

The scleractinian corals: a perspective

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ABSTRACT. Though scientific interest in scleractinian corals originated in the 16th century, the knowledge base continues to grow and is far from complete. The progress of the research on these organisms is represented here as an exponential process and its history may be divided into three periods. In the beginning, Plant period (1576-1727), these organisms were interpreted as plants. The Animal period (1727-2007) brought in their consideration as animals and includes three phases that introduce new research approaches (phase 1: variability, microstructure, transplantation; phase 2: multiple skeletal characters, global spatial and temporal attention; phase 3: life history, molecular biology). Recently, the number of sources of scleractinian knowledge has increased to five: morphology, paleobiology, ecology, life history and molecular biology. Scleractinian corals are no longer considered alone but as holobionts, along with their symbiotic zooxanthellae and other associated microbiota. The accumulated multidisciplinary data and new integrative concepts urge a holistic interpretation and have been indicating (since 2007) the commencement of the present, Holistic period. This analysis of the current status of scleractinian knowledge provides a list of proposed directions for future research.

KEYWORDS: Taxonomy, morphology, paleobiology, ecology, life history, molecular biology.

1. Introduction

Scleractinian corals have been of interest to scientists since the 16th century and yet our understanding of them remains far from satisfactory. Scientists forming the international Scleractinia Working Group recognized “that existing classification systems for scleractinians are inadequate, and a revised system that better reflects new molecular results needs to be adopted as soon as possible” (Budd et al., 2010). In addition to the higher classification, “generic definition of the Scleractinia remain[s] in chaos” (Stolarski et al., 2006). Though new research approaches over the past half century have contributed considerably to resolution of the taxonomy of this group, the existing concepts

are being challenged and accumulated data are in need of new interpretations. Presently, “the combined use of morphological and molecular tools holds great promise for ending confusion in scleractinian systematics” (Budd et al., 2010). Studies of life history and ecology also are contributing to the holistic understanding of the Scleractinia. This article reviews the progress of scleractinian knowledge and its current status and provides suggestions for future work.

2. History

The goal here is not to present a detailed history of scleractinian studies but rather to trace the progress and timing of research.

