Subspecific Differentiation and Ecological Characteristics of *Capitella capitata* (Fabricius, 1780) (Polychaeta, Capitellidae)

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Capitella capitata (Fabricius) has been collected from Dalian, Yantai and Qingdao in the Yellow Sea and Dachen Island, Zhejiang in the East China Sea during the invertebrate collecting trips organized by the Institute of Oceanology since the 1950s, where its number is absolutely dominant in the polluted waters. There have been a number of reports of this species in overseas, but none in China. Apart from describing the morphological and ecological characteristics of *C. capitata* in China seas, this paper presents a preliminary discussion of subspecific differentiation of this species, based on observation of preserved specimens in the Zoological Institute, Academy of Sciences, USSR, collected from the Russian Far East Sea, Artic Ocean, Black Sea and Mediterranean Sea, and literature.

I. Significance of *C. capitata* as an indicator species of polluted water

Marine pollution has been studied only in the recent ten to twenty years. There have been only few studies of the association between polychaetes and water pollution, except the recent works by Reish[35-40] in the US and Ryonosuke Kitamori[1-2] in Japan, which noted this species as an indicator of polluted water (especially sewage related to fecal material, garbage and rotten fisheries products). Reish[35, 37] divided the polluted waters in Los Angeles, California into heavily polluted zone, polluted zone, semi-polluted zone I, semi-polluted zone II and normal zone. In the heavily polluted zone where no animal inhabits, D.O. is virtually zero. In the polluted zone there are five animal species, among which *C. capitata* is numerically dominant absolutely; the mean D.O. is 3.5 ppm, water temperature 11.2 – 25.1 °C, and pH 7.6. Ryonosuke Kitamori[1] divided the polluted waters in Hiro Bay, Setonaikai, Japan into 4 zones: 1. heavily polluted zone; 2. polluted zone; 3. semi-polluted zone; 4. normal zone. *C. capitata* is also an indicator species of the polluted zone.

II. History of research in *Capitella capitata*

Capitella capitata, belonging to genus *Capitella* Blainville, 1828 (syn.: *Lumbriconais* Oersted, 1842; *Valla* Johnston, 1865), was first described very briefly as *Lumbricus capitatus* by Fabricius in 1780, based on types from Greenland. In 1957 Van Beneden recombined these animals and merged genus *Lumbricus* into genus *Capitella*. Later on, renowned polychaetologists Quatrefages (1865), Malmgren

(1867), Claparede et Mecznikow (1869), McIntosh (1874), Ehlers (1875), Levinsen (1883) and Webster and Benedict (1884) reported *C. capitata* in different regions, respectively, but did not note the variation in setal formula in the thorax. In the USSR, Czerniavshy based on intraspecific variation published 3 variants in 1881: *C. capitata* var. *prototypa*, *C. capitata* var. *intermedia* and *C. capitata* var. *similes*, which did not gain acceptance by later researchers (McIntosh[32], Fauvel[24] and Hartman[29]). Fauvel (1927) described *C. capitata* along the European coast in detail, especially noted its thoracic setal formulae, which was a significant contribution to the study of this species. Worth noting is the work on intraspecific differentiation by Hartman since 1947, especially since 1959, which has resulted in the publication of 4 subspecies and laid the foundation for further research in the intraspecific taxonomy. Meanwhile, Reish[35-40] and Kitamori[1-2] began ecological studies of *C. capitata* in polluted waters. Because of efforts of these researchers, we have now understood some characteristics of this species. It could be used not only as an indicator of water pollution, but also as a good material to study zoogeography and evolution.

III. Morphological and ecological characteristics of *Capitella capitata* found in China seas.

Capitella capitata capitata (Fabricius, 1780) (Fig. 1-3)

Literature list omitted

Sample collection sites: Yellow Sea: Malan River, Dalian, Oct. 29, 1958 (8 specimens), Oct. 18, 1963 (about 300 specimens), Laohu Beach, Oct 17, 1963 (750 specimens); Eastern Point, Zhibu, Yantai, June 29, 1957 (1 specimen), below Mountain Yantai, lower intertidal zone, June 19, 1957 (1 specimen); to the east of Qingdao Pier, July 26, 1950 (1 specimen), May 22, 1957 (3 specimens), June 6, 1957 (2 specimens), Qingdao Sea Water Bathing Beach May 7, 1963 (1 specimen), 1962-1964 monthly samples, to the east of Qingdao Pier (> 5000 specimens). East China Sea: Dachen Island, Zhejiang, June 10, 1963 (50 specimens).

