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Need for a more integrative approach to scleractinian taxonomy

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Abstract. The history of scleractinian taxonomy is divided into six periods: the original, purely typological, was based on scarce coralla material; the second, starting at the end of nineteenth century, originated with visiting natural habitat and established variability; the third commenced in the 1930s with detailed skeletal study; the fourth began in the 1950s with scuba access to coral habitat; the fifth began in the 1980s following fundamental discoveries in life history and molecular genetics; and the sixth started in 1995, when data from molecular genetics opened a new avenue for scleractinian megataxonomy, contradicting conventional gross-morphology taxonomy but resulting congruent with skeletal histology and ornamentation. Currently, there are four sources of scleractinian taxonomic information: morphology, paleobiology, developmental biology and molecular genetics. Taxonomy is important for understanding scleractinian biodiversity and reef conservation. However, the taxonomy is fragmented and the nomenclature tangled. The e-dimension benefits have not yet been realized and the New Taxonomy not yet arrived for scleractinians. Vision and teamwork are needed for a more integrative taxonomy. The Atlantic Scleractinia Initiative seeks to address the following points: massive sampling, study of the mesophotic habitat, collection access, analysis of phenotypic diversity, life history, geological history, molecular genetics, cyberinfrastructure and education of specialists.

Key words: Scleractinia, taxonomy, microstructure, biodiversity, reefs.

Introduction

For a long time, the taxonomy of scleractinians was based only on macromorphologic skeleton characters. This changed fundamentally in the second half of the last century, and even more during the last two dozen years, following a series of important discoveries related to skeletal ornamentation and histological microstructure, paleobiology, ecology, roll in the reef ecosystem, life history and molecular genetics. With new knowledge, the taxonomy became very complex, and it now plays a crucial role in the understanding of scleractinians, their biodiversity and importance for the fragile reef system.

This note provides a brief historical review of scleractinian taxonomy and an analysis of its current state, and concludes with recommendations for a more integrative approach.

History

The history of scleractinian taxonomy can be divided into six periods which demonstrate its accelerated development.

First period

Originally, studies were based on scarce coralla material found on beaches or during fishing activities, and the taxonomy was *purely typological*.

Second period

At the end of the nineteenth century, investigators began visiting the natural coral habitat. Field observations and systematized sampling demonstrated the presence of *scleractinian variability*. The forma category was introduced as a taxonomic subdivision of the species (Quelch 1886; Vaughan 1901, 1907). Transplantations first demonstrated induced change in coral growth form (Vaughan 1911). During the first half of the twentieth century, these corals did not attract much attention from zoologists. Two American paleontologists synthesized the knowledge on Scleractinia (Vaughan and Wells 1943; Wells 1956).

Third period

In late 1930s, in France, another paleontologist commenced a revision of the classical fossil coral collections, paying special attention to skeletal ornamentation and histological microstructure (Alloiteau 1952, 1957), and put together a team of specialists on scleractinians of different geological periods. The ornamentation of the radial elements was considered to reflect their histological structure and was used in the scleractinian systematic. The taxonomy was based on *more skeletal characters* than previously. Unfortunately, this improved taxonomic methodology was not applied for long outside the

disciples of the Parisian school, which may have been due to language barriers.

Fourth period

Starting in the 1950s, scuba made the *coral habitat accessible* for investigators. Pioneering work (in order of execution) in Jamaica (Goreau 1959, Goreau and Wells 1967; Wells 1973), the South Pacific (Chevalier 1968, 1971, 1975), Madagascar (Pichon 1964), the Red Sea (Scheer, 1964; Loya and Slobodkin 1971), Cuba (Zlatarski 1982) and Australia (Veron and Pichon 1976, 1980, 1982; Veron and Wallace 1984; Veron et al. 1977) established an extraordinary variability of the skeletal morphology on a global scale and shed light on the role of Scleractinia in the reef-building process. These findings coincided with the results of massive paleontological sampling of scleractinians from different geological periods, from their appearance in the Triassic to the present. The global spatial and temporal variability translated into serious taxonomic difficulties for species identification, which is basic for reef study. A reevaluation of the scleractinian taxonomy was needed (Zlatarski 2007). The last synthesis on scleractinians (Chevalier 1987) presented the enormous mass of information collected to date and the dilemmas of this period.

Fifth period

Since the 1980s, a series of *fundamental discoveries in life history and molecular genetics* broadened very quickly the existing scleractinian knowledge in uncharted aspects: long generation times and frequent propagation fragmentation (Potts 1984), simultaneous multispecific spawning (Harrison et al. 1984; Oliver and Willis 1987), reticulate concept for coral speciation (Veron 1995), lateral gene transfer or hybridization (Willis et al. 1997), astonishing growth forms in aquaria (Carlson 1999), coral symbiosis (Hoegh-Guldberg 1999), coral health and the role of microorganisms in relation to it (Rosenberg and Loya 2004; Reshef et al. 2006), and the notion of coral holobiont (Rosenberg et al. 2007). Research interest in scleractinians ceased to be focused exclusively on morphology. Instead it expanded widely in numerous new directions (Zlatarski 2007) and became an important and integral part of reef investigations. The time had come to reorient scleractinian research and for a basic change in the taxonomy.