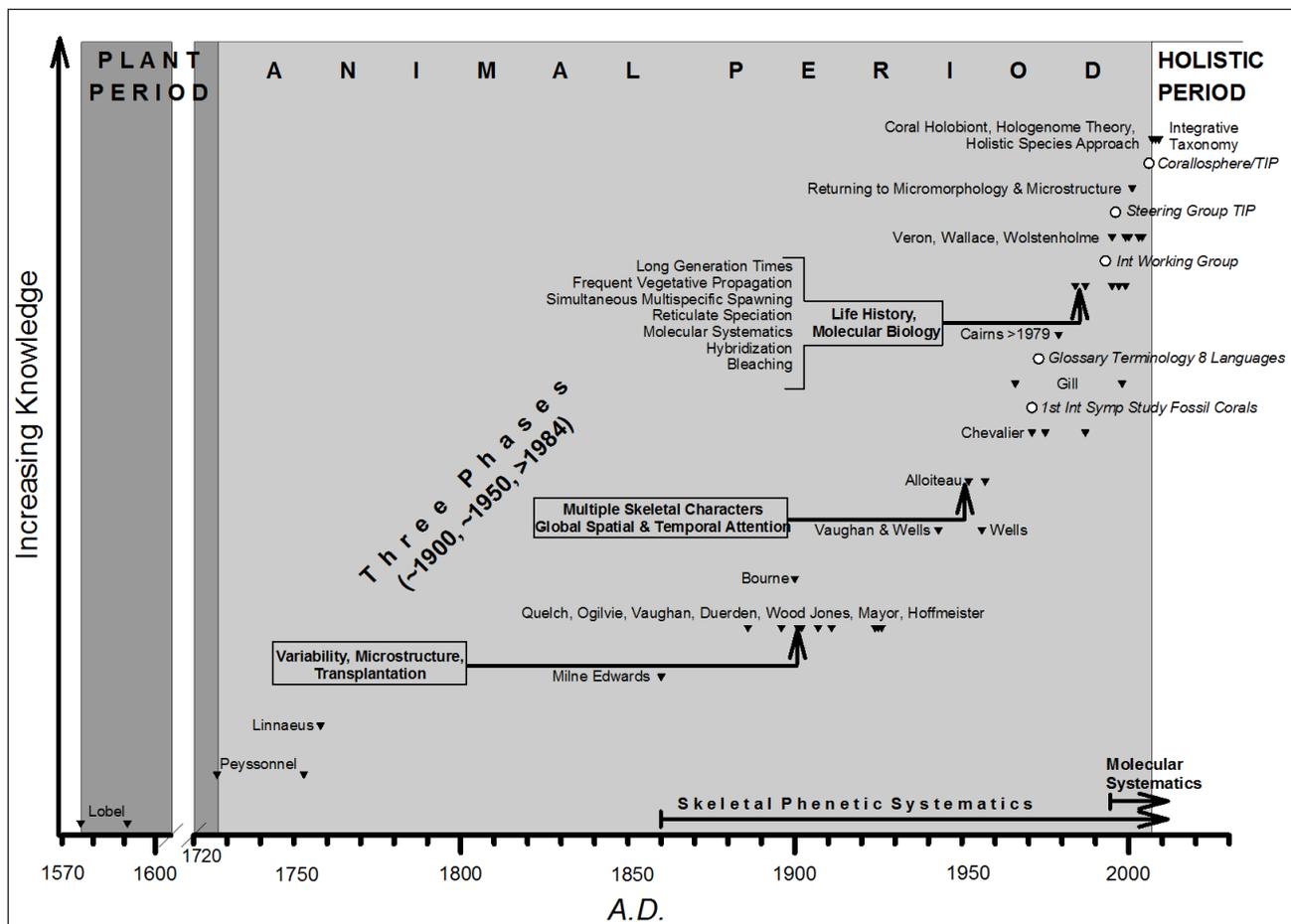


Figure 1. Progress of scleractinian knowledge. Legend: ▼ : A new step in research. ○ : Multinational collaboration.

The history of research on scleractinian corals may be divided into three periods. A graphical presentation of the progress of scleractinian knowledge reveals here an exponential growth (Fig. 1).

The **First period** (1576-1727) may be named the **Plant period**. During this time, scleractinian corals were interpreted as plants. M. Lobel illustrated two scleractinians, *Dendrophyllia ramea* and *Madrepora oculata* in 1576 and in 1591 (Vaughan & Wells, 1943), and naturalists illustrated many scleractinians as botanical objects.

The **Second period** (1727-2007) may be called the **Animal period**, during which scleractinian corals were considered animals. Peyssonnel was the first, in 1727 and 1753 (Vaughan & Wells, 1943), to maintain that they are not plants but animals. In 1758, the 10th Edition of Linnaeus's "Sistema Naturae" marked the starting point of zoological nomenclature. Initially, studied coralla were found fortuitously. The taxonomy was purely typological. Milne Edwards published "Histoire naturelle des Coralliaires" (1857-1860) based on living and fossil species.

This period includes three phases that introduce new research approaches. They are not applicable to the azooxanthellate representatives of the order because their predominantly deep-sea distribution made *in situ* access for study difficult, and those azooxanthellate corals living in shallow water are small and frequently cryptic. The time around the end of the 19th and beginning of the 20th centuries was marked by the **first phase (variability, microstructure, transplantation)**, which (except for microstructure) resulted from entrance into the natural coral habitat. During this phase, the extraordinarily rich variability of coralla was established, the species problem was considered and formae were introduced (Quelch, 1886; Vaughan, 1901, 1907; Hoffmeister, 1925, 1926). Aggregated colonies (Duerden, 1902) and growth forms (Wood Jones, 1907) were described. The new knowledge prompted transplantation experiments (Vaughan, 1911; Mayor, 1924; Mayor's work reviewed in Stephens & Calder, 2006). In addition, skeletal microstructure was applied as the basis of higher classification (Ogilvie, 1896). The order Scleractinia was created by Bourne in 1900. During the first half of the 20th century, paleontologists were leading the research and synthesized the results on scleractinians (Vaughan & Wells, 1943; Wells, 1956).

A **second phase of the second period (multiple skeletal characters, global spatial and temporal attention)** of research on Scleractinia marked the middle of the last century. By paying special attention to micromorphology and microstructure, the paleontologist J. Alloiteau (1952, 1957) founded a Parisian coral school whose members studied Scleractinia of all geological periods beginning with those of the Triassic (Sorauf et al., in this volume). His successor Chevalier (1971, 1975, 1987) started *in situ* research on living corals and published the most complete descriptions on skeletal variability ever produced. Gill (1966-1998 in: Lathuilière & Barta-Calmus, 1999) pioneered the study of functional micromorphology. SCUBA made the euphotic and the upper part of the mesophotic habitat accessible for research (Zlatarski & Martinez Estalella, 1982; Zlatarski, 2008, 2009). Since the 1970s, Cairns (2007) and Zibrowius (1980) published revisions of museum material and new collections of azooxanthellates.

