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THE EVOLUTION OF THE METAZOA

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PREFACE

It was with great pleasure that I accepted the invitation of the Editor of the Pergamon Press Zoological Series to publish in book form and in English, as an international language, the results of my research on the Cnidaria, the interpretations of this research, and the final effects of these interpretations. I was all the more pleased with this invitation because my first general study of this problem appeared 17 years ago during the turmoils of the Second World War, when I tried to save the existence of the Slovene Academy of Arts and Sciences at Ljubljana which was threatened by the occupying powers.

My book, *The Turbellarian Theory of the Cnidaria; The Phylogeny of the Cnidaria and Their Position in the Animal System* was published in a Slav language, in the language of the small yet progressive nation of Slovenes. Added to this text was a detailed summary written in an international language which could help various scholars to get acquainted with the contents of the book. The summary was written in German because I myself completed my studies at Vienna University.

Since the publication of this book many new elements have become known in the field of biology, and above all in zoology. Neither have I ceased with my studies: a whole series of special papers have been written by me in the meantime which are closely connected with problems that had only been touched on in the book. In the international literature there were a number of reactions to my book and to my subsequent shorter publications; this was especcially true for my article which appeared in the American review, *Systematic Zoology*. The publication of this article was made possible due to the generous help of an excellent translator, Professor A. Petrunkewitch. American and the English zoologists have shown particularly

great interest in my interpretations and ideas. I have, therefore, now a welcome chance to answer all the critical observations that have so far been made as regards my suggestions.

The present volume must not be simply considered as a second revised edition of the first volume even if I deal in both these books with the same or at least similar problems. This book is a completely new work: the foundations only of the two books have remained the same.

To these few words of preface I wish to add a few more words dictated by my feelings of indebtedness. Above all, I wish to thank all those critics of my earlier studies who have helped me to clarify many points that had previously been not clear. They must excuse me if I have occasionally used too vehement words that have been dictated "by the heat of the struggle." My wish has always been to convince them. I can not accept the suggestion made by a prominent scholar that such revolutionary novelties have to wait the till present generation dies out and the next generation becomes convinced of the correctness of the new concept.

My special thanks go to my dear friend, Professor Dr. Otto Steinböck (Innsbruck, Austria). He has not only critically read my manuscript; he has also always excelled as a noble colleague. Without any previous knowledge of our researches, we both came to the same conclusions regarding the origin of the Eumetazoa. Each of us has made his researches in his special group of animals: Professor Steinböck has mainly worked on the Turbellaria, and I myself mainly on the Cnidaria. Otto Steinböck came to the conclusion that the Turbellaria, i.e. the acoelous Turbellaria, must be the most primitive Eumetazoa, even before I was able to formulate the results of my studies. As a consequence of this discovery, Steinböck had correctly made important conclusions especially as regards the way the Eumetazoa had evolved, and as regards the previously firmly held theory of the germ layers. He did not, however, succeed in publishing the results of his research and his ideas. Just before the outbreak of the Second World War, Steinböck gave

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a lecture on this subject at the International Congress of Cytology at Stockholm. Only the title of this lecture has ever been published. This is how it happened that I was the first scholar to publish these ideas, in spite of the fact that I developed the same ideas later than Professor Steinböck: this has been due to various circumstances, among others, also to the outbreak of the Second World War. This fact, however, is not ultimately so important for the progress of the science itself; it is much more important that two researchers have reached quite independently the same conclusions; and that they continue to collaborate in a friendly way to prepare the way for the final reception of their ideas. It is unimportant that we differ in several unessential points; it seems that we will soon reach an agreement even on these points. The difficulties we have to overcome are great; we must struggle against interpretations and ideas which were considered inviolate since the days of the struggle for the victory of Darwinism and which were supported by such an authority as Haeckel, and by many other most prominent names. We must struggle against interpretations which have been considered as laws, i.e. as truths, and replace them by new suggestions.

