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Revision of the genera *Crangon fabricius* and *Sclerocrangon* G.O. Sars (Decapoda, Crustacea)

By N.A. Zarenkov

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Revision of the Genera Crangon Fabricius and Sclerocrangon G.O.Sars (Decapoda, Crustacea).

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Introduction

The genera Crangon and Sclerocrangon, to which the most common representatives of our fauna belong, are still poorly studied and interrelations are not clear.

The similarity of Sclerocrangon to the Antarctic representative of the family, Notocrangon antarcticus (Pf.) has been established long ago (Coutiere, 1917), but this question requires further clarification, because the relation between Crangon and Sclerocrangon is not determined. We must agree with L. B. Holhuis (1955) that the position of Notocrangon may only be clarified on the basis of a general revision of Crangon and Sclerocrangon, which are closely related to this genus. We believe that Nectocrangon should also be studied; the latter is an original genus and undoubtedly similar to the three mentioned genera.

J. G. de Man (1920) presents a most complete list of species of these genera. Together with the later described species (Bierstein and Vinogradov, 1951, 1953; Kobyakov, 1937, 1955; Chase, 1937; Yokoya, 1933, 1939; Yaldwyn, 1960; de Man, 1929), today we know more than 60 species classified as belonging to genera Crangon, Sclerocrangon, Nectocrangon and Notocrangon. With greater or lesser doubt, we consider four of these species to be synonymous with C. crangon (L.) extensively occurring in European waters. The Japanese S. gasuyeki Yok. is apparently synonymous to S. boreas Phipps; the South-African C. capensis Stimpson has not been preserved, as Dr. Chase (Washington, USA) was so kind to inform us, therefore, the existence of this species requires confirmation. Thus, we assume that there are 58 species in the four genera in question. Owing to the abundant collections of the Institute of Oceanology of the USSR Academy of Sciences, to the supply of material from the National Museum of the USA and from the Department of Hydrobiology of the Leningrad University*, I succeeded to study the structure of 39 species. In respect to the remaining species I had to limit myself to the use of literature data.

The studied genera are to a considerable degree based upon the peculiarities of the sculpture of body covers. The functional value of these characteristics is still not clarified and their utilization does not always lead to positive results. In particular this feature is very difficult to use in distinguishing Crangon from Sclerocrangon. Utilization of another characteristic, namely of the endopodite of II pleopod of a male is difficult, because this feature is unknown in the majority of species. Finally, the peculiarities in the structure of the gill apparatus are used for taxonomical purposes. It is believed /1762

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* In this connection I express my sincere gratitude to Dr. Chase and to Mr. Stuart, Director of the National Museum of the USA, as well as to E. I. Kobyakova, Assistant Professor at the Leningrad University.

that representatives of the *Crangon* species have an arthrobranch on the outer maxilliped, while *Sclerocrangon* has no such gill (Holthuis, 1955). However, K. H. Barnard (1950) believes that some of the *Crangon* do have arthrobranch on the outer maxilliped. Therefore, the possibility of using this characteristic requires a revision.

An analysis of data on morphology, on reproduction biology and on metamorphosis allowed us to conclude that species classified as belonging to *Crangon* and to *Sclerocrangon*, actually belong to five different genera. Diagnoses of the genera in question are shown below.

Taxonomy

1. Genus *Crangon* Fabricius, 1758. Type species *C. crangon* (Linné, 1798). Endopodite of II pleopod of a male is armed with pinnated setae along edges and terminally, and is longer than the appendix masculina. The sculpture of body covers is poorly developed. The genus consists of two subgenera.

Subgenus *Crangon s. str.* The type species of the genus is *C.* (*C.*) *crangon* (Linné, 1798). Arthrobranch on III maxilliped is in a reduced condition. One spine is located on the medial line of the carapace, the dorsal keels of VI abdominal segment are either scarcely traced or absent.

alaskensis Rathbun, 1902; almanni Kinahan, 1864; septemspinosa Say, 1818; alba Holmes 1900; crangon Linné, 1798; stylirostris Holmes, 1900; holmesi Rathburn, 1902.

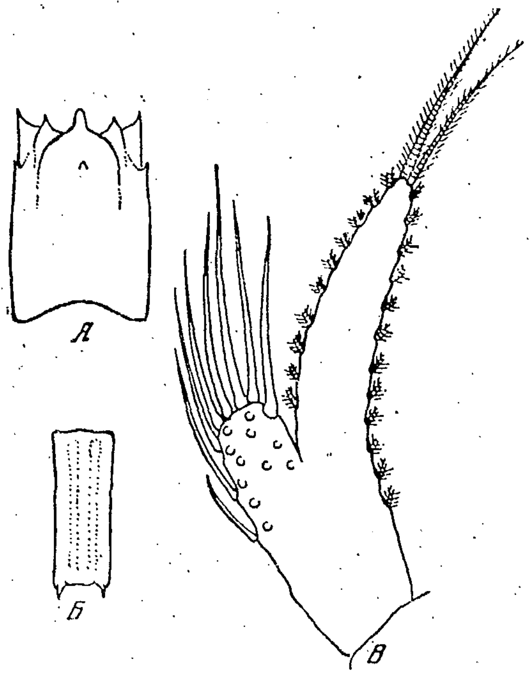

Figure 1. Crangon ralli Rathburn.

A - carapace; 6 - VI abdominal segment;

B - endopodite of II pleopod of a male.

Subgenus Neocrangon subgen. n.. Type species is C. (N.) communis (Rathbun, 1899). Arthrobranch on III maxilliped is absent. One spine is located on the medial line of the carapace, dorsal keels of VI abdominal segment are well pronounced, but do not reach the rear edge of this segment (fig. 1).

abyssorum Rathbun, 1902; ? geniculata Yokoya, 1933; resima Rathbun, 1902; communis Rathbun, 1899; ? joloensis de Man, 1929; ? sagamiense Balss, 1913; dalli Rathbun, 1902; nigricauda Stimpson, 1856; ? zacae Chase, 1937, 1937; franciscorum Stimpson, 1859; nigromaculata Lockington, 1877.