A **third phase of the second period (life history, molecular biology)** began in 1984 as a series of discoveries of new aspects of scleractinian nature including: evolutionary consequences of long generation times and frequent propagation through vegetative fragmentation (Potts, 1984), the existence of simultaneous multispecific spawning (Harrison et al., 1984; Oliver & Willis, 1987), the possibility for reticulate speciation (Veron, 1995), the usage of molecular systematics (Chen et al., 1995), the presence of introgressive hybridization (Willis et al., 1997), the impact of bleaching (Hoeg-Guldberg, 1999) and unusual growth forms in aquaria (Carlson, 1999). Veron (1995, 2000, 2003) summarized his worldwide observations on zooxanthellate Scleractinia. Both mitochondrial and DNA markers revealed incongruence with the conventional gross-morphology-based taxonomy when traditionally defined families were shown to be polyphyletic (Chen et al., 1995; Romano & Palumbi, 1997).

Wallace (1999) published a revision of *Acropora*, the most speciose scleractinian genus in the world, using the contemporary approaches. The returning of attention to the micromorphological and microstructural characters suggested a possibility for harmonizing skeletal and molecular data (Stolarski & Roniewicz, 2001). Difficulty in finding molecular markers suitable for differentiating species-level relationships compounded the problem of large-scale polyphyly. Scleractinian corals were shown to have slowly evolving mitochondrial genomes (Shearer et al., 2002). After analysis of morphological, molecular and reproductive criteria, Wolstenholme (2004) concluded that hybridization events of corals occur in nature but are not frequent. In the late 1980s Hoeksema began publishing on the taxonomy, ecology, phylogeny and biogeography of mushroom corals (Fungiidae) (Gittenberger et al., 2011).

At the beginning of this century we "have a greatly improved toolbox for studying scleractinian evolution" (Budd et al., 2010), but the knowledge about this group is coming in from different disciplines. As a consequence, results concerning morphology, paleobiology, ecology, life history and molecular biology need a holistic approach for analysis. The notion of the coral holobiont no longer considers the coral animal alone, but with its symbiotic zooxanthellae and all associated microbiota in connection with coral health, and has led to the theory of hologenome evolution (Rosenberg et al., 2007). These changes together with the holistic species approach (Zlatarski, 2007) and the increasingly integrative character of scleractinian research (Zlatarski, 2008, 2009) indicate the commencement of a **Third period** (2007-present), which may be named the **Holistic period**.

Multinational collaboration started with the First International Symposium on the Study of Fossil Corals in 1971 in Novosibirsk (Russia), where the International Committee on Fossil Corals was elected and the International Newsletter of ICFC (now Fossil Cnidaria & Porifera) was started. A glossary of equivalent terms for scleractinian studies in eight languages followed (Zlatarski, 1973), as well as the International Working Group on Scleractinian Corals (Löser & Rosen, 1993), the Steering Group for Revision of Scleractinia for the Treatise on Invertebrate Paleontology (TIP) (since 1996, led by Rosen), the CoralloSphere (since 2006, <http://www.corallosphere.org>) and TIP Project (Stolarski et al., 2006).

3. Current status

The species richness of Scleractinia has not even approximately been calculated. Recently 1,482 valid extant species were recognized, a little more than half of them zooxanthellate (Cairns, 2007). The higher taxonomic categories are pending revisions. Currently, "[c]oral taxonomy and systematics continue to be plagued by a host of problems" (Huang et al., 2009).

The sources of scleractinian knowledge today are various: morphology, paleobiology, ecology, life history and molecular biology. Their combined use for studying azooxanthellate scleractinians indicates the evolutionary origin of the Order deep in the Paleozoic (Stolarski et al., 2011).

Skeletal **morphology** has been studied since the dawn of scleractinian research and until less than two decades ago was the exclusive basis for scleractinian classification, but it still lacks information about variability and microarchitecture. Where sampling is insufficient (e.g., collecting only clear representatives of different phenotypes and ignoring specimens showing intermediate characters or bimorphic colonies), it presents an impediment for obtaining a more objective taxonomy because it shows only part of the phenotypes' picture. Neglected, the variability in different levels of biological organization (a structural element, corallite, colony, etc., Zlatarski & Martinez Estalella, 1982) also introduces a typological component into taxonomic practice and hinders understanding of intraspecific polymorphism, plasticity and the process of speciation. Study of taxonomically "atypical" portions of coralla may indicate that coral life is under stress (Nothdurft & Webb, 2009). Nanostructure data are promising for phylogeny analysis (Janiszewska et al., 2011). Information on skeletogenesis has shown to be important for conclusions on past and future climates, as well as for coral taxonomy (Clode et al., 2011). A novel non-destructive technique

