SPONGE PECULIARITIES AND THEIR IMPACT ON GENERAL BIOLOGY AT THE THRESHOLD OF 2000

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ABSTRACT

A survey of sponge research trends from 1870 to 2000 shows a turning point around 1970, with a growing expansion in number of papers, the rise of new fields such as ecology and the explosion of the new sector of applied research in the chemistry of natural products. Sponge research has had a major impact on general biology after the acknowledgement that sponges evolved early from a common ancestor with other animals. Sponge peculiarities, with the lack of tissues and organs and of well defined nervous and muscle systems, represent a key point to understand further animal evolution and their changes in organization.

A look to the future of sponge science shows the need for an extension of biological and genetic molecular research but also of basic knowledge coming from taxonomy and ecology. The here analyzed sponge research trends show that these sectors are in expansion also to-day.

KEY WORDS

Sponge research history, sponge research trends, sponge research impact on general biology, *Hox* gene.

INTRODUCTION

We are at the beginning of a new millennium and at the end of a century of great scientific achievements. It is largely acknowledged that in the second half of the 20th century, biology, especially with the rise of ecology and molecular biology and the related advanced biotechnologies, has reached the forefront of scientific development. But what is the present situation for sponges? To understand the present state of spongology, in relation to its contributions to general biology it is useful to give a retrospective view of the historical course of spongological research. But, firstly, I would like to make some remarks on the history of spongology in Italy.

It is well known that the contribution of Italian people to the pioneering phase of sponge study, with first illustrations of species and debates on the animal nature of Sponges was considerable during the sixteenth, seventeenth, eighteenth and the first half of the nineteenth century. Names such as those of Donati, Marsili, Spallanzani, Olivi, Risso, Nardo and Delle Chiaje, among others, are well known. On the contrary, a considerable eclipse occurred in the second half of the nineteenth and in the first half of the twentieth century. Only occasionally we find some Italian works on sponges, as the observations at the Zoological Station of Naples by LO BIANCO (1909) on their reproductive periods. Significantly, the first extensive studies on the Sponges of the Bay of Naples were performed not by Italians but by two foreign scientists, VOSMAER (1933) from the Netherlands and the Frenchman TOPSENT (1925).

The development of spongology in Italy in the second half of the twentieth century takes its origin from a somewhat fortuitous event after the end of the last world war in 1945. I was beginning my studies on Natural Sciences in Naples when I was charged by my professor of Comparative Anatomy and Zoology, Mario Salfi, an Ascidian specialist, to study sponges at the Zoological Station because "nobody studies Sponges in Italy". I found many difficulties in this because the only works on the sponges of the Bay of Naples, were the monograph by Vosmaer which has very nice illustrations. However, Vosmaer had an extreme tendency to lump species and the other very parsimonious and little illustrated paper of Topsent, could not help me too much. However, difficulties were overcome and I had after several students that worked on sponges and in turn instructed other students. Sponge study is difficult but also increasingly attractive in the framework of the modern biology. I think that this is the main reason why, compared with 50 years ago, a growing number of people in Genoa, Ancona, Bari, Naples, Perugia and elsewhere in Italy form a flourishing spongological community now.

SPONGE RESEARCH TRENDS FROM 1870 TO 2000

The review of sponge research trends reported here aims to give quantitative answers on some of the following questions. In what measure there was in the history of recent spongology an increase of published papers? And how this increase, regarded the different sectors, as systematics, cytology, ecology, etc. in which, conventionally, spongology may be subdivided? When significant new sectors have arisen? My data compare the number of publications in 14 triennia (in total 42 years) chosen with ten years intervals from 1870-72 to 1998-2000. The sources are Vosmaer's bibliography (VOSMAER, 1928) for the triennia 1870-1872 and 1880-82 and the Zoological Record for the other triennia from 1890-92 to 1998-2000 (MINCHIN, 1890, 1891, 1900, 1901, 1902; HANITSCH, 1892; SOLLAS, 1910, 1911,1912; WOODCOCK, 1920, 1921, 1922; BURTON, 1930, 1931, 1932, 1940, 1941, 1942, 1950, 1951, 1952; WARE, 1960, 1961, 1962; ANON., 1970, 1971, 1972, 1980, 1981, 1982, 1990, 1991, 1992, 1997-98, 1998-99, 1999-2000). In fact Vosmaer's bibliography is more complete for the first two triennia than the Zoological Record. On the contrary, Vosmaer's bibliography, which ends in 1913, becomes less complete than the Zoological Record from 1890 onwards, especially for the paleontological papers.

