# The scleractinian species – a holistic approach

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*To Boris Sergeevich Sokolov, the organizer of the first International Paleontological Symposium on the Study of Fossil Corals in 1971, for his enormous contributions to the field*

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**Abstract**: The widely recognized difficulty in defining the scleractinian species may be attributed to two factors: the objective nature of these elusive organisms, and the subjective impact of us as researchers. Shifts in areas of nomenclature, ethics and taxonomy can reduce our negative impact on the problem and require introspection on the personal, inter-colleague and international levels. The International Code of Zoological Nomenclature offers a tool for regulating nomenclature procedures, but it has been troublingly ignored recently. Ethical issues require appeals to our conscience, recognition of the necessity of publishing following peer review and use of quality tests. Taxonomy can be facilitated by constantly updated species notions and approaches. The scleractinian species concept followed the evolution of the species notion in general and the enrichment of knowledge about these corals. The past two decades dramatically changed our understanding of scleractinians with discoveries concerning such life history aspects as long generation times and propagation through fragmentation, synchronous multispecific spawning, hybridization, ocean currents, symbiosis and life in aquaria. A holistic approach to defining scleractinian species requires recognition of the implication of life history traits and usage of three types of criteria – morphological, molecular and reproductive – as well as the cooperation of specialists. Scleractinian species taxonomy can benefit considerably from the bridging of paleontological and neontological techniques. Suggestions for future strategies in scleractinian species taxonomy are offered.

**Key words:** Scleractinia, nomenclature, taxonomy, life history

**Contents**



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## 1. INTRODUCTION

The tradition of the International Association for the Study of Fossil Cnidaria and Porifera (IASFCP) of convening an international symposium every four years presents an excellent opportunity for the review and discussion of our work and for the mobilization of our collegium toward meeting existing challenges. For the 1995 Madrid Symposium, SANDO (1997a) prepared a remarkable analysis of the history of the Association and an excellent state of the art of Late Paleozoic corals (1997b). At the 1999 Sendai Symposium, FEDOROWSKI (2001) successfully focused attention on Upper Paleozoic coral studies, insisting on improved species procedures. It is time to turn to Scleractinia.

The scleractinian species is notoriously difficult to define and there has been "no consensus as to why this problem exists" (KNOWLTON & BUDD, 2001). This paper argues that this difficulty is attributable to two factors: the objective nature of these elusive organisms, and the subjective nature of us as researchers. There are three areas in which our subjective impact may hinder resolution of the scleractinian species – nomenclature, ethics and taxonomy – and shifts in these areas can lead to more objective results. This requires introspection on the personal, inter-colleague and international level. Because coral nature is, except within the narrow boundaries of certain controlled experiments, independent of our will, our only hope for developing a more objective species concept lies in constantly striving for improved research techniques and approaches.

Recently discovered life history traits of these organisms have enriched our knowledge by adding new aspects to the scleractinian species. As a result, morphological criteria should be combined with molecular and reproductive criteria in the process of species identification. The appeal to integrate all aspects of scleractinian species in a holistic approach requires that investigators unify their efforts and coordinate research into a more efficient collaboration.

## 2. NOMENCLATURE

"Zoological nomenclature is the system of scientific names applied to taxonomic units [...] of extant or extinct animals" (ICZN, 1999). "The International Code of Zoological Nomenclature is a system of rules and recommendations originally adopted by the International Congress of Zoology and, since 1973, by the International Union of Biological Sciences [...]. The objects of the Code, whose author is the International Commission on Zoological Nomenclature, are to promote stability and universality in the scientific names of animals and to ensure that the name of each taxon is unique and distinct" (ICZN, 1999). The provisions of the current, fourth, edition supercede those of the previous editions as of 1 January 2000.

The task of continually updating and improving the Code and issuing new editions presents a constant challenge for the scientific community because, as noted at the end of the Preface to the third edition, "[n]o Code is perfect. None will please everyone" (ICZN, 1999). Nevertheless it is the best existing instrument for the regulation of nomenclature.