Prostomium conical, two dark eye spots prominent only in few specimens.

Thorax 9 setigers, the first 7 with fine capillary chaetae and the last two with hooks only. Dioecious, male genital pore between thoracic segments 8 and 9, with 4 bundles of stout genital chaetae, the anterior two bundles each has 5 chaetae, darker in color, pointing against each other with the two posterior lighter-color bundles (Fig. 1a). Female genital pore dorsal, between thoracic segments 7 and 8. Thoracic segments larger than abdominal segments, with especially numerous surfacial wrinkles. Abdomen long, with 5-6 times as many segments as the thorax. Hooks in both the thorax and abdomen with an apical transparent hood (Fig. 1b). Specimens from the Yellow Sea and East China Sea identical to those in Japan, normally small in size, with large individuals measuring 56 mm long and 2 mm wide (widest part of the body). Live specimens blood red, ethanol preserved specimens light yellow or pale. In Qingdao, sexually mature specimens can be collected nearly throughout the year. My observation shows that the late spermatids and sperm resemble those described by Frazen[25] (Fig. 2a,b). The oocyte large, with a diameter of approximately 20 µm (mistake in the original paper, should be 200 µm, as shown in Fig 3a), whitish and semi-translucent, deposited in a thin mud tube. Early embryos develop inside the tube. Early ditrocha larvae (Fig. 3b) found in the tube not translucent, with a preoral protochocha and preanal telotrocha. Five days later they have 2 eye spots, their gut full with oil droplets, their body enlarged, but still without segmentation or chaetae. Thirteen days later they have 13 setigers, the first 1-3 setigers with capillary chaetae only, and setigers 4-8 with hooks only (fig. 3c). At this developmental stage the larvae escape from the tube and adopt a pelagic life. We can often collect larvae of this stage through towing around Qingdao Pier.

C. capitata is a dominant species of polluted areas. In the Yeollow Sea and East China Sea collecting sites, the polluted waters are biogenic (fecal material, garbage etc.) and the substratum is black mud with a foul H_2S odor. No animal lives in the heavily polluted zone around the discharged channels, where D.O. is zero, and H_2S content high (H_2S contents are relative values measured by qualitative H2S test paper pretreated with lead acetate). In the polluted zone *C. capatata* dominates. In Qingdao, the D.O. is approximately 3 ppm, the pH is 7.6, and the chlorinity is 15.87 ppt. H_2S content is lower as compared to the heavily polluted zone. The density of *C. capitata* in April is 127,200/m^2; this species accounts for 60-97% of all groups of animals, and the biomass is 1,068 g/m^2. In Lahu beach, Dalian, the density is 75,900/m^2, and the biomass is 325 g. In the polluted zone of Dachen Island, Zhejiang (small individuals), the density is 33,600/m^2, and the biomass is 52 g/m^2. In the polluted community in Qingdao, in additional to *C. capitata*, there are polychaetes *Etone longa* (Fabricius), *Glycera chirori* Izuka, *Nephtys*1) *polybranchia* Southern, *Lumbrinereis*2) *debilis* Grube, *Polydora* (*Carazzia*) *paucibranchiata* Okuda, *Armandia lanceolata* Willey, mollusks *Venerupis variegate* (Sowerby) and *Mya arenaria japonica* Jay, crustaceans *Corophium homoceratum* Yu and *Dimorphostylis asiatica* (Zimmer). Apart from polluted areas, *C. capitata* is also found in various biological communities in the mid and low intertidal zones, such as among the roots of *Zostera* sp., among *Enteromorpha* spp., *Balanus amphitrite albicostatus* Pilsbry and *Chthamalus challengeri* Hock, albeit in small numbers.

Footnotes 1) (and 2)). We used to adopt *Nephthys* and *Lumbricornereis*. According to the rule of priority *Nephtys* and *Lumbrinereis* are valid names erected earlier, which are now used by researchers in various countries.

