course includes much less eggs. The egg size might differ somewhat, but there are not yet enough data to make further discussions about this.

The essentially specific morphologies stable throughout the range of variation are as follows in studied chaetognaths.

(1) General appearance of the body: Though the proportional length of the tail segment may slightly be larger in smaller individuals matured rapidly at higher temperature, the approximate proportion of this segment in respective size ranges is fixed specifically. The stiffness and transparency of specimens are specific, too, although some delicate variation has been reported.

(2) Essential structure and arrangement of lateral fins: The distribution of the ray-less-zone is included here.

(3) Essential feature of the corona ciliata: The length of the corona will naturally be decreased and the sinuation will become less marked in smaller individuals.

(4) Outline of the pigment fleck of eyes: Stable in most species, though the individual fluctuation and the change with age should be checked in some species.

(5) Structure and situation of the seminal vesicle.

(6) Essential armature formulae: In spite of some slight differences found between individuals in the same range of body size but grown in different circumstances, the armature formula will continue roughly in a series among the different forms of different body sizes in the same species.

(7) Existence or absence of the intestinal diverticulae.

Taxonomy of the Studied Species

The taxonomy of the species discussed above may be summarized as follows:

(1) *Aidanosagitta crassa* (Tokioka)

      typical form (open waters of lower temperature)

      f. *naikaiensis* (Tokioka) (embayments of higher temperature)

      f. *tumida* (Tokioka) (embayment waters)

         summer type

         winter type

(2) *Sagitta tenuis* (Conant)

      typical form (mainly in embayment waters of higher temperature and

            salinity, = *popovicii* Sund)

      f. *friderici* (Ritter-Záhony) (open neritic waters of lower temperature)

type *euneritica* (Alvariño) (in California Current)

type *peruviana* (Sund) (in Humboldt Current)

Some other types may be defined in the world seas.

(3) *Zonosagitta bedoti* (Béraneck)

typical form (neritic waters, = *nagae* Alvariño)

f. *minor* (Tokioka) (tropical waters, but not oceanic; = ? *polyodon*
                                        Doncaster, = *bedoti* by Alvariño)

f. *littoralis* (Tokioka and Pathansali) (tropical embayment waters of lower
                                                    salinity, = ? *bruuni* Alvariño)

(4) *Flaccisagitta lyra* (Krohn)

typical form

lyra-type

gazellae-type (? young stage of f. *scrippsae*)

f. *scrippsae* (Alvariño) (marginal waters of Subarctic region, adjoining
                                        subtropical region)

Flaccisagitta gazellae (Ritter-Záhony) (already separated)

(5) *Aidanosagitta neglecta* (Aida) ⎫
                                                          ⎬ (? already separated)
Aidanosagitta oceania (Gray) ⎭

Conclusion

There have been known in many planktonic animal groups such as chaetognaths, pelagic tunicates, molluscs, crustaceans, protozoans, etc. a number of pairs, trios or groups of species that are closely related one another, but respectively living in water masses different but adjoining one another. When any twins of such pairs are neritic or eurythermal, it is worthy to check again the validity of these species. The complete absence of any intermediate forms cannot be the prove to separate the species, because the threshold effect will bring about the perfect separation in morphology.

The separation of allied species has been made in many cases for the reason that there are no intermediate forms between the two and respective forms are distributed limitedly in different water masses. I myself ever followed this (for instance, Tokioka 1959, p. 364). However, when the question concerns the neritic (inevitably eurythermal and euryhaline) or oceanic but eurythermal species, and when the twins are distributed separately but in adjoining different water masses, it is very likely that the twins are only different generations of the same single species, developed respectively under different environmental conditions. The different features are ecotypic. They are evidently only phenotypic in the case of *Aidanosagitta crassa* f. *tumida* and possibly also in some of the cases concerning the relations between the typical form of *Aidanosagitta crassa* and its f. *naikaiensis*, *Flaccisagitta lyra* and its f. *scrippsae*, and between different forms of *Zonosagitta bedoti* or *Sagitta tenuis*; in such cases the barrier be-

tween the adjoining water masses is not structured so sharply that it is very difficult to pass across it. The barrier will be strengthened by such vertical currents as divergence or convergence, and with the increase of the steadiness and distictness of these currents the interbreeding between the adjoining populations will become more difficult and the different features will become genotypic. This might be the case for those, in which the distributional areas of two forms are far separated by another intervening form. And it is not deniable that these are showing some significant step in the specific differentiation. Anyhow, in checking actually the validity of those species, the crucial examination of the nature of differentiated morphologies will be the only clue.

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