Sixth period

So much has been learned over the past dozen years, as molecular genetics opened a new avenue for scleractinian megataxonomy (Chen et al. 1995; Veron et al. 1996; Romano and Palumbi 1996; Romano 1996; Romano and Cairns 2000). Strikingly, due to the findings of homoplasious gross-morphology characters, the results were non-congruent with the conventional taxonomy, based on macromorphologic characters. Most traditional supra-families and some families and genera were recognized not to be monophyletic units and this led to a taxonomic impasse. Not surprisingly, the solution came from the previously-introduced (during the third period) but neglected methodology of more detailed morphological study, and from rediscovering the septocentric scleractinian taxonomy (Stolarski and Roniewicz 2001; Stolarski and Russo 2002; Fukami et al. 1994; Cuif et al. 2003; Stolarski and Vertino 2007). Importantly, it turned out that *the molecular information is congruent with data of skeletal histological structure and ornamentation*.

Today

The current situation

Today there are four sources of scleractinian taxonomic information: morphology, paleobiology, developmental biology and molecular genetics. Use of all four is necessary for optimal success. Taxonomic decisions based on only a portion of the available sources are neither satisfactory nor justified. Taxonomic projects are no longer possible for the solo investigator and require teams and networks.

Fundamental biological and taxonomic issues such as species definition and the process of speciation continue to be the subject of discussion. The question of how much reproductive isolation is required between "good" species remains open (Abbott et al. 2008) and applies frequently to scleractinians. Also for these corals, phenotypic plasticity (environment-induced changes in morphology) is usually not distinguished from intraspecific genetic variation (polymorphism) (Todd 2008). The latter offers a probable explanation for the existence of some instances of morphogenesis extravaganza. For example, in environments with calm waters, a lack of hard substratum and the presence of very fine sediments, it looks like mutational accidents were not eliminated by selection, and evolution led to exuberant endemic colony astogeny. In the same train of thought, the endemic morphological richness of the Lower Cretaceous scleractinians of Diplocteniopsidae (Zlatarski 1968) is reminiscent of speculations regarding the origin of the rich Burgess shale fauna (Mayr 2001).

The taxonomy is fragmented in a number of ways and for a variety of reasons. First, some taxonomic works are purely descriptive while others have a predominantly phylogenetic orientation. Neither extreme benefits taxonomic efforts. Second, researchers rely on literature published during a very long period, the last 250 years, and it is not always

easy to access this literature. Third, the publications are in various languages, requiring a certain linguistic ability. Fourth, investigators need to study the existing collections, but sometimes these are not available or access to them is restricted. Fifth, the research facilities are frequently far from the natural habitat. In addition to all of these obstacles, taxonomists need to untangle a multitude of nomenclatural challenges.

These impediments pose serious challenges and require a reorganization of the taxonomic work utilizing all available sources as well as a mastery of professional skills, nomenclature and ethics.

The e-dimension

In the face of our current taxonomic difficulties and the gathering clouds over coral reef survival, there is a silver lining in the potential offered up by electronic communication. It has quite aptly been stated that taxonomy is made for the Internet (Godfray 2002). The cyberinfrastructure offers on a global scale not only ways for accessible and efficient communication between investigators, but it is also diminishing the disadvantages caused by the fragmentary character of taxonomy. Taxonomic work may benefit from the online availability of rare publications; digitized collections and virtual usage of types and specimens; storage of rich descriptive data and illustrations; and reduction of the distance between researchers and major institutions. The e-dimension is open to a wide audience, including "purist" taxonomists, specialists dedicated to reef conservation, educators and laymen. It permits taxonomy to be vested with authority and at the same time not to be authoritarian. The advantages of the e-dimension for scleractinian taxonomy are yet to be realized.