Articles 79 and 80 of the Code (ICZN, 1999) are dedicated to the List of Available Names in Zoology and to the proper treatment of the Parts of the List. An interna-

tional association such as the IASFCP, in consultation the International Commission on Zoological Nomenclature, might propose that the Commission adopt a Part concerning Cnidaria. It would be appropriate to form a committee on nomenclature in the IASFCP.

LATHUILIÈRE (1996) has proposed a novel "spectral" approach, previously used for Foraminifera, for coral nomenclature, in cases of "periodic occurrence of transgeneric highly variable specific units (spectra) in the fossil record." This is an interesting addition to the field that requires further attention, and is consistent with the Code's goal of promoting stability in scientific names.

Recent years witnessed a troubling increase in the number of cases in which the requirements of the Code have been ignored. The new species names in *Corals of the World* were the object of a subsequent monograph in order to be legalized (VERON, 2000, 2002).

Whenever a manuscript goes directly from the author's computer to a publishing house, it cannot benefit from peer review.

Scleractinian studies require the use of infrasubspecific entities whose names are excluded from the provisions of the Code. Present-day methods of study are making the usage of these entities necessary and more frequent, but they are named in inconsistent ways. An agreement between investigators concerning their nomenclature will facilitate any comparison of obtained results and future research. Because they fall outside the scope of the Code, the names of infrasubspecific entities are not subject to regulations concerning their type material, making this another area in which the joint effort of specialists is desirable in order to preserve valuable material.

## 3. ETHICS

In theory, it is widely accepted that "science functions best only when all actions are open to question, and when we require the highest levels of accountability" (KRAUSS, 2003). Yet, in our field, with the exception of the Code of Ethics, which is "a guide to good usage in nomenclature" (ICZN, 1999), and which only has the status of recommendations, there are few documents regulating ethics. This makes peer review especially important. Also useful are the instructions some scientific journals provide to authors in the form of ethical advice and warnings. Finally, the editors of most scientific journals are sensitive to and on the lookout for ethical issues.

Research would benefit from the development of techniques for the control and evaluation of our work. In this respect, SANDO (1997b) provided us with a very useful tool for gauging the efficacy of presented results. He introduced quality tests with five categories concerning the usage of type specimens of type species, and applied them to Late Paleozoic corals. He suggested to the IASFCP that research quality issues be addressed and warned us of the danger of a "proliferation of inaccurate concepts of global biostratigraphy, phylogeny, and biogeography."

FEDOROWSKI (2001) provided us with another example of frankly addressing these important quality issues for Paleozoic corals when he noted "a trend [...] toward superficial identifications, based on a single, incomplete solitary corallite or a small fragment of colony with random transverse sections and longitudinal sections commonly off center. As a result, the complete morphology of holotypes and intraspecific variability

of the majority of Upper Palaeozoic rugose coral species remain unknown." This reminds us that the time for facing these types of questions for Scleractinia is long overdue.

In a broad sense, good ethics requires investigators to study all existing material and data pertinent to their research project. Yet how this can be done in the case study of Caribbean scleractinians while the collection of the eminent Tom F. GOREAU has remained stored and unavailable for the past three decades? Another rich collection, from Yucatan, Mexico, has spent the last two decades in boxes without of information about specimen localities. The sole surviving large collection gathered by SCUBA-diving in natural habitat, the more than 30-year-old Cuban collection, has been largely preserved (approximately 80%) with its accompanying documentation.

Furthermore, the mere fact of preserving samples with data concerning their locality does not facilitate their use. Information on the exceptional plasticity and variability of Scleractinia would be available to investigators if the curators of coral collections were to organize 3-D photo libraries and make information available electronically through the internet, a process in which our IASFCP could play a leading role.