The number of papers was assessed for each triennium and recorded both for the neontological and paleontological literature. An analysis of the development of sponge research sectors was made only for the neontological literature. Considering the introductive character of this speech I have singled out only general sectors. Indeed, a further subdivision in more specialized topics was not an easy task, especially after 1970, due to a growing tendency to the interdisciplinary blend of methods and subjects shown by several papers. Obviously, there is a different degree of completeness of the Zoological Record lists in different triennia. It is likely that the accuracy increases with later issues, those after 1970, that are compiled not by single authors but by the staff of the Zoological Society of London. The last triennium runs from 1997-98 to 1999-2000, the latest report to be published, so the ten year gap with the previous triennium could not be respected. A subjectivity in paper repartition among different sectors cannot be avoided. I think, however, that these biases should not alter substantially the general trends here illustrated.

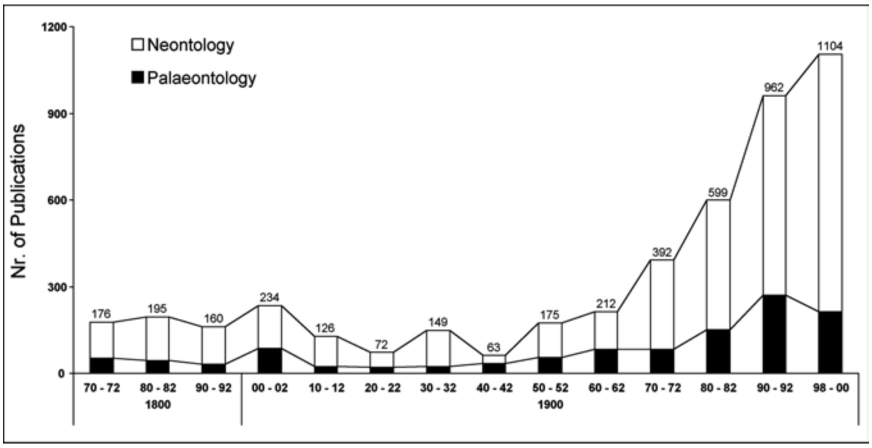

Fig. 1. The trend in general sponge publications between 1870 and 2000. Publication number refers to triennia.

The general trend of sponge neontological and paleontological publications is shown by Fig. 1 The record regards a choice of 14 triennia, and then a total of 42 years between 1870 and 2001.

The total number of recorded publications was 4619 (3450 for Neontology and 1169 for Paleontology). Neontological publications represent 74.7 % and paleontological ones 25.3 % of the total number of publications. The trend shows clearly a recent sharp increase in number of publications. This increase for neontology is evident after 1970 and for paleontology only after 1980.

It is interesting to compare sponge publication trend with that of other groups. It was possible to make this comparison with another group of lower metazoa, that of Hydroidomedusae. Research trend in Hydroidomedusae (GRAVILI *et al.,* 2000), reports the total number of publications for year (not for triennia) and between 1910 and 1997. The trend is roughly similar to that of sponges (also in the total number of publications). There is an increase after the second war, a little before that of sponges, and depressions in relation to the two world wars. There are however some differences. A difference in the stronger recent increase of sponge publications is due to the peculiar sector of natural products, which accounts for more than one third of the neontological sponge papers published after 1980. The other, and more significant, difference is a decline of hydroidomedusan publications after 1990, a decline linked essentially to a reduced production in the systematics and ecology areas. On the contrary, sponge trend shows that systematics and ecology areas expanded in the last triennium 1998-2000. It is likely that this depends, at least in part, on the strong renewal of the naturalistic sector of spongology through advanced and biology-related research on systematics and ecology.