IV. Subspecies of *Capitella capitata*

I). Up to date *C. capitata* has the following 7 subspecies (including a new subspecies described in this article):

1. *Capitella capitata capitata* (Fabricius, 1780)

The main characteristics of this "typical" subspecies: thoracic setal arrangement being fine capillary chaetae only in the first 7 segments, and hooks in segments 8 and 9 (Fig. 4a). It mainly inhabits intertidal zone, especially estuarine low salinity, anoxic, polluted areas, and is an indicator species of polluted water.

A comparison of our specimens collected from Yellow Sea and East China Sea with those deposited in the Zoological Institute, USSR, collected from the Russian Far East seas (Sea of Japan, Sea of Okhotsk, Bering Sea), Franz Josef Is., which is quite close to the type locality (Greenland), White Sea, and Novaga Zemlya, Barents Sea shows that these specimens have very similar thoracic setal arrangement, which should belong to the same type (Fig. 4a). In addition, the specimens from Vancouver, reported by Berkeley[20], and from Alaska, reported by Pettibone[34] should also be of the same type. This "typical" subspecies thus has a continuous distribution in northern Pacific, in the east coast extending southward to California and in the west coast extending southward to Dachen Island, Zhejiang.

In 1960, Ryonosuke Kitamori[1] described a new subspecies waters (*C. capitata japonica*) based on specimens collected from Setonaikai, Japan. From the description and figures the thorax appears to have 8 segments, and the setal formulae are 6S + 2G♂ and 6S + 2H. (Since) having 8 thoracic segments is a special case in this species, I communicated with Kitamori in 1963 about this issue by letter, and in his reply he stated that his specimens all had 9 thoracic segments, (but because) the chaetae in the first segment are small they are easily mistaken as having 8 segments. Thus, the specimens from coastal Japan have thoracic setal formulae identical to those from the Russian Far East seas, and Yellow Sea and East China Seas of our country. This subspecies should thus be considered as a synonym and its use be discontinued.

2. *Capitella capitata ovincola* Hartman, 1947.

Hartman (1959) lowered the status of the new species, *C. ovincola*, described in 1947 based on specimens collected from Monterrey Bay, American Pacific coast at water depths of 60-80 m to subspecies *C. capitata ovincola*. This subspecies inhabits the egg capsules of squid *Loligo*; its segments 1 -5 have fine capillary chaetae only, and segments 6-7 have both fine capillary chaetae and hooks, and segments 8 and 9 have hooks only. The thoracic setal formulae are 5S + 2S/H + 2G♂, 5S +2S/H + 2H (Fig. 4d).

3. *Capitella capitata floridana* Hartman, 1959

Hartman (1959) also described another subspecies *C. capitata floridana* from specimens collected in the egg capsules of squid *Loligo* sp. in St. Andrew Bay, Florida. This subspecies is very small, with a length of only approximately 6 mm, and its thoracic setal arrangement is especially unique, with only fine capillary chaetae in the first 4 segments, and hooks in the subsequent 5 segments. The setal formulae are 4S + 3H + 2G♂, and 4S + 5H (Fig. 4c).

4. *Capitella capitata tripartita* Hartman, 1961

Hartman (1961) described *Capitella capitata tripartita*, based on specimens found inside the egg capsules of squid (likely *Loligo opalescens* Berry) in San Pedro (46.36 m) and Mugu Canyon (119 m), California. The adults are 9-90 mm long. In San Pedro she collected 100 specimens in total. This subspecies has capillary chaetae only in segments 1-3, and the notopodia of segment 4 have capillary chaetae only, or both the noto- and neuropodia have capillary chaetae and hooks. Segment 5 has both capillary chaetae and hooks. In segment 6, the notopodia have both fine capillary chaetae and hooks, whereas the neuropodia have hooks only. In segments 7-9 the chaetae are all hooks, or in segment 7 the notopodia have both fine capillary chaetae and hooks. The setal formulae are: notopodia 3S + 4S/H + 2G♂, neuropodia 3S + 2S/H + 4H♂; notopodia 3S + 4S/H + 2H♀ or 4S + 2S/H + 3H♀, neuropodia 3S + 2S/H + 4H♀ (Fig. 4f).