It is difficult to resist the temptation of sharing the story of a particularly remarkable and commendable moral gesture in the field of fossil corals. On 5 January 1977, Yury I. TESAKOV was defending his D. Sc. Dissertation (later published as a book – TESAKOV, 1978). As a result of populational, biocoenosic and biostratigraphic analysis, TESAKOV radically revised the Tabulata species concepts of his mentor, Academician Boris Sergeevich SOKOLOV. Everyone nervously awaited the crucial opinion of the highly respected and well-positioned SOKOLOV. After recognizing the defender's achievements, SOKOLOV congratulated TESAKOV and declared that his next task would be to destroy his own previous work (personal communication), demonstrating his commitment to the pursuit of truth in science.

## 4. TOWARD AN INTEGRATED LIFE HISTORY APPROACH TO THE SCLERACTINIAN SPECIES CONCEPT

The scleractinian species concept and low-level taxonomy has closely followed both the evolution of the species notion of organisms in general and the long process of our deepening knowledge about this group of lower invertebrates. Currently existing species concepts may be grouped into five main categories: phenetic, biological, phylogenetic, ecological and cohesive (WINSTON, 1999). The first four are well known. The cohesive concept was introduced by TEMPLETON (1989). "The cohesion species is defined as an evolutionary lineage or set of lineages with genetic exchangeability and/or ecological interchangeability" (TEMPLETON, 2001). By integrating the previous concepts, it is the most inclusive species notion to date, and was applied to scleractinians by MÁRQUEZ et al. (2002).

The first species concept to be employed was the phenetic (or morphological) concept. Until the end of the nineteenth century, corals were not investigated in their natural habitat, and the reigning typological approach was based on scarce material merely sent to specialists for laboratory study, or resulting from very limited fieldwork.

QUELCH (1886) and VAUGHAN (1901, 1907) were the first to pay serious attention to the exceptional variability of scleractinian corals. VAUGHAN described different formae

(1901) and so at the beginning of the twentieth century the phenetic notion was enriched by a new, very important aspect of scleractinians, namely **variability**.

In the late 1930s, the French school of ALLOITEAU (1957) began very detailed studies of fossil Scleractinia and described considerably more morphological characters. In 1960, his successor CHEVALIER commenced extensive SCUBA-diving investigations in the natural habitat of coral life in the South Pacific, which culminated with his posthumously published synthesis in 1987. His detailed descriptions of the microstructure of skeletal elements remains unparalleled and offers valuable information on the nature of scleractinians.

Starting in the early 1960s, TESAKOV actively studied the variability of Tabulata (TESAKOV, 1978), and radically amended their low-level taxonomy introducing various infrasubspecific categories.

The variability in fossil scleractinians urged species revision (ZLATARSKI, 1963) and led from 1970 to 1976 to a rich underwater sampling in depths to 70 m and laboratory investigation of Cuban Scleractinia. As result, variability was described on ten levels of biological organization (ZLATARSKI, 1982). Nonetheless, many questions continue unresolved, especially regarding low-level taxonomy (such as structural elements, corallites, colonies and infrasubspecific entities).

In the 1970s, VERON and colleagues launched an extremely broad research resulting in a monograph series on extant Eastern Australian Scleractinia that again demonstrated the extraordinary plasticity of corals and the difficulty of species identifications. This spirit prevailed during the Coral Taxonomy Workshop held in 1976 on Marshall Island, attended by the world coral leader of that time, John WELLS, and many of his fellow active coral researchers (VERON, 2001). A year later, WELLS commented with reserve that it was "unlikely that there would ever be a single internationally applicable taxonomic framework for corals" (VERON, 2001).

The necessity of serious changes in coral species taxonomy was demonstrated by the fact that the issue independently surfaced in the work of several investigators of fossil as well as extant corals (TESAKOV, ZLATARSKI, VERON, KRASNOV, LATYPOV), and when they happened to meet in 1979, they immediately organized a workshop on intraspecific variability and categories (LATYPOV, 1998). Around the same time, LANG (1984) emphasized the need to focus on the variability of non-skeletal characters in scleractinian taxonomy.

The discoveries of the last two decades have enormously changed our knowledge of scleractinians and have assisted us in better grasping their nature. The newly described aspects of life history summarized below have enlarged the scope of species definition and prompt us to integrate them under a holistic approach.

