

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 diameters.

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 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.

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

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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

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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?

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

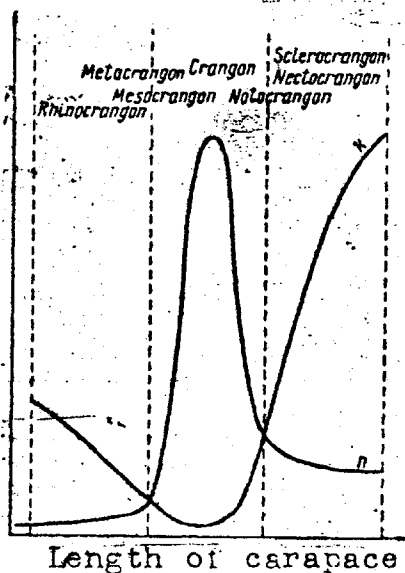


Figure 8. Ratio of body dimensions to the number and size of eggs in a clutch in various genera of Crangonidae

We must assume that the Crancon 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 Crancon, therefore, a decrease in the number of laid eggs must take place. This condition is observed in the Metacrancon 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 Mesocrancon groups, and possibly to Rhynocrancon, 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 Sclerocrancon 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.

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; Bonnett, 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 existence of a complete cycle of larval development, because in a clutch of a M. intermedia female we found a zoea larva. Most probably the female was fixated at the very moment of the hatching of larvae and fully formed zoeae 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 <sup>with</sup> 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 perfecting adaptations of burying in the ground. Generalization of the Sclerocrangon 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.

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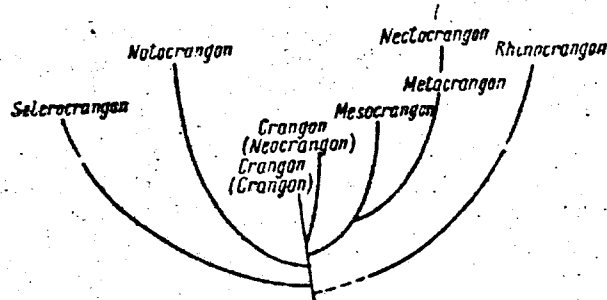


Figure 9. Diagram of the phylogenetic relations of certain genera of Crangonidae.

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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 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 dependency of the genera *Notoocrangon*, *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. *Notoocrangon* is a specialized Antarctic genus.