5. *Capitella capitata oculata* Hartman, 1961

Hartman (1961) described a new subspecies – *C. Capitata oculata*, based on specimens collected from 15.25 – 637 m in California. This subspecies is very small, with a length of only 3-24 mm. The eyes are present throughout the life. Its thoracic setal formulae are the same as in the "typical" subspecies: 7S + 2G♂, 7S + 2H. Interestingly, this subspecies is the host of copepod *Monstrilla capitellicola* Hartman, 1961. Among the 14,145 specimens she checked, Harman[31] found 114 specimens containing one to few parasitic *M. capitellicola*.

6. "South African" subspecies?

The specimens, collected from Table Bay and identified as the "typical" subspecies by Day (1961)[22] have unique thoracic setal formulae: notopodia 4S +

2S/H + 1H + 2G♂, neuropodia 4S + 2S/H + 3H♂; notopodia 7S + 2H♀, neuropodia 6S + 1S/H + 2H♀ (Fig. 4g). Day raised the possibility that this is a variant differentiated in South Africa1). From the description of the setal arrangement, it is very likely a subspecies formed in the southern hemisphere as a result of geographic isolation. Because the few specimens available for Day's observation, the specimens might not be representative of the sampled population. Meanwhile, due to the lack of South African specimens for comparison, we stop our note here. This issue should be further studied in the future.

7. *Capitella capitata europaea* subsp. nov. (Fig. 4c)

Literature list omitted

Sample collection sites: Mediterranean Sea and the Black Sea (Karada, Sewastopor, and Odesa – note: these are Russian place names, Latinized unofficially according to the pronunciations by JWQ, see the original paper for the Russian words). Specimens are lodged in the Zoological Institute, Academy of Sciences, USSR.

The new subspecies differs from other subspecies mainly in thoracic setal arrangement (Fig. 4c). Based on setal formulae this "European" subspecies can be further divided into two populations: (1) High salinity population (salinity > 18 ppt) around Mediterranean Sea – notopodia 6S + 1S/H + 2G♂, neuropodia 6S + 3S/H♂; noto- and neuropodia 6S + 3S/H♀. (2) Low salinity population (< 18 ppt) along the coasts of Black Sea and Sea of Azov - notopodia 6S + 1S/H + 2G♂, neuropodia 6S + 1S/H + 2H ♂; noto- and neuropodia 6S + 1S/H + 2H♀ [Fig. 4c(b)].

Geographic distribution: Mediterranean Sea, Spanish coast, England, North Sea, Sea of Azov, Black Sea.

II). Preliminary discussion of the subspecific differentiation

Given the lack of information from South America and southern hemisphere for comparison, it is difficult to provide a thorough analysis about the origin of *C. capitata* and its subspecific differentiation. Up to date it has 7 known subspecies. The "typical" species (probably the primitive one, although there is no fossil data to support) has thoracic setal formulae of 7S + 2G ♂, 7S + 2H. It is distributed in Greenland, Franz Josef Land Islands, Barents Sea, Kara Sea, White Sea, Chukchi Sea, west Pacific coast from Bering Sea, Sea of Okhotsk, Japan Sea, coastal Japan, Yellow Sea to Dachen Island, Zhejiang, East China Sea, east Pacific coast from Alaska, Vancouver to California, southern hemisphere distributed in Estrecho de Magallanes, South Georgia Is., Bouvet Island, Kerguelen Island(in the literature, the thoracic setal arrangement in the specimens from southern hemisphere is usually unclear) (Fig. 5). This "typical" subspecies is eurythermal and has a wide distribution. It has a center of modern geographic distribution in cold temperate regions and is bipolar; it has not been reported from the tropical seas. In Feb. 3, 1964 in Qingdao, when the temperature of coastal water reached -2 °C, we were still able to collect female worms whose bodies full of mature oocytes, indicating it was still reproductive at this low temperature. Thus, it is beyond doubt that *C. capitata* was soriginated as a cold water species. From the current distribution pattern, it appears that this species had a continuous distribution in ancient times from Greenland, Barents Sea, Kara Sea through Chukchi Sea to the Pacific, and currently this species still forms a continuous distribution along the east and west coasts of the Pacific. In addition to temperature, anoxic polluted environment is also an important determinant of the distribution of this "typical" subspecies. Under favorable temperature conditions, C. capitata can thrive in anoxic, h2S rich water. The specimens reported by Reish[35-40] and Kitamori[1-2] from the polluted waters all belong to this subspecies. Up to date no other subspecies have been found in polluted waters.