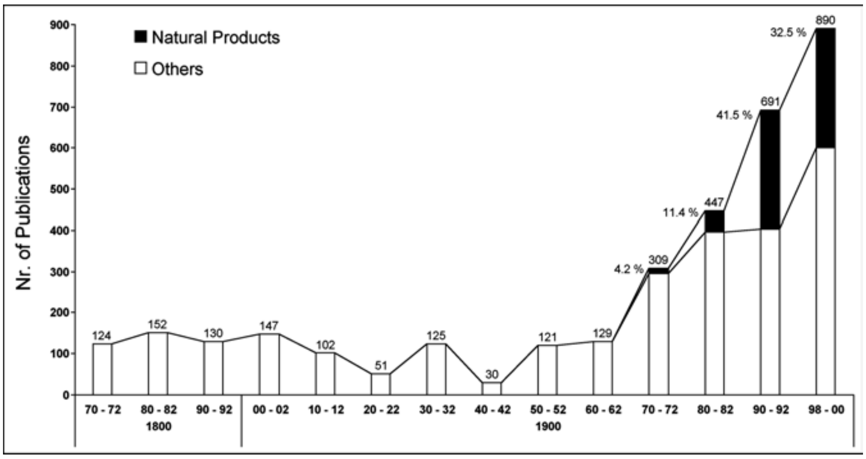

Fig. 2. The trend in sponge neontology publications between 1870 and 2000 The rise of the natural product sector, with indication of percentages on the total publication number, is put in evidence.

The strong impact of the special applied study of natural products on the recent growth of sponge neontological publications is shown in Fig. 2. The percentages of this sector on the total production are 4.2 % in 1970-72, 11.4 % in 1980-82, 41.5 % in 1990-92 and 32.5 % in 1998-2000. The natural product publication number remains stable in the last two triennia (287 in 1990-92 and 289 in 1998-2000) and the percentage decrease is due to the stronge increase of the other sector publications and, in the last triennium, especially those of the naturalistic (systematics and ecology) sector.

For neontology the number of publications until 1970-72 is a little more than 100, except for two depressions during the two world wars, depressions that clearly persist for a significant period after the wars. In 1950-52 and 1960-62 the publication number did not exceed that recorded for the last decades of the nineteenth century. The growth after 1970 is documented by more than 300 publications for 1970-72, more than 400 for 1980-82, about 700 for 1990-92 and 900 for 1999-2001. For paleontology the diagram shows many oscillations and there is no clear evidence of depressions in relation to the world wars (Fig. 1, 3).

The two curves, neontological and paleontological, have a different pattern as shown by the variations in percentages of the paleontological publications The percentages fluctuate irregularly between 19 % on the total in 1930-32 and 55 % in 1960-62 (Fig. 3). In 1940-42 the paleontological publications slightly exceeded the neontological ones. Both show a recent growth in number. The number of paleontological publications, always less than 100 before 1980-82 rises to 150 in 1980-82 and to more than 200 in 1990-92 and 1998-2000.

Trends in sponge research sectors in neontology are represented in Fig. 4. The following sectors were singled out; a systematic sector subdivided into faunistic-descriptive taxonomy and general systematics, phylogeny and evolution including biogeography; an ecology sector with autoecological, synecological and applied topics; a natural product sector; a biology sector comprehensive coverage of all its branches from cytology to physiology, biochemistry, genetics, molecular biology, reproductive biology, sponge cultivation, etc; an "others" sector for treatises, biographies, divulgation, etc.