based on micro-computed tomography was introduced for measuring skeletal growth (Roche et al., 2010). Existing museum collections may be useful for determining long-time biodiversity changes (Hoeksema & Koh, 2009; Hoeksema et al., 2011). However, no large extant coralla collections are realized recently, and the old are not always available or digitally documented, with the exception of the Dana types digitized on the Smithsonian Institution web pages and the Cuban collection of 4,980 SCUBA-collected specimens from the early 1970s available in multimedia format with digital photos of all specimens.

Paleobiology continues to contribute knowledge on past biodiversity and coral evolution, and is now also contributing to examinations of ecology, climatology, biological interaction, life strategies and reef building. Paleocological analysis of assemblages under sediment input (Sanders & Baron-Szabo, 2005), paleoenvironmental implications of free-living colonies (Sorauf & Harries, 2009, 2010; Harries & Sorauf, 2010), the roles of clone-clone interactions in building reef framework (Fagerstrom & West, 2011), fossil clonal fusion (Helm & Schülke, 2000), conspecific and heterospecific interactions in nonextant material (West et al., 2011), and the evolutionary importance of hybridization in the geological past (Budd, 2010; Zlatarski, 2010) have received attention. Paleocology is placing the modern biodiversity crisis in an historical context (Pandolfi, 2011). Scleractinian evidence contributes to paleoclimatology by no supporting permanent El Niño (ENSO) during the Pliocene warm period (Watanabe et al., 2011). Caribbean paleontological records are being used for identifying analogues to 21st century Earth conditions (Klaus et al., 2011). Caribbean coral reef development over the last 28 million years was shown to be independent of scleractinian diversity and this poses a question for researchers and reef managers, to choose between encouraging reef development or maximizing diversity of reef-corals (Johnson et al., 2008). Data of fossil corals were used for the analysis of generation, senescence and “hopping” of paleobiodiversity hotspots (Renema et al., 2008). There are indications of repeated loss of coloniality and symbiosis in scleractinian evolution (Barbeitos et al., 2010). The skeletal growth information is under-exploited (Lough, 2008). The coral “fossil record remains a largely untapped resource for understanding evolutionary rates and patterns” (Knowlton et al., 2006).

The migration of species farther from the equator, phase shifts and alternative states on coral reefs are changing our knowledge of scleractinian **ecology** and have implementation in paleocological interpretations (Precht & Aronson, 2004; Norström et al., 2009; Yamano et al., 2011). The research is focused predominantly on shallow waters. Experiments demonstrated the functional significance of light-induced morphological plasticity (Ow & Todd, 2010) and environmental control on corallite morphology (Klaus et al., 2007). The latter work showed that the characters in thin sections are more useful for species identification while the characters of calical surface provide information for interpreting the adaptive significance of species differences. The phenotypic differences between ecomorphs were found to be maintained in sympatry despite evidence of hybridization (Carlson & Lippé, 2011). The studies of mesophotic habitat noted high biodiversity and endemism, but the mechanisms for these patterns have not been established (Lesser et al., 2009). Also, the expected recruitment of larvae of deep water origin into shallow habitats was not always confirmed (van Oppen et al., 2011). The effect of ocean acidification on corals is presently the focus of study (Erez et al., 2011).

Recent years have brought considerable contributions to scleractinian **life history**. “The ongoing global renaissance in coral reproduction research” (Harrison, 2011) established data on sexual reproduction for 444 species. Of them, 64.5% are hermaphroditic broadcast spawners, 19.5% gonochoric spawners, with fewer hermaphroditic and gonochoric brooders and a number of species demonstrating mixed sexual patterns/sex change. Multispecific spawning was recorded in many reef regions. Pioneering achievements include: analysis of systematic and biogeographical patterns in the reproductive biology (Baird et al., 2009), correlated evolution of sex (gonochorism/hermaphroditism) and reproductive mode (brooding/spawning) (Kerr et al., 2011) and observations that hybrids can be more fit than both parents,

occupy new niches and have a bioconstructive role (Budd, 2010; Zlatarski, 2010). The questions of coral allorecognition and xenorecognition (Rinkevich, 2004), chimerism (Puill-Stephan et al., 2009), skeletal calcification (Allemand et al., 2011) and diseases (Rosenberg & Kushmaro, 2011) received attention. The established evolutionary significance of hybridization is now posing a serious challenge to conservation policy and legislation because of the ignoring of the hybrids (Richards et al., 2010). The finding that climate change induces demographic resistance to disease in novel coral assemblages is important for projections concerning ecosystems under climate change (Yakob & Mumby, 2011).