2. Mesocrangon gen. n. Type species is M. intermedia (Stimpson, 1860). Endopodite of II pleopod is armed with pinnated setae along edges and terminally. Arthrobranch on III maxilliped is absent. There are two spines or tubercles on the median line of the carapace, one lateral spine in the gastral area. VI abdominal segment is cylindrical and has 2 distinct keels that do not reach the rear edge of the segment. Suborbital spine is separated from the orbital edge by a narrow cleft (fig. 3).

intermedia Stimpson, 1860; ? volki Birstein et Winogradov, 1953; ? munitella Walker, 1898.

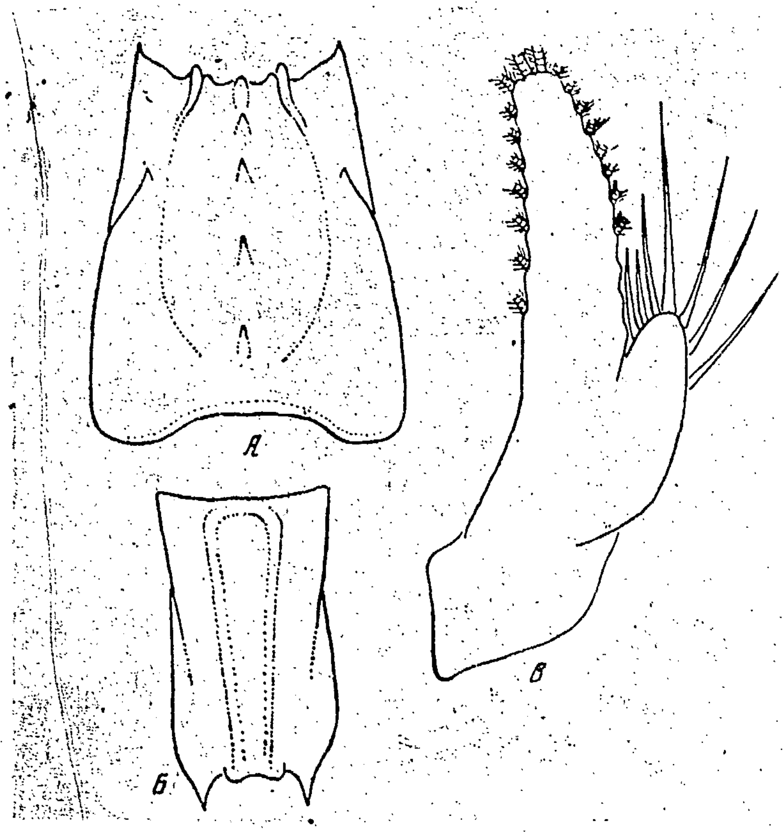

Figure 2. Nectocrangon crassa Rathbun.

Same symbols as in figure 1.

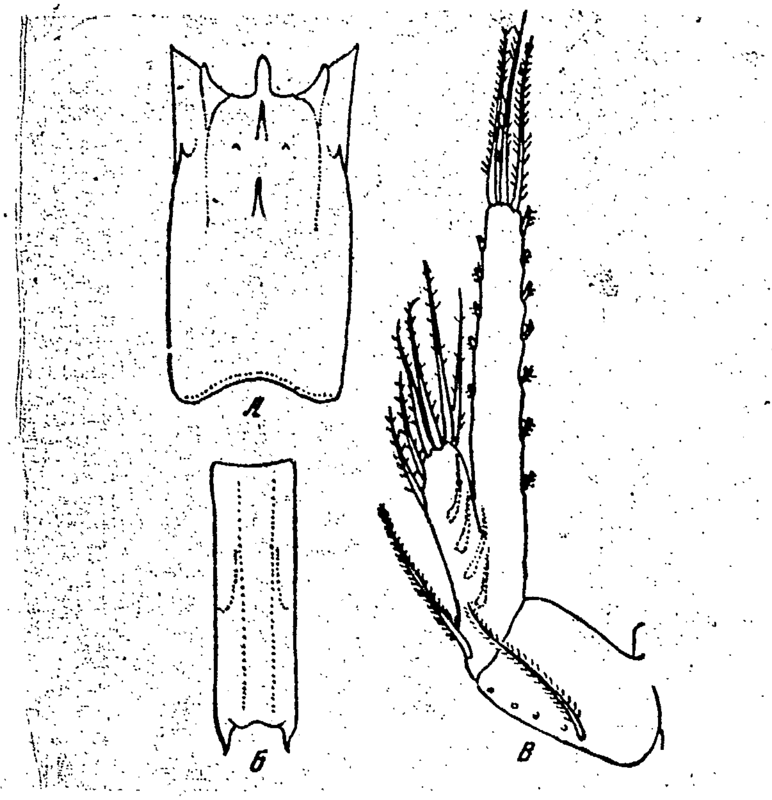

Figure 3. Mesocrangon intermedia (Stimpson).

Same symbols as in figure 1.

3. *Metacrangon* gen. n. Type species is *Met. variabilis* (Rathbun, 1902). Endopodite of II pleopod is armed with pinnated setae along the edges and terminally. The arthrobranch on III maxilliped is absent. There are three spines on the medial line of the carapace and one lateral spine in the gastral area. Dorsal keels of VI abdominal segment are pronounced, but do not reach the rear edge of the segment. The rear lower corners of VI abdominal segment form laterally directed wing-like lobes. The front edge of the carapace is raised, the suborbital spine is separated from the orbital edge of a narrow cleft (fig. 4).

acclivis Rathbun, 1902; monodon Birstein et Winog., 1951; richardsoni Yaldwyn, 1960; angusticauda de Haan, 1849; hellmarlei Stebbing, 1914; munita Dana, 1852; robusta Kobjakova, 1935; jacqueti A. M. Edw., 1881; ? nipponensis Yokoya, 1933; spinirostris Rathbun, 1902; knoxi Yaldwyn, 1960; ochotensis Kobjakova, 1955; spinosissima Rathbun, 1902; laevis Yokoya, 1933; procax Faxon, 1893; variabilis Rathbun, 1902; lomae Schmitt, 1921; ? trigonorostris Yokoya, 1933; ? longirostris Yokoya, 1933.