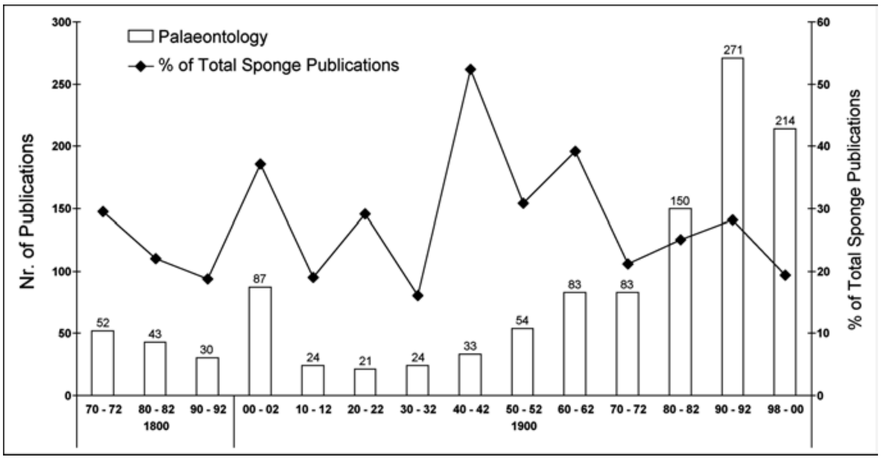

Fig. 3. The trend in sponge paleontology publications between 1870 and 2000. The fluctuation of the percentage on the total number of sponge publications is put in evidence.

Sponge research trends show a dominance (more than half of the total number of publications) of the naturalistic area (systematics and ecology) until 1960-62. In 1970-72 there is a balance of the naturalistic area and other sectors but after 1970-72 the naturalistic area decreases to little more than one third of the total publication number. This decrease in percentage is essentially due to the rise of the natural products sector and so, in conclusion, it may be said that the naturalistic area keeps well until the more recent years. However, the transformation of the naturalistic area is significant. Until 1960-62 the dominance in this area was held by the faunistic and descriptive taxonomy sector. In 1970-72 there is a sharp increase of the ecology sector and after, especially in 1998-2000, the growth of the general systematics-phylogeny-evolution sector: but the faunistic and descriptive taxonomy sector is also flourishing in 1998-2000.

As previously stated, a subdivision of the main areas into more detailed topics, especially ecology and biology, could not be made because it was too difficult, especially after 1970-72. The number of specialized topics such as cell aggregation, immunology, cell motility, bacterial symbiontology, etc. becomes much greater while, on the other hand there is a blend of research methodologies and themes, with boundary research lines that reflect general tendencies of modern biology. Sometimes it is difficult to assign a paper to either the naturalistic or biological area.

The most significant aspects of the sponge research trends, shown by this 130 years-long analysis, emerge particularly after 1970-72. The trend becomes characterized by a sharp increase in the whole scientific production, an impressive growth of the natural products sector, a constant expansion of the naturalistic area (systematics and ecology sectors, especially for the ecology and advanced systematics topics), a sharp expansion of the biology area in 1970-72, but also its virtual stasis in the following triennia; and, reflecting general tendencies of recent biology, the proliferation of specialized topics and the blend of research methodologies and subjects.

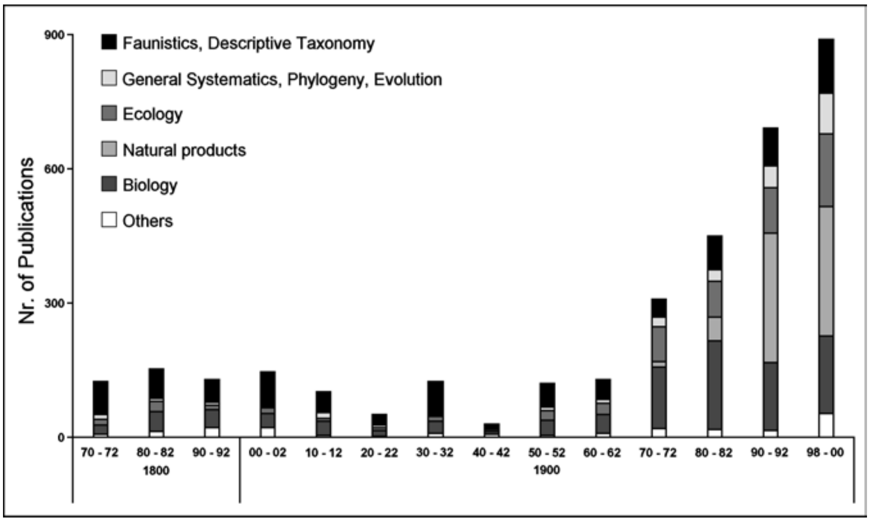

Fig. 4. Trends of different sectors of sponge neontological research between 1870 and 2000. Comment in the text.