Moving in chronological order through significant recently described aspects, we can begin with the recognition of **long generation times**, in some cases spanning centuries, and **frequent propagation through vegetative fragmentation**, raising the question of whether in general most corals "experience physiological senescence" (POTTS, 1984).

Around the same time came the momentous discovery of **simultaneous multispecific spawning** (HARRISON et al., 1984) as a method of coral reproduction, bringing forth a new important aspect. The scale of this phenomenon was observed to be so large that sometimes gametes congregate on the sea surface to form "slicks" up to a few kilometers long (OLIVER & WILLIS, 1987).

Veron (1995) synthesized his prolific work, emphasizing the role of another aspect, **ocean currents**, and offering a reticulate hypothesis for scleractinian speciation.

The recognition of simultaneous multispecific spawning led to the opening of a completely new important chapter in the scleractinian story, namely the great potential for lateral gene transfer, or **hybridization** (Willis et al., 1997).

Recently the intricate character of coral **symbiosis** (Hoegh-Guldberg, 1999; Omori et al., 2001; Banin et al., 2001; Fine & Loya, 2002) has added another puzzling life history trait.

Finally, **life in aquaria** has provided not only great possibilities for controlled experiments, but has also revealed some astonishingly dramatic changes in scleractinian growth forms (Carlson, 1999), probably illustrations of pedomorphosis and peramorphosis due to extreme stress.

It is now widely recognized that scleractinian species are in constant dynamics. There are incipient species, established species, hybrids, syngameon clusters and single species, the latter being reproductively isolated and genetically cohesive. The process of applying an integrated life history approach requires us to employ three possible criteria: morphological, molecular and reproductive. The optimal efficiency of these applied techniques depends on the nature of the material studied and the cooperation of specialists operating different criteria. The proposed holistic approach to the definition of the scleractinian species is an open system and can be improved upon to incorporate new insights.

## 5. RECOMMENDATIONS

A holistic approach to the scleractinian species requires the joint effort of specialists. IASFCP can play an important role in this process by organizing a workshop on the subject, the results of which would reported on at the next international symposium. The following recommendations are offered in connection with such a proposed initiative. The list is not complete and colleague additions are requested and welcome.

- Sample not only "clear" species, but representatives of all kinds of phenotypes, ecological conditions and life history traits by using infrasubspecific entities that have regulated names and types.
- Make valuable collections available, organize 3-D photo libraries and use the cyber infrastructure to promote access to existing data.
- Bring closer paleontological and neontological approaches through reciprocal illumination. The importance of actualistic studies is recognized, but detailed microstructural and ontogenic paleontological studies also provide very valuable information. For example, the accurate position of Fungiidae, confirmed by DNA study, was "foreseen 16 years before by Gill" (Gill, 1981; Lathuilière, 1996). Similarly, the investigation of the ontogenetic development of the thecal structure made by Stolarski (1995) was pointed out eight years later as an "additional means of resolving the identity of juvenile corals" from Indo-Pacific Reefs (Babcock et al., 2003).
- Focus on variability at low-levels of biological organization: structural elements, corallites (especially heteromorphic colonies, bimorphic colonies and pathological wedges) and infrasubspecific entities (Zlatarski, 1982).

- "[S]tudies at the population/species interface" are necessary for "progress in applying molecular genetics to the problem of speciation" (HARRISON, 1991 *sensu* TEMPLETON, 1994).
- Contribute to a better understanding of the structure and function of cross-fertilization barriers (MILLER & van OPPEN, 2003).
- Reveal different reproductive strategies (FUKAMI et al., 2000, 2003).
- "[E]xplore the existence of a stabilized 'morphometric code,' a morphological set of buffering rules used repeatedly by members of any species, regardless of enviromental factors" (GATEÑO & RINKEVICH, 2003).
- Increase the taxonomic resolution of scleractian recruits (BABCOCK et al., 2003).
- Direct attention to scleractinian immigrants (FINE et al., 2001).
- Explain how bleaching impacts on coral strategies (FINE & LOYA, 2003; FINE et al., 2002a, 2002b).
- Rationalize the genetic economies controlling the length of the clonal life span and the problems of physiological senescence.
- Analyze the "energy investment into tissue and skeleton in corals" (ANTHONY et al., 2002).
- Interpret the biocalcification proxy (STOLARSKI, 2003).