I also wish to express my warmest thanks to the distinguished publishing house of Pergamon Press which has made possible the publication of this book in such a full presentation. I am also grateful to Dr. Janez Stanonik, the translator of the present text, the original of which was written in German; he has completed his task, which has certainly not been easy, to my full satisfaction.

JOVAN HADŽI

INTRODUCTION

It was in 1903, 58 years ago, that I, then a young man who had just left the classical grammar school at Zagreb, went to Vienna to study Natural Sciences and above all my beloved Zoology at Vienna University. For this study I was well prepared. Whilst at school, I had made a large collection of zoological objects. I had learnt the richness of forms and the ways of life of the animal world through my diligent study of Brehm's work on the Lives of Animals as well as through my field studies. At Vienna my teachers were the two professors of zoology, Carl Grobben and Berthold Hatschek, particularly the latter under whose guidance I also worked on my dissertation thesis.

During my second year at university, a public aquarium was purchased in Prater by some young Austrian biologists supported by their prosperous parents; in it they established a modern biological research institute—The Prater Biological Experimental Testing Station (Die biologische Versuchsanstalt im Prater)—and I applied as one of the first to this place to learn there the methods of scientific research. Dr. Hans Przibram, then Privatdocent, was the head of the department; he is the author of the well known synoptic work on Experimental Zoology. *Hydra* was my first object of study. There were numerous green *Hydra* in a half-darkened concrete basin; their exterior looked rather pale. This induced me to transfer the same *Hydra* into a completely darkened place. When these *Hydra* began to procreate I could observe what I had actually expected: their ova were without the symbiotic green algae so that finally there were at least some colourless "green" *Hydra*. Other tests and researches were made in the same place. In 1906 my first results were published in Roux's *Archiv für Entwicklungsmechanik*.

From here I went to the Zoological Institute of Vienna University which was at that time headed by the famous zoologist, Councillor Prof. Dr. Berthold Hatschek. Besides him there were also on the staff Prof. Dr. Karl Camillo Schneider, a well known comparative histologist of Invertebrata, Prof. Dr. Heinrich Joseph, a comparative cytologist, and Dr. R. Zwicklitzer who worked as assistant. I remained faithful to *Hydra* and so I chose "The Nervous System of *Hydra*" as my theme for the doctoral thesis. I succeeded in using methylene blue as an *intra-vitam* colouring of the complete nervous system of *Hydra*. In spring 1908, when I was in the eighth semester of my studies, I became a Doctor of Philosophy. In 1909 the results of my thesis were published in the Institute's journal *Arbeiten der zoologischen Institute Wien und Triest*. This work has never been surpassed by any other study in the same field, it has been quoted everywhere, and the pictures published in it have often been reproduced. Because of the early appearance of this work and because of the other works written by me on *Hydra* and other hydroids (gemmation, migration of nematocysts, etc.) that soon followed, it was not strange that after a lapse of years I have been looked upon at various congresses of zoologists and other meetings as being a son or even a grandson of the "Old Hydra—Hadži."

After the completion of my studies and after I had passed in 1907 the state examination, I returned to my country (Zagreb in Croatia, now Yugoslavia). Here I came, after a short stay at the local Zoological Museum, to the University Institute of Comparative Anatomy, headed by Prof. Dr. Lazar Car. I still continued to remain faithful to hydroids as well as to other Cnidaria and Coelenterata. It was only when I was called, at the end of the First World War, to the newly founded Ljubljana University (Slovenia, Yugoslavia) that I extended the sphere of my interest to some groups of land Arthropoda (Chelicerata), particularly those which inhabit underground caves.