The New Taxonomy

The 2005 international Biennial Conference of the Systematic Association held in Cardiff, Wales a symposium entitled "The New Taxonomy," and published Special Volume Series 76 (Wheeler 2008, ed.). Participants argued for the important new role of taxonomy in the understanding and conservation of biodiversity. Attention was focused on the inadequacy of funding for taxonomic work and education; the need to support descriptive taxonomy, which is the basis of identification and phylogeny but has recently been the neglected Cinderella of taxonomy; and the urgency of e-taxonomy, networks, museum engagement, democratization of taxonomy and planetary scale projects. Taxon knowledge communities, "people with similar interests and expertise connected through cyberinfrastructure such that they may interact, collaborate and even compete with one another on a much accelerated time scale," (*ibid*.) have taken on important significance. Taxon knowledge communities lead to virtual taxon knowledge banks in which the following are available in a cost-effective and environmentally-friendly manner: literature, 3-D digitized and georeferenced specimens, identification tools, maps, field guides and all of the pertinent information from all taxonomic sources. At the present time, the international scientific community is enabling a New Taxonomy through large-scale projects and programs such as: Encyclopedia of Life (EOL), Global Biodiversity Information Facility (GBIF), Planetary Biodiversity Inventories (PBIs), Legacy Infrastructure Network for Natural Environments (LINNE), European Distributed Institute for Taxonomy (EDIT) and Creating an e-Taxonomy (CATE). The book "The New Taxonomy" is loaded with energy and vision and presents a call to arms "for the taxonomy and museum communities to come together and to organize, plan, innovate and initiate the most ambitious period of exploration in the long history of taxonomy" (*ibid*.).

Ways forward

The scleractinian taxonomy is still far from realizing the progress and advantages of contemporary taxonomic science. How this can be efficiently addressed? Taxonomic work can be oriented top-down or down-up. Both ways are useful. The latter is practiced more frequently and is more matched to everyday necessities. Teamwork can be organized on various different scales: planetary, regional or special task forces. The volume of work and the nature of species composition makes it recommendable to start regionally.

Toward an Atlantic Scleractinia Initiative

The following must be addressed for the success of a future integrative approach to Atlantic scleractinian taxonomy:

- *Massive sampling.* Comprehension of scleractinian variability and plasticity requires massive sampling, which lately is hardly ever applied.
- *Study of the mesophotic habitat*. Despite the well-established scleractinian presence in the mesophotic habitat in Jamaica (Goreau and Wells 1967), Cuba (Zlatarski 1982), Bahamas (Reed 1985), Barbados (Macintyre et al. 1991), Curacao and Bonaire (Bak et al. 2005) and Mexico (Zlatarski 2008), recent attention has mainly been focused on shallow waters.
- *Collection access*. There is much to be done. The collection of T. F. Goreau has for more than three decades remained unavailable in storage.

Among the large monograph collections, only the Cuban one is well-preserved in the National Aquarium in Havana (Zlatarski 2004), but unfortunately, for reasons beyond the control of the host institution, it is out of reach for many researchers. The corals at the Smithsonian Institution, Washington, D.C., serve as a good example of well-inventoried and available specimens. For the Atlantic province, digitized collections and virtual usage of types and specimens are not yet available.

- *Analysis of phenotypic diversity*. Knowledge of phenotypic diversity at all levels of biological organization, from structural elements to high systematic categories, is basic for taxonomic work. The phenoid delineation is a first step for making sense of taxon structure. Its usefulness became evident when taxonomic problems identified and decisions made decades ago (Zlatarski 1982) were recently validated by molecular studies (Zlatarski 2008).
- *Life history*. The insufficiency of data on the life history of Atlantic scleractinians presents an obstacle for a better understanding of the species as a basic taxonomic unit. Systematized observations and experiments in natural habitat and aquaria are needed.
- *Geological history*. The application of the reversed principle of uniformitarianism can facilitate the explanation of particular cases of evolution. For example, the presence of considerably smaller and more delicate scleractinian colonies in Golfo de Guacanayabo, Cuba, as compared to the rest of Caribbean (Zlatarski, 1982), may be viewed together with the endemic morphogenesis observed in Lower Cretaceous scleractinians of Diplocteniopsidae in Bulgaria (Zlatarski 1968). It is likely that evolution in an environment of calm waters, the lack of a hard bottom and the presence of very fine sediments resulted in a different colony astogeny in a very limited temporal and spatial range.
- *Molecular genetics*. As a new, very powerful and expensive taxonomic tool, molecular genetics should be used after the completion of a systematized sampling process corresponding to phenotypic diversity and life history traits, in coordination with interested researchers.
- *Cyberinfrastructure*. A website for Atlantic scleractinian taxonomy is needed to form a taxon knowledge community and taxon knowledge bank, and to provide easy and inexpensive access to literature, collections and all pertinent documentation for specialists and others interested in scleractinians and reefs. The experience of writing the Treatise on Invertebrate Paleontology for Scleractinia by means of a website could be helpful in designing a website for extant Atlantic scleractinians.
- *Education of specialists*. The necessity to make use of four sources of taxonomic information requires fundamental changes in educational programs in order to prepare specialists to able to meet the more stringent requirements of the New Taxonomy.

Ultimately, all of the foregoing recommendations will be fruitless in the absence of a collaborative spirit in forging strategies and working together in the most efficient and integrative way. This is especially important at a time when taxonomy plays such a crucial role for the understanding of scleractinian biodiversity and the conservation of coral reefs.

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