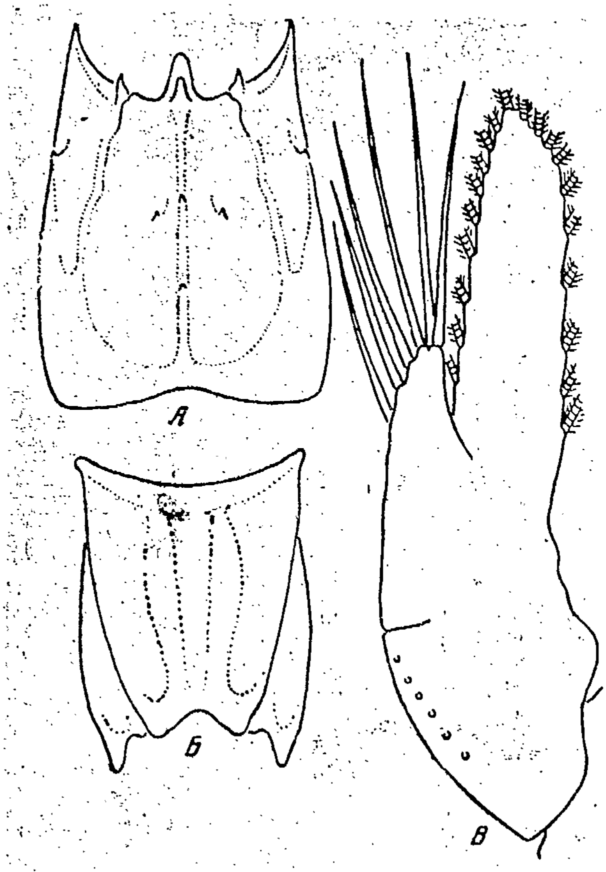

Figure 4. Metacrangon robusta (Kobjakova).

Same symbols as in figure 1.

4. Nectocrangon Brandt, 1837. Type species is N. lar Owen, 1839. Endopodite of II pleopod of a male is armed with pinnate setae along the edges and terminally. This endopodite is longer than appendix masculina.

Arthrobranch on III maxilliped is absent. Two or three spines are located on the median line of the carapace, keels of VI abdominal segment are well developed, but do not reach the rear edge of this segment. The front edge of the carapace is raised; closely arranged rostrum and orbital spines form a tube-like receptacle for eyes (fig. 2). The dactylopodites of IV and V pereiopods are flattened.

alaskensis Kingsley, 1882; dentata Rathbun, 1902; levior Rathbun, 1902; californiensis Rathbun, 1902; hozawai Yokoya, 1939; ovifer Rathbun, 1902; crassa Rathbun, 1899; lar Owen, 1839; sadoensis Yokoya, 1933; tovamaensis Yokoya, 1933.

5. Rhynocrangon gen. n. Type species is R. sharpi (Ortmann, 1895). Endopodite is armed only with one or two terminal setae and is longer than appendix masculina.

Arthrobranch is absent on III maxilliped. Three spines or low tubercles are located on the median line. Dorsal keels of VI abdominal segment are pronounced (fig. 5).

alata Rathbun, 1902; sharpi Ortmann, 1895.

6. Sclerocrangon G. O. Sars, 1883. Type species is S. Boreas Phipps, 1774. Endopodite is highly reduced, appendix masculina is large and armed with thick bare setae. Arthrobranch is absent on III maxilliped. /1766 There are at least 3 spines on the median line of the carapace. Dorsal keels of VI abdominal segment are pronounced and pointed; these points sometimes protrude beyond the rear edge of the segment. The lower rear corners of VI abdominal segment form pointed wing-like lobes directed towards the sides (fig. 6).

atrox Faxon, 1893; derjugini Kobjakova, 1937; salebrosa Owen, 1839; boreas Phipps, 1774; ferox G. O. Sars, 1877; zenkevitchi Birstein et Winogr., 1935.

7. Notocrangon Coutiere, 1905. Type species is N. antarcticus (Pfeffer, 1887). Endopodite is fully reduced, appendix masculina is thin, long and has several short terminal spines. Arthrobranch is absent on III maxilliped. There is one spine on the median line of the carapace. VI abdominal segment has pronounced dorsal keels that reach to the rear edge of the segment (fig. 7).

antarcticus Pfeffer, 1887.

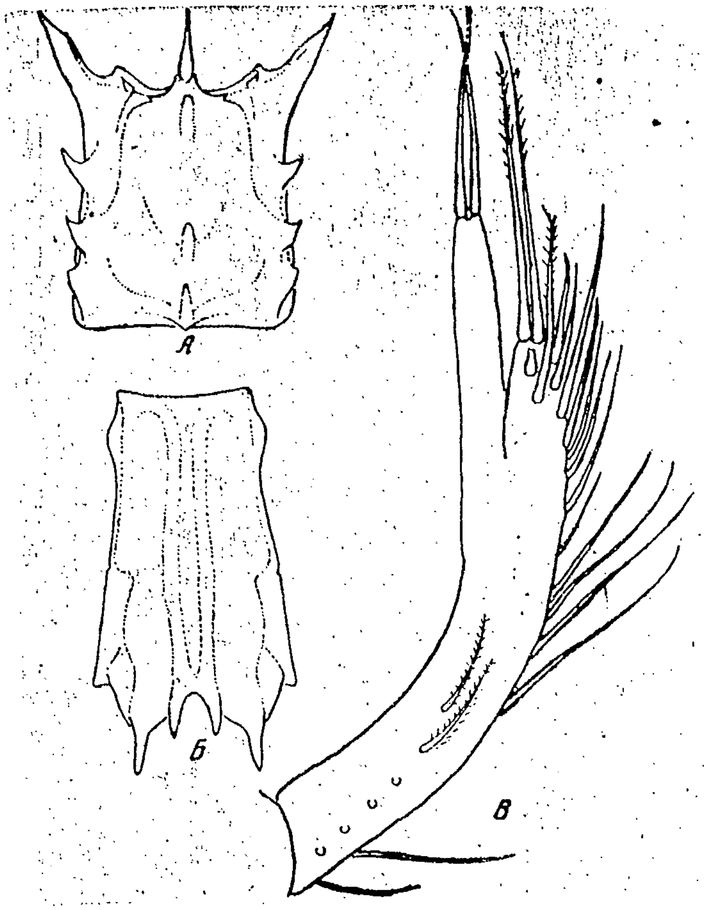

Figure 5. Rhynocrangon sharpi (Ortmann).