THE IMPACT OF SPONGE RESEARCH ON CURRENT GENERAL BIOLOGY PROBLEMS

It is interesting to evaluate the impact that recent sponge research has on current problems of general biology.

It is very important to acknowledge that sponges are not a separate lineage from other metazoa, but that they evolved early from a common ancestor with all other metazoa. They are near, as emphasized by MÜLLER (2001), to the hypothetical ancestral animal, the Urmetazoa, from which the metazoan lineages diverged more than 600 mya. This may be considered as a copernican revolution for spongology because now sponges are included in the system of all other metazoa, to which man belongs. The question of greater or less affinity of sponges with other animals has long been a debated question and opinions ranged from their clear cut separation from metazoa as parazoa to their affinity with metazoa, not even eumetazoa. But now, through molecular data, it has been ascertained that Porifera should be considered as the most primitive recognizable metazoa. The peculiarities of sponges, such as the lack of tissues and organs and that of definite nervous and muscle systems seem to be related not to divergence but to a primitive condition, of a cell and not a tissue and organ organization degree. Sponges have, as shown in recent years by Müller and others, the molecular systems needed for the pluricellular organization of tissues and organs and also the biochemical substances and basic molecular structures for nervous conduction, contractility and locomotion.

As summarized by VACELET (1999) they have receptors and ligands homologous to other metazoa, collagen type IV specific to the basal membrane, g-crystallins, a protein of the vertebrate eye lens, molecules and genes involved in signal transduction, immunorecognition and neurotransmission, that are largely shared with other metazoa. But, renouncing to form definite tissues and organs they have maintained an extraordinary freedom in development and organization. How and why this happened for sponges and not for the other metazoa is clearly a crucial problem for animal evolution. I think that an exploration of the sponge genome and of its regulatory gene systems and gene expression mechanisms, in comparison with those of more organized animals could be very interesting to understand the evolution of genome plasticity, a basic question also for what has been called the Cambrian explosion of animal phyla.

Sponges show many inexpressed potentialities which were expressed in the other and more advanced animal phyla. Why has this happened? Why have sponges, in spite of their great diversity and ecological diffusion, maintained - substantially - the same primitive and cell-level body plan for 580 million years?

I agree with the suggestions made by both LEVI (1999) and VACELET (1999) that the essential distinction between sponges and the other metazoa is not in the occurrence of special filter feeding structures such as channel system and choanocyte chambers but in their degree of cell organization which allows for cell motility and transdifferentiation, plasticity of organization and the absence of true tissues and organs. As already indicated, this view is supported by the Precambrian chinese fossils and also by some deep sea living sponges that lack choanocytes and an aquiferous system.

The history of sponges like that of other groups is full of evolutionary events, extinctions and innovations that gradually brought us to the modern sponge fauna. A significant evolutionary change followed the rise of modern coral reefs in Triassic and Jurassic when sponges were outcompeted by madreporarians as important reef builders (SARÀ, 2000). Sponges found new habits with an enhancement in ecological plasticity and adaptability to different habitats and then in biodiversity. These changes left the fundamental body-plan unchanged. Also in deep sea conditions, as for the carnivorous sponges, a regression of filter feeding structures including choanocyte chambers and the need of larger prey ingestion are recorded. These impressive changes do not signified a body plan transformation with the acquisition of cnidarian structures as digestive cavity and nervous system that could be induced by the new feeding system. We know other conservative animal groups such as the brachiopods, are outcompeted in many habitats by the more advanced bivalve mollusks, but their relict condition is more comparable from an ecological point of view to that of some sponge living fossils, such as the few surviving sclerospongiae or lithistids rather than to the whole and to-day well flourishing sponge phylum. On the other hand, the conservative success of sponges is a different problem from that of bacteria and protists. Considering the fundamental role that bacteria and protists have in all ecosystems, their role, of course, is not comparable with that of sponges.