Subspecific differentiation has not been found along the western Pacific coast as the specimens from Baring Sea to Dachen Is., East China Sea all belong to the "typical" subspecies. This is probably due to the lack of research in this region. In California, east Pacific coast sympatric subspecific differentiation was found at the same time; up to date there are 4 subspecies (localities in Table 1): *C. c. capitata*, *C.c. ovincola*, *C.c. tripartita*, and *C.c. oculata*, which is an interesting phenomenon requiring further study. With exception of the "typical" species, which inhabits coastal polluted zone, the other three subspecies have all been differentiated due to a parasitic relationship. *C. c. ovincola* and *C. c. tripartita* have significant genetic differentiation due to a parasitic life inside the egg capsules of squid *Loligo*; whereas *C. c. oculata* itself is a host of a species of copepod; (these relationships) are discussed below. *C.c. ovincola* has a farther distribution (36 °N, 121 °W), a body length reaching 60 mm, and was found in the egg capsules of squid *Loligo* sp. at water depths of 60-80 m. *C.c. tripartita* was found in San Pedro (33° 38' N, 118° 14' W, 46.3 m) and Mugu Canyon (34° 05' N, 119° 05' W, 119 m) in egg capsules likely to be *Loligo opalescens*. Although this above two subspecies were both found in squid egg capsules, the areas are different and the *Loligo* species are probably different. Their morphology differs significantly (Fig. 4d and f). According to the thoracic setal formulae they should belong to different types; furthermore, the neuropodia of *C. c. ovincola* are relatively thick and large. These two different subspecies were probably formed as a result of separation due to parasitic life in the egg capsules of different species of *Loligo*. Unfortunately the identity of the *Loligo* spp. remains unknown. This issue should be studied further. The main characteristic of *C. capitata* is anoxic, which is also shared by the two parasitic subspecies living inside squid egg capsules. Worth noting is *C.c. oculata*, a highly differentiated subspecies with a vertical distribution of 637 m. It is no longer anoxic and can live in deeper waters, and has developed sense organs – eyes, which are present throughout the life. This subspecies is small, with a length of only 3-24 mm, and setal formulae completely identical to those of the "typical" subspecies. Interestingly, Hartman, after observing a large amount of specimens (population density 60,000 /m^2), found this subspecies to be the host of copepod *Monstrilla capitellicola*, indicating it is special physiologically and ecologically. In summary of the above, the 4 subspecies found at the same time along California were not formed as a result of geographic separation. They involve complicated biological issues, should be regarded as sympatric ecological and physiological subspecies, but could have a phylogenetic relationship as well (sorry this is a direct translation – be honest I don't fully understand this sentence).

Along Florida, west Atlantic coast and Texas, two species of *Capitella* have been reported. *C. capitata floridana*, reported by Harman[28] in 1959 based on specimens collected from St. Andrew Bay inside egg capsules of *Loligo* sp., has thoracic setal formulae significantly different from those of other subspecies. In addition, its size is very small, with a length of 6 mm only. Again this is another ecologically and physiologically distinct subspecies. Worth noting are the specimens Hartman [28] collected from Port Aransa, Texas and Andrews Bay, Florida and identified as the "typical" subspecies, which have somewhat different setal formulae. Although in the notopodia the formula is 7S + 2H; but in notopodia it is different: 6S + 3H (Fig. 4b), which resembles that of the "European" subspecies in the Black Sea and the Mediterranean Sea, which also has fine capillary chaetae in the first 6 thoracic segments (6S), but different patterns in the 3 subsequent segments: 3S/H or 1S/H + 2H. From this analysis it appears that this is likely a transitional region for *C. c. capitata* and *C. c. europaea*. We suggest that the differentiation of this transitional type be related to water temperature. *C. capitata* originally is a cold water species. In the west Pacific coast where its distribution extends to Dachen Is. at 28 °N, there has not been a report of such transitional type. However, in east Pacific coast the subspecific differentiation occurred at 36 °N. In addition to more research work, this may be related to the higher temperature in waters of the same latitude along the east coast. Texas and west coast of Florida are located in tropical eastern America-Asia region, with high water temperature, which might have stimulated the formation of the transitional type. *C. c. europeaea* is morphologically distinct from the "typical" subspecies. From current distribution pattern it appears to have been formed as a result of geographic separation.