Molecular biology has changed the way we think about the systematics and the evolution of the Scleractinia, although we are just beginning to realize its full potential. The lack of diversity in mitochondrial DNA makes it more difficult to establish intraspecific relationships with this type of genetic marker. Molecular analyses revealed that while the extant Scleractinia are monophyletic, families within the order are not (Fukami et al., 2008). Even more striking than the general lack of congruence within families is the amount of gross-morphological convergence between species in geographically distinct ocean basins (Fukami et al., 2004). Studies are focused on exploring the use of micromorphological, microstructural and nanostructural skeletal characteristics along with genetic data to present a more complete picture of the Scleractinia (Cuif et al., 2003; Benzoni et al., 2007; Budd & Stolarski, 2009, 2011; Budd et al., 2010; Kitahara et al., 2010; Gittenberger et al., 2011; Huang et al., 2011; Janiszewska et al., 2011). Molecular data also contribute to understanding reef connectivity by demonstrating historic and current patterns of connectivity between populations (Hellberg, 2007), the developmental and regulatory pathways in corals (Grasso et al., 2008; Schwarz et al., 2008), the innate immunity and resistance to infection (Vollmer & Kline, 2008), and the hologenome’s response to environmental change and coral-specific gene families with predicted roles in calcification (Shinzato et al., 2011).

4. Future directions

Recent progress in scleractinian research has accumulated a considerable base of temporal and spatial information pending new interpretation and urging efficient holistic, multidisciplinary scientific collaboration. The following is a list of proposed directions for further attention, and serves as an appeal for discussion and steps toward future research in these areas:

- Material – expand the sample size of material collected to tap the phenotypic and genotypic diversity, the geological past, and the ecological distribution of species (Hoeksema et al., 2011), photo-digitizing collections in multimedia format, using the Coral Virtual Microscope Database System of the Coral Disease and Health Consortium, strong partnership between natural history collections holders and global change biologists (Johnson et al., 2011), develop standards for holistic collection of material and photodocumentation and organize virtual species museum (idea of Dr. V. Kosmynin, personal communication);
- Phenotypic variation – study variability at multiple levels, exploring plasticity (Shaish et al., 2007), intraspecific polymorphism and hybrids;
- Ontogeny – gain further insight into reproduction, septal insertion, astogeny, pathology and senescence and exploit skeletal growth records;
- Functional macro- and micromorphology – bring to light these important aspects of morphology;
- Paleobiology – focus research on temporal morphological diversification, reversed actuopaleontology (Zlatarski, 2010), forecasts from the past, sea-level changes as speciation “pumps”, species reshuffle for biodiversity conservation (Precht & Aronson, 2004), the importance of hybridization in the geological past and fossil behavior;
- Molecular biology – connect new molecular findings with taxonomic revision, engage in more integrative collaborations and maximize the potential of molecular techniques in life history, physiology, ecology and skeletogenesis;
- Skeletogenesis – further explore the interrelation between

animal and skeleton, and how the genes of soft organisms control the formation of an extracellular 3D-skeleton, particularly the physiology of skeletogenesis (ion transport, organic matrix characterization);

- Mesophotic and deep-sea habitats – prompt scleractinian research and evaluate their conservational and evolutionary potential;
- Speciation – better understand hybridization, histocompatibility and chimeras;
- Coral holobiont and reef ecosystem – direct attention to their coevolution in temporal and spatial dimensions;
- Integrative approach to harmonize the data of all sources of knowledge;
- Preparation of specialists – workshops of the International Association for the Study of Fossil Cnidaria and Porifera, the Projects Corallosphere/TIP and the Integrative Graduate Education and Research Traineeship;
- The importance of coral hybridization urges re-evaluation of species and ecosystem conservation approaches and including scleractinian hybrids in conservation policy and legislation.

5. Acknowledgements

Thanks to Mrs. Margaret McNulty of the Barrington Public Library in Rhode Island for her assistance in obtaining access to many publications and to Mrs. Vera Zlatarski for improving the English. The manuscript benefited a great deal from the suggestions of Dr. S. Cairns, Dr. G. Webb, Dr. V. Kosmylin and two reviewers, Dr. J. Sorauf and an anonymous one. The second author contributed to this article with respect to molecular biology.

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