Symbols see figure 1.

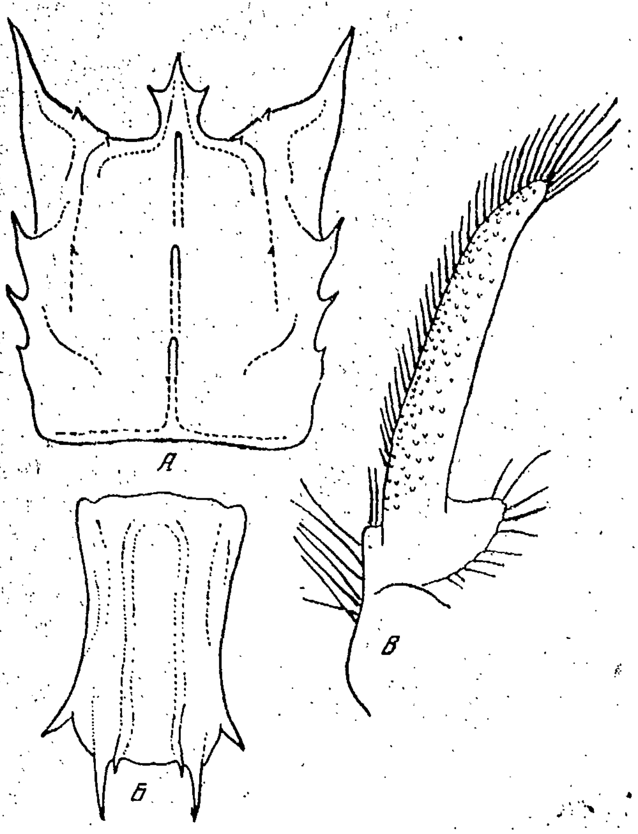

Figure 6. Sclerocrangon derjugini Kobjakova.

Symbols see figure 1.

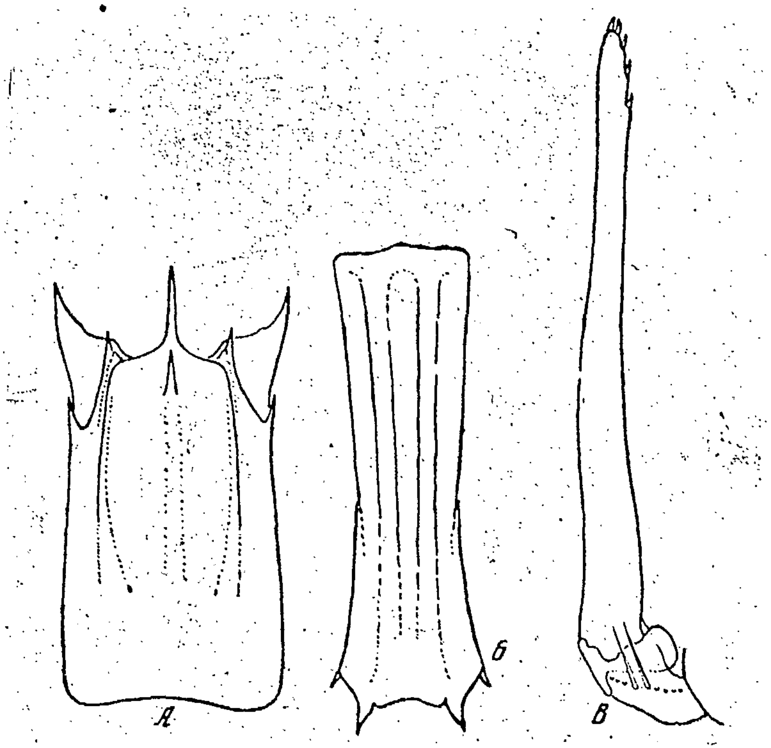

Figure 7. Notocrangon antarcticus (Pfeffer).

Symbols see figure 1.

Certain Forms of Evolution

Morphological changes that took place in the evolution of genera in question consist, probably, in the following:

1) growth of appendix masculina and reduction in the size of endopodite of II pleopod ;
2) reduction of the arthrobranch of III maxilliped;
3) hardening of body covers, increase in the sculpture of carapace and abdomen.

Furthermore, there are grounds to assume that in certain cases a change in the size of eggs carried by a female took place, as well as changes in the body dimensions. Let us discuss each of the changes separately.

1. It is known that changes in the relative dimensions of individual organs are usually explained by differences in their relative rates of phylogenetic growth (Huxley, 1932; Rensh, 1960). Such an approach seems also to be justified in our research, since the studied shrimps differ considerably in respect to their body size. Furthermore, the clarification of the forms of the phylogenetic growth of appendages of II pleopods of a male presents a possibility of determining the /176

peculiarities of this feature in various genera. For this purpose we have studied the phylogenetic growth of appendix masculina and of endopodite of II pleopod of a male in respect to the carapace in species of various genera. It was demonstrated here that the relative size of these appendages differs from genus to genus, but cannot serve as a generic characteristic. More definite results were obtained, when we studied the phylogenetic growth of endopodite in respect to appendix masculina. It turned out that the index of the allometrid growth <u>b</u> in various genera is generally in reverse relation to <u>a</u> (table 1). The latter value characterizes the size of embryos. In genera <u>Sclerocrangon</u> and <u>Rhynocrangon</u>, which differ from other genera in a special structure of II pleopod of a male, <u>a</u> is greater than one. Therefore, <u>Notocrangon</u>, whose endopodite is completely reduced, is represented by a widely deviated branch not directly connected to <u>Crangon</u>.