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## References

ALLOITEAU, J., 1957: Contribution à la systématique des Madréporaires fossils. – **I** , texte, 462 p., 5 tabl., **II**, atlas, 286 fig., 20 pl., Paris (C. N. R. S.).

ANTHONY, K.R.N., CONNOLLY, S.R. & WILLIS, B.L., 2002: Comparative analysis of energy allocation to tissue and skeletal growth in corals. – Limnol. Oceanogr., **47** (5): 1417–1429.

BABCOCK, R.C., BAIRD, A.H., PIROMVARAGORN, S., THOMSON, D.P. & WILLIS, B.L., 2003: Identification of scleractinian coral recruits from Indo-Pacific Reefs. – Zoological Studies, **42** (1): 211–226.

BANIN, E., ISRAELY, T., FINE, M., LOYA, Y. & ROSENBERG, E., 2001: Role of endosymbiotic zooxanthallae and coral mucus in the adhesion of the coral-bleaching pathogen *Vibrio shiloi* to its host. – FEMS Microbiology Letters, **199**: 33–37.

CARLSON, B.A., 1999: Organism responses to rapid change: What aquaria tell us about nature. – Amer. Zool., **39**: 44–55.

CHEVALIER, J.-P., 1987: Ordre des Scléractiniaires (Systématique with Beauvais, L.). – In: GRASSÉ, P.-P. (Ed.): Traité de Zoologie, **III** Cnidaires, Anthozoaires, 3, 403–764, Masson.

FEDOROWSKI, J., 2001: Upper Palaeozoic coral studies: where we are and where we should be. – Bull. Tohoku Univ. Museum, **1**: 1–6.

FINE, M. & LOYA, Y., 2002: Endolithic algae: an alternative source of photoassimilates during coral bleaching. – Proc. R. Soc. Lond., B, **269**: 1205–1210.

FINE, M. & LOYA, Y., 2003: Alternate coral-bryozoan competitive superiority during coral bleaching. – Marine Biology, **142**: 989–996.

FINE, M., ZIBROWIUS, H. & LOYA, Y., 2001: *Oculina patagonica*: a non-lessepsian scleractinian coral invading the Mediterranean Sea. – Marine Biology, **138**: 1195–1203.

FINE, M., BANIN, E., ISRAELY, T., ROSENBERG, E. & LOYA, Y., 2002a: Ultraviolet radiation prevents bleaching in the Mediterranean coral *Oculina patagonica*. – Marine Ecology Progress Series, **226**: 249–254.

FINE, M., OREN, U. & LOYA, Y., 2002b: Bleaching effect on regeneration and resource translocation in the coral *Oculina patagonica*. – Marine Ecology Progress Series, **234**: 119–125.

FUKAMI, H., OMORI, M. & HATTA, M., 2000: Philogenetic relationships in the coral family Acroporidae, reassessed by inference from mitochondrial genes. – Zoological Science, **17**: 689–696.

FUKAMI, H., OMORI, M., SHIMOIKE, K., HAYASHIBARA, T. & HATTA, M., 2003: Ecological and genetic aspects of reproductive isolation by different spawning times in *Acropora* corals. – Marine Biology, **142**: 679–684.

GATEÑO, D. & RINKEVICH, B., 2003: Coral polyp budding is probably promoted by a canalized ratio of two morphometric fields. – Marine Biology, **142**: 971–973.

GILL, G.A., 1981: The fulturae ("compound synapticulae"), their structure and reconsideration of their systematic value. – Acta Paleont. Polonica, **25** (3–4): 301–310, 4 pls.

HARRISON, P.L., BABCOCK, R.C., BULL, G.D., OLIVER, J.K., WALLACE, C.C. & WILLIS, B.L., 1984: Mass spawning in tropical reef corals. – Science, **223**: 1186–1189.