For more than 40 years I have collected experience and knowledge about Cnidaria and Coelenterata, constantly thinking about

their real nature. Though dogmas are characteristic for religious systems, yet the same can also be found in science. One such dogma was, and it still is, the belief in the primary simplicity of *Hydra*, and even more so of Hydrozoa, and so too with Cnidaria and Coelenterata. It is well known how difficult it is to fight against dogmas, particularly when they have been accepted for so long, when they have been supported by renowned scholars, and when they appear to be well founded. My initial researches have shown that *Hydra* is in no way so simply organized as the simple structure of its body would seem to indicate when considered from a crudely anatomical point of view. Soon I saw the first pillar of the proud structure of Coelenterata collapse. It has been almost generally accepted that *Hydra* and its closest relatives are not primarily solitary animals but that, instead, they are derived from ancestors that were able to form cormi. Naturally, this discovery alone could not suffice to make all Hydrozoa the secondarily simplified Eumetazoa. Nevertheless, with this a good beginning was made.

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CHAPTER 1

CNIDARIA AS THE ONLY COELENTERATA

The Systematic Position of the Spongiae

The next step, apparently without connection with the former, was made when some well-known researchers especially Sollas and Delage, came to the conclusion that the Spongiae must not only be placed far from the immediate vicinity of Cnidaria, but also that they must be completely separated from the Coelenterata and even from all the remaining real Metazoa, the Eumetazoa; they must appear completely isolated as an independent type, as Parazoa or Enantiozoa. We must consider this separation as being definite, and, in my opinion, nothing can be changed in this respects by recent attempts made particularly by Miss O. Tuzet and her collaborators.

On the basis of works of older investigators, especially the researchers into the ontogeny of Spongiae (Metschnikoff, Delage, etc.) it is no longer necessary to defer d the special position that the Spongiae have as Parazoa (Sollas) in the animal classification. Recently, however, a tendency has arisen which aims at a revision of this point of view and tries to bring Spongiae back amongst the other Metazoa. The French school in particular, which created the term Enantiozoa (Delage), attempts to cancel out the progress that has been achieved; Tuzet points in this connection mainly to the following evidence: (1) According to her School, the Spongiae have a nervous system; (2) the choanocytes are found in the other Metazoa; (3) the stretching out and the pulling in of a part of the blastoderm observed in the

embryos of Spongiae is not a completely isolated case (*Volvox*). On the basis of all this, Tuzet comes to the conclusion that Spongiae are genuine Coelenterata, and are thus Eumetazoa and not Parazoa. In this she is followed by many zoologists, even by scholars who are not French (Remane, Jägersten, Alvarado).

Considered critically, one can see that the arguments proposed by Tuzet in favour of the old thesis which holds that Spongiae are Coelenterates, have a rather weak foundation. The existence of a nervous system is in no way proved for Spongiae, yet it is of great importance in this connection and Tuzet tries hard to prove the contrary. The pictures of thin sections that have been shown by Tuzet and her collaborators, have been seen by many investigators and I, too, have able been to see them. Yet no one—with one exception that will be mentioned later—has classified these cells of the central stratum with plasmatic processes, as genuine ganglion-cells or even nerve cells. They have always been identified as simple cells of the connective tissue from the central stratum which is filled up with jelly. In all probability these cells are as much, or perhaps slightly more, irritable and able to conduct excitement much as any other animal cell. In order to prove that these cells, or at least some of them, really have a nervous character it would be necessary to apply successfully special selective stains, as for example methylene blue which colours the nerve cells selectivily *intra-vitam*. If this has not been done, then at least it would be necessary to carry out some neurophysiological experiments, and achieve a positive result.

The general behaviour of Spongiae as well as the kind of reactions they show to various stimuli, make it completely improbable that Spongiae could possess a real net of nerves, let alone sensory nerves, as these can with certainty be considered to exist, e.g. in *Hydra*. Some time ago, von Lendenfeld sketched such nerve cells in pictures published by him, yet nobody believed his allegations or his beautiful pictures. And even, if there were some of these cells that exist—not

that they do!—they would be a *lucus a non lucendo*, since they would be physiologically meaningless.