I think that sponges are not relict animals or living fossils but a flourishing modern fauna living with their primitive organization degree as ancestors of the whole animal evolution. They represent for the evolutionary biology an essential element to understand the presently ignored mechanisms that determined the metazoan body-plan diversification and the rise of the evolutionary key innovations of the animal kingdom.

Another important problem for evolutionary biology is: what were the ancestors of sponges and then of other metazoa? The classical view of separate unicellular eukaryote ancestors for the three multicellular eukaryote kingdoms of Plantae, Fungi and Animals, that address, essentially on paleontological, morphological and embryological data, to a choanoflagellate ancestor for sponges and other metazoa (WAINRIGHT *et al.,* 1993) has been recently challenged by MÜLLER (2001) who proposed a common ancestor for Plantae, Fungi and Animals, based on molecular grounds, as they all share a series of common cell adhesion and intracellular signaling molecules. This is supported by the ZOCCHI *et al.* (2001) data that suggest an ancient evolutionary origin of a temperature signaling cascade in a common precursor of metazoa and metaphyta. However, metazoa including sponges show innovative molecular devices such as highly developed receptor and signaling systems for cell interactions, new immune molecules and morphogens and novel extracellular organic skeletal elements as the collagen.

Other questions arise regarding whether sponges are monophyletic, paraphyletic or even polyphyletic and which higher metazoan groups are directly derived from them. Sponges, in the adult stage, are sedentary organisms that have in common, with the previously indicated significant exceptions, a filter feeding systems with a single layer of flagellated cells (choanocytes) that pumps a unidirectional water current through their body (BERGQUIST, 1978) and especially a fundamental body-plan of cell level organization. Otherwise, they are heterogenous in their morphofunctional structure and in their molecular affinities with other animal groups. Morphofunctional organization clearly separates the Hexactinellida and the sponge-like extinct group of Archeocyatha from the other sponges. According to MEHL *et al.* (1998) and MÜLLER (1998) paleontological, morphofunctional evidence and some molecular data supports the splitting of the monophyletic Porifera into the two subphyla of Synplasma, with the class of Hexactinellida, and the Cellularia, with the classes Calcarea and Demospongiae. For MÜLLER (1998) Hexactinellida with syncitia branched off from a common ancestor before Calcarea and Demospongiae, and Calcarea are closer to the higher metazoans.

In contrast, ADAMS *et al.* (1999) suggest that Porifera may be a paraphyletic and even a polyphyletic group of animals, on the basis of ultrastructural and molecular evidence. According to ADAMS *et al.* (1999) Demospongiae and Hexactinellida form a well-supported clade while excluding Calcarea, which are more closely related to other diploblasts and form a clade with Ctenophora. However, in a recent analysis of the origin of bilaterians made by PETERSON & DAVIDSON (2000), (even if of doubtful phylogenetic origin), Ctenophora are considered as the bilaterian sister group on the basis of shared developmental and genetic characters. This raises again a debated question of general phylogenetics: to what extent molecular-based phylogenies fit with morphological, embryological and paleontological based ones?

The metazoan phylogeny traced by PETERSON & DAVIDSON (2000) on the basis of *Hox* gene evolution puts the sponges with only one Hox-like gene (a proto-*Hox* gene) before the Cnidaria with two *Hox* genes. These are likely to have been derived from the duplication of the proto-*Hox* gene. The Cnidaria are followed by the Ctenophora with three *Hox* genes. Moreover, for PETERSON & DAVIDSON the

Porifera and Cnidaria *Hox* genes are not involved in any sort of A/P vectorial patterning mechanism while the third ctenophoran *Hox* gene is a central class *Hox* gene shared with the bilaterians and then possibly involved in the fundamental body plan structure. However, the function of *Hox* genes in lower Metazoans is controversial. For example, FINNERTY & MARTINDALE (1999) suggest the existence of a gene of *Hox* cluster integrated into animal axial differentiation also in cnidarians, such as corals. This view is supported also by FERRIER & HOLLAND (2001). Sponges, in contrast with cnidarians, are however put before the duplication of the proto-*Hox* gene in the anterior and posterior *Hox* genes.