2. Evolutionary changes in the gill apparatus consisted in a reduction of arthrobranch of III maxilliped. This gill appears exclusively in <u>Crangon</u> (Crangon) and occurs in reduced state. Presence of such a gill should be considered as a primitive feature and, therefore, the subgenus <u>Crangon</u> retains the most primitive state. Loss of this arthrobranch takes place already within the confines of the <u>Crangon</u> genus (subgenus <u>Neocrangon</u>); this process, we believe, took place independently in each of the other groups.

Table 1

Indices of the allometric growth of appendages of II pleopod of a male ($y = ax^b$, where y is endopodite and x is appendix masculina)

Genera	Number of species	Number of measurements	a	b
Metacrangon gen. n.	8	17	1.05	1.16
Crangon L.	13	31	1.46	1.32
Sclerocrangon G. O. Sars	5	44	0.45	1.32
Mesocrangon gen. n.	1	9	1.63	0.75
Rhynocrangon gen. n.	2	6	0.10	1.90

3. Peculiarities of the sculpture of body covers reflect the character of the evolution of genera. Intensification of sculpture takes place in the direction from Crangon and Mesocrangon to Sclerocrangon and Rhynocrangon. The species of the Sclerocrangon genus are the largest ones among the Crangonidae, and therefore, the strong development of their sculpture may possibly be explained by a change in body proportions during the process of phylogenetic growth. However, the Rhynocrangon species, which have the richest sculpture, at the same time are the smallest animals, therefore, the above-suggested assumption in respect to Sclerocrangon, is inapplicable in the present case. Similar difficulty arises when we study the genus Metacrangon, the representatives of this genus have a richer sculpture than Crangon, but smaller body dimensions.

Strong development of sculpture and considerable body dimensions present a particularly illustrative feature of Sclerocrangon; this refers both to the shallow-water and to deep-water representatives. An increase in the body dimensions became possible because of the hardening of covers, a feature ensuring the necessary mechanical strength. Intensification of sculpture and reduction in the endopodite of II pleopod of a male must be considered as a result of allometric growth. The /1768 bathyal *S. derjugini* has a spine in the gastral area of carapace, same as in *Metacrangon*. Nevertheless, any grouping together on this basis would be artificial. Apparently, such a spine is a remnant of a pronounced oblique ridge running in *S. boreas* along the gastral area. We believe that an increase in dimensions is the most important moment in the evolution of this genus, and this, as it will be shown below, had an effect upon reproduction biology. One might also have thought that this characteristic would have effect upon the position of the animal in the food cycle system. However, this is not exactly the case. Representatives of *Sclerocrangon* (*boreas*, *zenkevitchi*) (Sokolova, 1957; Turpayeva, 1948) same as the representatives of *Crangon* (*crangon*, *almanni*, *abyssorum*, *communis*) are carnivorous animals feeding upon polychaetous worms, bivalved mollusks, amphipods and echinoderms. The representatives of *Crangon*, *Nectocrangon* and *Sclerocrangon* are, however, mentioned as food objects of benthophagous fish (Bylacheva, 1948; Gordeyeva, 1954; Logvinovich, 1949; Mikulich, 1949, 1954; Popova, 1954; Skalkin, 1963). Nevertheless, there are reasons to believe, that owing to greater dimensions, representatives of *Sclerocrangon* become inaccessible to certain benthophages. Finally, one could also have connected the large dimensions of the Sclerocrangon species with their relative preference to life in cold water, as applied in general (Skadovsky, 1955); however, the largest S. salebrosa is more thermophyllic than the remaining representatives of the group.

Occurrence of epiphytous organisms attached to the upper side of the body permits us to consider the way of life of some of the species. We find barnacles Spirorbis and bryozoans on S. boreas, we find hydroids and foraminifers on S. zenkevitchi; in the latter species these animals attach themselves not merely to the top of the body, but also to its sides. It is difficult to imagine that the described phenomenon could have taken place, if these animals spent most of their time buried in the ground. This applies particularly to S. zenkevitchi. The very long rostrum, a morphological characteristic of this species, makes his ability to dig itself into the ground rather improbable. In the abyssal, where the given species lives, the food objects are more scattered than in shallow waters and do not form similar accumulations. Therefore, this animal must carry out prolonged searches for food and acquires the ability of a more active locomotion. Such peculiarities place S. zenkevitchi in a somewhat special position among the other representatives of the genus, which evidently maintain the ability to bury themselves into the ground to a greater degree. On the other hand, we observed in an acquarium how a large *S. boreas* specimen dug itself into the ground leaving uncovered nothing but the upper portion of its body. Similarity in structure and absence of any significant inter-species differences permit us to assume that the majority of the *Crangon* species lead a similar way of life, and just as *C. crangon* and *C. septemspinosa* is able to dig itself into the ground either completely, or partly. To such behavioural feature corresponds a reticulate fine mottled pattern of the upper side of the body formed by the chromatophores and corresponding to the fine-grained ground into which these animals bury themselves. *C. communis*, *dalli*, *franciscorum* and *stylirostris* have a similar pattern, a fact entitling us to suspect a similar way of life also in respect to these species. Intensification in the carapace sculpture observed in the *Nectocrangon* and *Metacrangon* genera consists in an elevation of the front edge of the carapace together with the rostrum and the orbital spines, this results in lowering of the surface of the gastral area and formation of a depression. These characteristics are best pronounced in *Nectocrangon*, the representatives of this genus being characterized by a tubular receptacle for eyes formed by drawing-together and pulling uppwards the rostrum and orbital spines.

Furthermore, flat and widened fingers of the last pereiopods are characteristic of Nectocrangon. Both characteristics should be considered as adaptations to a more perfect burying in the ground during which the eyes should remain above the surface. We have no immediate observations on the behaviour of these animals, therefore, an explanation of the expediency of the discussed characteristics is conjectural. It is, however, possible to assume that in the series Metacrangon - Nectocrangon a specialization took place in the direction of the perfection of the burying method. /1769

Undoubtedly, Nectocrangon is the most specialized genus among the studied shrimps and unlike other shrimps it has short pterygostomous spines turned frontwards and inwards. This feature may facilitate the animal's locomotion in the ground and indiates a burying way of life. Judging by the peculiarities of the carapace structure, the Mesocrangon genus was also developing in the direction of adaptation to burying in the ground. The gastral area of M. intermedia and volki is depressed, the orbital edge of the carapace is elevated, and at the base of the orbital spine we have a deep notch, which is very characteristic of Nectocrangon.