Lévi (1956) made, after the publications of the school of Tuzet had become known, an extensive and critical histological study of Spongiae, and did not report any finding of a nervous system or of nerve cells in Spongiae. Neither could such a finding be confirmed by others, e.g. G. Eberl (Eberl, 1950), an excellent histologist from Vienna who used numerous staining techniques in her work. Yet in spite of all this the propositions as well as pictures published by Tuzet have found acceptance in many schoolbooks, especially in France.

Neither did Miss Tuzet succeed with her—it can be truly said—attempt to disprove the law of the supposedly inversed sequence of body layers in Spongiae. As is well known, Metschnikoff and many other famous zoologists after him, among them particularly Yves Delage, have shown that in the ontogenies of Spongiae, the early morphogeny proceeds along very particular lines. We get the impression that during the morphogeny of Spongiae a process takes place that is opposite to the process which can be observed in Eumetazoa. The primitive "ectoderm," i.e. the foremost part of the spongula, develops into the definite "entoderm," and the primitive "entoderm" into skin, this into the "ectoderm." For this reason Spongiae have been called Enantiozoa (i.e. animals with the two strata of body inversed) by Delage. Naturally, this inversed character is relative only i.e. in comparison to the development that can be observed in Eumetazoa. In fact, we have here a particular characteristic of Spongiae which has been developed during the course of their own phylogeny. It is therefore better not to speak in connection with Spongiae about an ecto- or an entoderm but rather to use special names, e.g. *pinacoderm* and *choanoderm*. The facts themselves cannot be changed. Yet Tuzet gives a description of an isolated case among Calcispongiae where the extroversion of the spongula blastoderms can be observed. A comparison with the only slightly similar case in the

ontogeny of *Volvox*, is in this connection completely out of place. *Volvox*, is in fact a real alga in spite of its slight resemblance to an animal (its spheric form, free swimming ability). The very rare appearance of an organelle in some Eumetazoa which resembles more or less the "collar" of the choanocytes in Spongiae is too insignificant to be used as a proof to support the thesis that Spongiae are really Coelenterata, and it can be explained by the fact that both Parazoa as well as Eumetazoa arise from the ancestors of Flagellata (i.e. the scattered appearance of similar genes).

Disregarding the fact that the arguments brought forward by Tuzet cannot be considered sound, we must emphasize that the principal mistake in this kind of reasoning lies in the wrong belief that individual morphological or morphogenetic features and characteristics can represent the special type of organisation of Spongiae; in reality, this is represented by their special "nature," so as to say by the whole spirit of the organisation of Spongiae, and by their way of life. Again and again it is necessary to point out that the Spongiae have neither a digestive canal nor an oral opening. To this one could remark that in this respect Spongiae do not represent a unique case; even among the genuine Eumetazoa there are some in which we can find neither an oral opening nor a digestive canal, e.g. among the extreme endoparasites, or in the strongly aberrant *Pogonophora*. Nevertheless, there is a basic difference between Spongiae and these cases observed in Eumetazoa. It is beyond any doubt that in the case of the parasitic Eumetazoa and the freely living Pogonophora the absence of the oral opening and of the digestive canal is nothing but a secondary phenomenon. Spongiae, on the other hand, indubitably have primarily neither an oral opening nor a digestive canal, and this is a consequence of their special organisation. The feeding system with its numerous pores, the canal system with layers of choanocytes in chambers separated from each other that serve to maintain the flow of water, the larger aperture for the discharge of surplus water, and many other things, all this is

unparalleled in other animals. In addition to this comes the special kind of ontogeny.