Another open question is the evolutionary significance of the motile larval stage of sponges that, in contrast to the sedentary adult phase, shows polarity and bilateral symmetry and also the expression of some *Pax* and *Bar* type genes suggesting their possible function in photoreception as indicated by LEYS *et al.* (2000) The evolutionary importance of sponge larvae is emphasized if we connect the view of PETERSON & DAVIDSON (2000) that many stages of animal evolution and many regulatory inventions preceded the advent of the complete *Hox* gene complex and its role in A/P patterning, required by the zootype hypothesis, with the findings of remarkable micrometazoan fossils dated to mid-Neoproterozoic times: (BENGTSON, 1998). Among these are not only poriferan and cnidarians embryos but also bilaterian embryos similar in scale and form to the recent marine larval morphologies: the hypothesis of a larval nature of the Precambrian metazoan microfossils suggests a sort of animal explosion at the larval level long before the well known Cambrian explosion of adult metazoan phyla and this may suggest their neotenic origin. But, there is also the contrasting hypothesis that the ancestral bilaterian animals were small but possessed an adult like body plan. This also in consideration of the fact that feeding marine larvae were successive to the Cambrian explosion of the adult phyla (RAFF, 2000).

It is interesting to note that these problems have been taken into consideration outside the spongologist community by general biologists as shown by the recent insertion in the programs of the Laboratory of Molecular Evolution of the Zoological Station of Naples of a research line on the esonic and intronic genome structure of sponges and on the phylogenetic position of sponge classes.

Sponges are very important not only for general evolutionary problems but also for several aspects that are peculiar to sponges and in the meanwhile of great relevance in biological actuality. Time limits constrains me only to an abridged list. The outstanding potentialities of sponges in reproduction and regeneration represent a stimulating research field of reference for the present focus on staminal cells and cloning. The existence of a primitive unspecialized conductive and contractile system in sponges is a basic leading to the understanding of the evolution of neurosensory and locomotory systems in animals. The occurrence of precursors of an adaptive immune system in sponges, besides the innate (MÜLLER *et al.,* 1999) is a trait that links sponges to the higher evolved animals such as mammals. The extraordinary richness of natural products found in sponges shows their biochemical versatility and stimulate research on the functioning of their genetic system. The general occurrence of intimate endosymbioses of sponges with bacteria, where bacterial biomass may also outweigh sponge biomass suggests that sponges are complex organisms with all the related problems for physiology, biochemistry, genetics and evolution. The bonds that link sponges to their aquatic environment, water and sediment, are more intimate than that for any other free animal group, and therefore raises peculiar physiological and ecological problems. The extraordinary extent of variability and phenotypic plasticity in sponges stimulates taxonomic and evolutionary studies also in relation to the species problem, always a current question for all organisms but especially for sponges.

CONCLUSION

What we can say about the future of sponge research? The future is, obviously, difficult to predict but some possible developments were envisaged during the problem analysis carried out for this paper. Certainly, it may be foreseen that molecular genetic research, which until now has been little developed in relation to the advanced animal models, will increase considerably, to clarify biological problems that regard sponges not only as such but as the ancestors of the animal kingdom. In particular I think that is not too ambitious, to hope that a sponge genome sequence will be produced further into the future. Among the organisms that are now on the road to being sequenced are *Tetrahymena*, fungi, the honey bee, a mosquito, the squid, tunicates, the chicken, bats, the pig and the chimp. Why not sponges, considering their peculiarities and exceptional phylogenetic position?

On the other hand, it is important to remember that any advanced research, in sponges as in other groups, requires the basic naturalistic knowledge derived from taxonomy and ecology. I think that we are all aware that what we know of the basic taxonomy and ecology of sponges, in spite of the amount of work till now produced, is always too little and many exciting discoveries wait us "around the corner". "The crop is large but, unfortunately, workers are few". However, in spite of the present heavy shortage of positions and funds for basic research, we should be optimistic for the future.

The more recent trends in sponge research decribed here indicate that in spite of all the difficulties the interest in the naturalistic area is always alight, and this is a good sign for future.

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