Acquiring certain special features common to the latter genus, the species of the Mesocrangon genus preserve a structure of VI abdominal segment characteristic of the poorly specialized Crangon. Therefore, a segregation of Metacrangon from Mesocrangon is difficult, but the latter may be considered formally as a transitional group from typical Crangon to typical Metacrangon. Apparently, it would be more correct to believe that Mesocrangon undergoes an evolutionary development that is basically parallel to Crangon → Metacrangon.

A small original group Rhynocrangon consists of smaller species. It developed in the direction of sculpture intensification. A specific structure of appendix masculina permits us to assume that this group segregated from the main trunk at an early stage of development.

In certain structural peculiarities of the carapace, Notocrangon may be contrasted to all the other genera. We note primarily the characteristic shape of rostrum, which is compressed in lateral direction and turned up, as well as the presence of median ridge on the dorsal surface of the carapace. Such features are characteristic of the actively swimming shrimps, for example, of the Pandalidae or Hippolytidae, but in the overwhelming majority of Crangonidae, who live basically on the ground, this ridge on the carapace is absent and the rostrum is usually compressed in the dorsal-ventral direction. The deep-water C. abyssorum, for example, is an exception, its rostrum is elevated and compressed from sides. Another peculiarity is the structure of the bottom front corner of the carapace, which is pronounced elongated from the ventral and orbital areas, a characteristic not observed in representatives of all the other genera (fig. 7). The position of pterygostomous spines is also characteristic. The genera Crangon and Metacrangon are characterized by relatively short pterygostomous spines, in the former genus they are forward directed, while in the latter one, both forwards and inwards. In Sclerocrangon and Rhynocrangon genera, uniting representatives with the most developed sculpture, these spines are considerably larger and are directed forwards and to the sides. Notocrangon approaches Crangon in the development degree of sculpture, it resembles Sclerocrangon and Rhynocrangon in its structure of the pterygostomous spine. The functional importance of these features remains unknown, but one must assume, that having preserved the more or less primitive type of the carapace structure and of the structure of VI abdominal segment, which is characteristic of Crangon, the Antarctic genus has acquired certain peculiar features. Among the latter the structure of the bottom front corner of the carapace has no analogies in other studied species, while the structure of rostrum and the presence of a median dorsal keel on the carapace indicate possibility of a rather mobile way of life.

/1770

Differences in the dimensions of appendages are a characteristic peculiarity in the majority of Crangonidae, a phenomenon which in Paracrangon is brought to complete reduction of II pereiopods. In the studied species II and III pairs of pereiopods are in reduced condition. S. W. Kemp (1916) considered this characteristic to be common to "group V", which includes Crangon s. lato, Sclerocrangon s. lato, Nectocrangon and Prionocrangon, thus giving this characteristic the rank of a suprageneric feature. We have studied the relation between the width of the distal portion of merus of II and III pereiopods and the width of the distal part of the claw of I pereiopod in 34 species and have not detected any significant differences between genera and individual species. This ratio fluctuates from 0.13 to 0.21 within each genus. Apparently there is no reason to believe that a considerable reduction of these appendages took place here. Therefore, we agree with Kemp that the reduced state of II and III pereiopods is characteristic of this group as a whole.

Peculiarities in the Reproduction Biology

Already Coutiere (1917) noted the structural resemblance of egg-clutches in Crangon and Sclerocrangon expressed in a considerable thickness of the clutch in the dorsal-ventral direction. It is, however, more expedient to study other features. We have studied the number of eggs in clutches (in the future, for the sake of brevity, this will conditionally be called "fecundity") and the dimensions of eggs in 34 forms. Utilization of these characteristics is faced with a number of difficulties. It is known that the fecundity changes in animals with age; this has been proven, for example, in the case of C. crangon (Havinga, 1929). Consequently, in order to obtain the compared data, one should study the age changes in fecundity. However, in the majority of instances this turned out to be impossible. Such a source of errors appears to be the most important one, but its importance should, however, not be overestimated. In the studied genera females are always larger than males[*], therefore, the

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[*] In literature, as a rule, the total body length is indicated from the tip of rostrum to the end of telson. More accurate are the measurements from the rear edge of orbit to the rear edge of carapace shown in our work. In the studied forms the carapace constitutes one quarter of the total body length, a fact which we utilized in the conversion of published data on the total length into the length of carapace.

rather numerous published data on the maximum body length in various forms, most probably, are referred to females; only forms known in one signle individual may constitute an exception. Dimensions of egg-bearing females studied by us are close to the maximum dimensions of corresponding species indicated in the literature, therefore, our data on the fecundity generally are close to the maximum possible ones, i.e., they are comparable. There are reasons to believe that the egg size is subject to changes because of the effect of certain factors. For example, C. crangon with a carapace length of 15.4 millimetres has eggs 0.50 x 0.45 millimetre in size, while according to M. W. Lebour's data (1931) they are 0.56 x 0.40 millimetre; with carapace length of 37.0 millimetres, S. salebrosa has eggs of the following dimension: 2.15 x 2.10 millimetres, while according to Bals' data (1914), in an individual of unknown size, they are 1.75 x 1.75 millimetres. One may see that fluctuations in eggs in respect to body length are insignificant. Another source of error should be pointed out, namely, the possible change in the egg shape, which is usually ovate, during the fixation process and under effect of mechanical causes. The dimensions of the first cause remain unknown, however, in our material, which is fixated by means of alcohol, this error will remain more or less the same; the second cause of error, on the other hand, may be avoided by utilizing the geometrical average of the large and the small diametres.

Finally, there is one more source of error, i.e., the possibility of losing a smaller or greater amount of eggs when catching the animal, or during its /1771 storage. This refers to a lesser degree to species forming the Sclerocrangon genus, eggs of these species are firmly attached, and to a greater degree, to the species of Crangon genus. The latter have more eggs per clutch and only in exceptional cases the losses may change their total number in any considerable degree. In the smallest species constituting the Metacrangon group, the eggs are relatively large and usually few in number. Thus, in the latter case, the relative number of lost eggs may be considerable, and the fecundity too low. Taking into consideration the value of mentioned sources of errors, we have approached the analysis of the obtained data with care and have limited ourselves to determination of common features. Among such features the following appear to be evident.