In short, many issues are involved in subspecific differentiation. Geographic separation should not be the only cause of such differentiation. Other complicated biological and genetic mechanisms may be involved. Bacci (& La Greca) (1953) used genetic and morphological evidences in a study of the subspecific differentiation in *Ophryotrocha puerilis* Claparede et Mecznikow (Dorvilleidae). Due to the lack of specimens from the east Pacific coast for comparison, the discussion in this article should be regarded as preliminary, and a further discussion should be pursued when more information is available in the future.

V. Summary

1. The *C. capitata* reported first time from Yellow Sea and East China Sea of our country is identified as the typical subspecies *C. capitata capitata* (Fabricius), which has a wide distribution in northern Pacific. It is numerically dominant in the polluted waters of the east and west coasts of the Pacific where oxygen levels are low and H_2S levels high, and it can thus be used as an indicator of marine polluted water.
2. Up to date 5 subspecies of *C. capitata* have been described, among which *C. capitata japonica* Kitamori, 1960 is a synonym of the "typical" subspecies. The author, after comparing specimens from the Black Sea, Mediterranean Sea, Barents Sea and Russian Far East seas, erected *C. capitata europaea* subsp. nov. for specimens from the Black Sea and European Mediterranean Sea, and constructed a diagram to illustrate the thoracic setal arrangements for the different subspecies.
3. This article presents a preliminary discussion about the origin and subspecific differentiation in *C. capitata*. This species is bipolar, with a modern distribution center in cold temperate northern Pacific. An analysis of the 4 subspecies in California indicates they were not formed by geographic separation, instead (the subspecies differentiation) might be related to deeper biological issues. They are sympatric ecological and physiological subspecies, and may have close phylogenetic relationship, especially for *C. capitata oculata*. The west coast of Florida and Texas may be a transitional region for *C. capitata capitata* x *C. capitata europaea*.

References omitted.
English abstract omitted.

Figure legends not translated because they have both English and Chinese versions. Table 1, To simplify the table I have only translated the words in Chinese.

Subspecies	Collection locality	Water depth (m)	Remarks
C. c. capitata	Los Angeles … and San Pedro to New Port …	Intertidal polluted zone	
C. c. ovincola	Monterrey Bay …		Parasitic inside the egg capsules of squid *Loligo* sp. …
C. c. tripatita			Parasitic inside the egg capsules of a squid likely to be *Loligo opalescens* …
C. c. oculata			Host of copepod *Monstrilla capitellicola* …

End of paper

Remarks by JW Qiu:

This article was translated by Jian-Wen Qiu from the Chinese version of the paper published in Oceanologia et Limnologia Sinica 6(3): 260-271 in 1964. Sergio Salazar supplied a pdf file of the original paper, which was kindly provided by Julia Dunaeva, librarian in the Zoological Institute of Saint Petersburg, Russia. The translation was prompted by the comments of Sergio Salazar, who initiated the discussion of the taxonomic problems with *Capitella capitata* in the polychaete discussion group in July 2006. We hope this will help those who determine to clarify the taxonomic confusion with this important species. Although the work was conducted in the early 1960s, some conclusions may still be valid, i.e., it is a cold water species and the larvae of dominant form along the coasts of Yellow Sea leave the adult tube when they have about 13 setigers. The following paper contains more updated information about this species in Qingdao – note the paper is in English and it reports three sibling species.

Wu B, Qian P, Zhang S (1988) Morphology, reproduction, ecology and isoenzyme electrophoresis of *Capitella* complex in Qingdao. Acta Oceanol Sinica 7 (3): 442-458.

Anyway, please let me know if you need clarification with the translation. Sergio has also taken the trouble of converting the original file in Chinese into a small pdf file so that it is easier to download from a website or send through e-mail.

Best wishes,

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