Finally, when we study attempts to construct the phylogeny of Spongiae as if they had the nature of Coelenterata (Remane, Jägersten)—these attempts must be considered as quite unsuccessful—then it actually becomes clear that Spongiae are really something "exceptional," and that they have developed independently from Protozoa, most probably out of Choanoflagellata. (Hadži, 1917). Yet even here it remains impossible to get ahead without a grain of imagination; we must use it to construct the phylogenetic processes of sponge evolution since it is completely hopeless to expect that we will ever run into any new documents which will help us to construct an actual phylogeny of Spongiae. Naturally enough, such an artificial construction, too, must be based on the actual facts that are now accessible. The scheme must be as close as possible to reality.

Since the Spongiae with their structure, their way of life, and their individual development represent something different from all other Metazoa, it must be expected, and actually reckoned with, that their phylogenetic evolution, too, was a special one. It is therefore quite improbable that the ancestors of Spongiae could be similar to gastraea. Here we run into very great difficulties when we try to construct the origin of Spongiae. We cannot expect any palaeontological evidence. We must limit ourselves to comparative morphology where, too, we are completely unable to make any progress without some imagination. Nevertheless, our scientific imagination—let us call it so, though it is usually called speculation—must be kept in check and within the limits of probability. The reconstruction must correspond to the factual material that is available.

On the basis of my studies on Spongiae (Hadži, 1917) I constructed a phylogeny of Spongiae and submitted this to the International Congress of Zoologists at Budapest in Hungary (Hadži, 1929). This construction was later somewhat improved

and is reproduced in the present volume (Fig. 1). According to this hypothesis the evolution of Spongiae progressed completely independent from that of Eumetazoa. The starting point was probably the freely swimming colonies of Mastigophora of the subtype Choanoflagellata. The subindividuals were

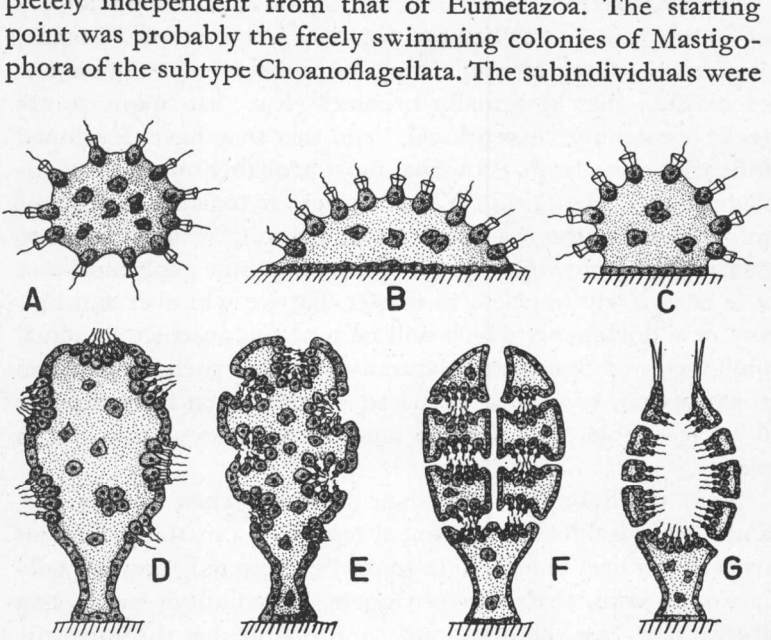

Fig. 1. Hypothetical construction of the evolution of the sponges. A, free swimming phase resembling *Proterospongia* sp.; B—C, the beginning of the sessile phase; D—E, erect phase with the formation of chambers; F, primitive phase of the heterocoelic state; G, homocoelic phase. (After Hadži, somewhat altered.)

kept together by means of a richly secreted jelly in a way which can even now be observed among Choanoflagellata in the genus *Proterospongia*. The existence of this form of Choanoflagellata, which was first described by Saville Kent, was disbelieved and it was considered that we did not have here an independent animal but rather a surviving fragment of a real sponge. In the meantime, another species of the same genus has been described, so that now we have not only the old species *Proterospongia haeckelii* S. Kent, (Gröntved, 1956; Lackey,

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