Table 2

Data on the fecundity and egg dimensions.

Species	Number of eggs per clutch	Size of eggs	Species	Number of eggs per clutch	Size of eggs
angon alba	850	0,60×0,53	Nectocrangon dentata	246	2,25×2,25
abyssorum	61	0,75×0,60	N. crassa	448	1,50×1,05
alaskensis	—	0,75×0,55	N. lar	980	1,40×1,15
almanni	—	0,80×0,48	N. ovifer	—	2,00×1,15
communis	2200	0,90×0,75		—	
crangon	7000	0,50×0,45	Sclerocrangon atrox	—	3,33×2,62
dalli	4290	0,50×0,45	S. boreas	448	2,75×2,85
franciscorum	3500	0,58×0,48	S. derjugini	143	4,85×5,00
nigromaculata	7700	0,40×0,38	S. ferox	133	3,00×2,20
nigricauda	6100	0,50×0,40	S. salebrosa	1735	2,15×2,10
resima	334	0,68×0,75	S. zenkevitchi	52	3,72×2,00
septemspinosa	1680	0,65×0,50	Metacrangon acclivis	5	1,75×1,60
stylirostris	4500	0,60×0,53	M. knoxi	45	1,50×1,80
			M. robusta	25	2,01×2,50
esocrangon intermedia	79	1,05×0,70	M. spinirostris	25	2,00×1,60
volki	62	0,65×0,65	M. variabilis	29	2,30×2,20
inocrangon sharpi	573	1,15×0,95	Notocrangon antarcticus	890	2,00×1,52

The lowest fecundity is characteristic of the Metacrangon group, which is represented by the smallest forms with relatively large eggs. Medium-sized and very fecund, the Crangon have very small eggs. The Sclerocrangon genus consists of the largest forms and holds a medium position in respect to the fecundity and is similar to Metacrangon in respect to the relative size of eggs.

In the Mesocrangon the fecundity is just as low as in Metacrangon, but the relative egg size is approximately the same as in the Crangon genus. The fecundity of the genera Rhynocrangon, Notocrangon and Nectocrangon is approximately identical to Sclerocrangon, but in respect to the relative dimensions of eggs the first three genera may be placed between Sclerocrangon and Mesocrangon.

The absolute egg dimensions increase in the following order: Crangon - Mesocrangon - Rhynocrangon - Nectocrangon - Metacrangon - Notocrangon - Sclerocrangon (table 2). The following explanation is suggested for the mentioned facts. Owing to larger body-dimensions, representatives of Crangon and Sclerocrangon are capable of carrying a clutch of considerable weight; however, in the first case this is effected through a greater number of small eggs, while in the second case, by a small number of large ones. As we know, the embryo development in large eggs is considerably prolonged. Indeed, in species of the Sclerocrangon genus, which lay very large eggs, the pelagic larvae are absent, while in the Crangon genus, which has small eggs, there are five larval stages. Notocrangon and Nectocrangon, with larger eggs than Crangon, and smaller than Sclerocrangon, are characterized by a shortened metamorphosis. We may expect by analogy that Rhynocrangon, which has approximately identical eggs, also has a shortened development. Species of the Metacrangon group, owing to their small dimensions, carry only a small number of rather large eggs, and in this case a shortening of the development is also probable. Undoubtedly such considerable differences in the egg dimensions and in the value of fecundity have the purpose of maintaining the numbers. In the Crangon genus this is achieved through a high fecundity compensating the high mortality among planktonic larvae, a mortality, which apparently occurs in the genera Notocrangon and Nectocrangon (possibly also in Rhynocrangon and Metacrangon), because of shortened ontogenesis, and in Sclerocrangon, because of their care for offspring. But why did these conditions happen? Why, for example, doesn't Sclerocrangon carry a considerable number of small eggs, and Crangon a small number of large ones?

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n is the number of eggs per clutch; the index of the dimensions of an egg is $k=\sqrt{\text{large diametre} \times \text{small diametre}}$.

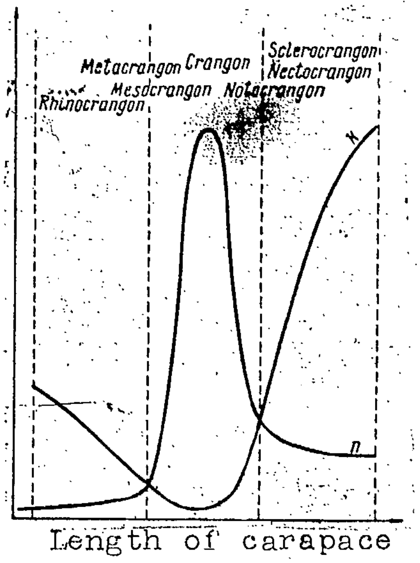

Figure 8. Ratio of body dimensions to the number and size of eggs in a clutch in various genera of Crangonidae

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We must assume that the Crangon genus, which is rather primitive, maintains its initial position; there is no basis to believe this to be a secondary phenomenon. It is natural that smaller forms cannot have clutches of same size as in Crangon, therefore, a decrease in the number of laid eggs must take place. This condition is observed in the Metacrangon genus. However, the preservation of numbers by means of a high fertility rate has a definite lower limit below which a survival of a sufficient number of planktonic larvae scarcely becomes a statistical probability. Small forms belonging to the Mesocrangon groups, and possibly to Rhynocrangon, are apparently incapable to carry more eggs than a critical number, therefore, in these groups the evolution led to the creation of the ability to lay large eggs. Thanks to this ability a shortening in the metamorphosis could have appeared in both groups. This shortening in the metamorphosis could ensure a sufficient survival rate of juveniles. In the evolution of Sclerocrangon occurred a possibility of increasing the fertility rate owing to increase in body dimensions. Apparently, however, the phylogenetic growth which took place in the present branch occurred in such a manner, that the growth rate of eggs surpassed the one of the body. It follows from here, that in the course of phylogenetic growth, in those concrete instances where this growth occurs, the increase in the fertility rate does not necessarily attain any greater size. Furthermore, and this is the most important part, the young shrimps hatched from eggs are in need of a space under the abdomen of the female. Even Sclerocrangon, a rather large animal, is unable to carry simultaneously several thousand juvenile individuals.

The ratios of egg dimensions to fertility are shown in fig. 8 in a general form. Such relations have an adaptational character and have a certain significance in the establishment of phylogenetic ratios. First of all, we have an argument in favour of the concept of the primitiveness of the Crangon genus and of the specialization of other genera. Evidently, Sclerocrangon must be considered among the latter as the most specialized group.

Concerning the Duration of Metamorphosis. /1773

Data on larval development, perhaps because of their incompleteness, do not add many significant contributions to the problem of the phylogenetic relations of the studied genera. Pelagic larvae of five stages are known in C. almanni, crangon (Lebour, 1931), franciscorum, *nigricauda*, *nigromaculata*, (Israel, 1936; Bonnott, 1932) and are completely absent in *boreas* (Gurney, 1942), *ferox* (Wollebaek, 1909), *zenkevitchi* (Birstein and Vinogradov, 1953). It is believed that in the genus *Nectocrangon* the development is shortened (Stephensen, 1916). Our data confirm the above-mentioned phenomena: we have discovered female *N. crassa* on whose pleopods larvae of late stage with developed pleopods were attached. Conversely, in the *Mesocrangon* genus we must assume the existance of a complete cycle of larval development, because in a clutch of a *M. intermedia* female we found a zoaea larva. Most probably the female was fixated at the very moment of the hatching of larvae and fully formed zoaeae were visible through the cover of other eggs of this clutch. Similar to the Arctic *Sabinea septemcarinata*, the development of *Notocrangon* has three larval stages (Gurney, 1942); furthermore, the structure of larvae in both species shows traits of similarity. Gurney sees in these facts an argument in favour of taxonomical isolation of *Notocrangon*, a statement with which one must agree. Nevertheless, it would have been wrong to utilize these facts as an argument in favour of the similarity of the two genera. Shortening of ontogenesis leading to the viviparity is characteristic of many invertebrates in the Arctic and Antarctic, and is considered as an adaptational feature originating indepently in unrelated groups. Similarity traits in the Sabinea and Notocrangon larvae are difficult to evaluate at the present time, insofar as the structure of the majority of other species remains unknown. Seven Notocrangon larvae in our collection have a carapace that is 3.00 to 3.35 millimetres long. Exopodite of I pleopod and the setae of exopodite in uropods, the anal shield and the disarticulatedness of pleopods give ground for classifying these larvae as V stage indicated by M. V. Lebour (1931) for Crangon, i.e., to III stage of Notocrangon. Numerous larvae detected by W. T. Calman (1907) are, according to this author, at IV and V stages (i.e., at II and III stages of the Notocrangon), and their brief description corresponds completely to the structure of our larvae. Thus, until now the larvae of I to II stages of Notocrangon remain without description. In respect to the already known facts it should be said that the Notocrangon larvae are generally close in structure to the Crangon larvae differing from the latter exclusively in presence of a dorsal spine on carapace, lateral on the V abdominal segment and in a longer rostrum (Gurney, 1942). The taxonomical importance of these features still remains unknown; nevertheless, it is evident, that in the structure of larval stages Notocrangon differs from Crangon only insignificantly.

Conclusion.

There are two opposite viewpoints in respect to the evolutionary relations of the *Crangon* and *Sclerocrangon* genera. Ortmann (1895) believed that the evolution went in the direction from *Sclerocrangon* to *Crangon* and led to simplification of body sculpture. Borradaile (1916) considered *Crangon* as a less specialized group from which *Sclerocrangon* was derived. The latter viewpoint appears to us to be better founded. Nevertheless, certain morphological peculiarities permit us to consider, that the specialization also takes place in the *Crangon* genus.

The evolution of the genera *Mesocrangon*, *Metacrangon*, *Nectocrangon* went along the path of perfectioning adaptations of burying in the ground. Generalization of the *Sclerocrangon* /1774 is connected with the increase in body dimensions, but the nature of this phenomenon remains unknown. The *Rhynocrangon* genus shows a sharp convergence in sculpture to *Sclerocrangon*, but is not immediately connected with the latter genus. The *Notocrangon* genus retains similarity with *Crangon* and acquires characteristics, which have no analogies in other genera. The immediate ancestor of *Notocrangon* is unknown. Proposed representatives are shown in fig. 9.

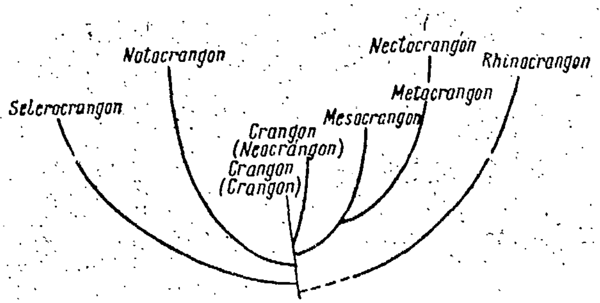

Figure 9. Diagram of the phylogenetic relations of certain genera of Crangonidae.

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REVISION OF THE GENERA CRANGON FABRICIUS AND SCLEROCRANGON G. O. SARS (DECAPODA, CRUSTACEA)

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Summary

An analysis of the structure of carapax and abdomen, of the appendages of the II pleopode of males and of the gill apparatus of 58 species showed the necessity to separate three new genera, Mesocrangon, Rhinocrangon and Metacrangon, and of two subgenera, Crangon and Neocrangon of the genus Crangon; this analysis proved the independency of the genera Notocrangon, Sclerocrangon, Nectocrangon and Crangon. Comparative-anatomic data and biological facts show that the evolution of some genera consisted in the improvement of the mode of burying into the bottom and was sometimes related to an increase in body size and a change in fecundity, egg size and the character of larval development. Notocrangon is a specialized Antarctic genus.