HOEG-GULDBERG, O., 1999: Climate change, coral bleaching and the future of the world's coral reefs. – Marine & Freshwater Research, **50**: 839–866.

International Commission on Zoological Nomenclature, 1999: International Code of Zoological Nomenclature, Fourth Edition – XXIX + 306 p. London (International Trust for Zoological Nomenclature).

KNOWLTON, N. & BUDD, A.F., 2001: Recognizing coral species present and past. – In: JACKSON, J.K., LIDGARD, S. & MCKINNEY, F.K. (Eds.): Evolutionary patterns: growth, form, and tempo in the fossil record in honor of Alan Cheetham. – 97–119, Chicago & London (Univ. Chicago Press).

KRAUSS, L.M., 2003: The citizen-scientist's obligation to stand up for standards. – New York Times, 22.04.2003: D3.

LANG, J.C., 1984: Whatever works: The variable importance of skeletal and non-skeletal characters in scleractinian taxonomy. – Palaeontographica Americana, **54**: 18–44.

LATHUILIÈRE, B., 1996: Is morphology a good way to understand the evolution of corals? – Paleontological Society Papers, **1**: 81–105.

LATYPOV, Y.Y., DAUTOVA, T.N. & MOSHCHENKO, A.V., 1998: The principles and methods of the cnidarian classification. 244 p., Vladivostok (Dalnauka) (in Russian).

MÁRQUEZ, L.M., VAN OPPEN, M.J.H., WILLIS, B.L., REYES, A. & MILLER, D.J., 2002: The highly cross-fertile coral species, *Acropora hyacinthus* and *Acropora cytherea*, constitute statistically distinguishable lineages. – Molecular Ecology, **11**: 1339–1349.

MILLER, D.J. & VAN OPPEN, M.J.H., 2003: A 'fair go' for coral hybridization. – Molecular Ecology, **12**: 805–807.

OLIVER, J.K., & WILLIS, B.L., 1987: Coral-spawn slicks in the Great Barrier Reef: preliminary observations. – Marine Biology, **94**: 521–529.

OMORI, M., FUKAMI, H., KOBINATA, H. & HATTA, M., 2001: Significant drop of fertilization of *Acropora* corals in 1999: An after-effect of heavy coral bleaching? – Limnol. Oceanogr., **46** (3): 704–706.

POTTS, D.C., 1984: Generation times and the Quaternary evolution of reef-building corals. – Paleobiology, **10** (1): 48–58.

QUELCH, J.J., 1886: Report on the reef-corals collected by H. M. S. Challenger during the years 1873–76. – Report on the scientific results of the voyage of H. M. S. Challenger during the years 1873–76, Zoology, **XVI**, 203 p., XII pl.

SANDO, W.J., 1997a: A silver platter-History of the International Association for the Study of Fossil Cnidaria and Porifera and trends in cnidarian and poriferan research, 1971–1994. – Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica), **91** (1–4): 5–33, Madrid.

SANDO, W.J., 1997b: Late Paleozoic coral genera and subgenera. State of art, 1814–1994. – Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica), **91** (1–4): 61–71, Madrid.

STOLARSKI, J., 1995: Ontogenetic development of the thecal structures in caryophyliine scleractinian corals. – Acta Palaeontologica Polonica, **40** (1): 19–44.

STOLARSKI, J., 2003: Three-dimensional micro- and nanostructural characteriastics of the scleractinian coral skeleton: A biocalcification proxy. – Acta Palaeontologica Polonica, **48** (4): 497–530.

TEMPLETON, A.R., 1989: The meaning of species and speciation: A genetic perspective. – In: OTTE, D. & ENDLER, J.A. (Eds.): Speciation and its consequences. – 3–27, Sunderland, Massachusetts (Sinauer).

TEMPLETON, A.R., 1994: The Role of molecular genetics in speciation studies. – In: SCHIERWATER, B., STREIT, B., WAGNER, G.P. & DESALLE, R. (Eds.): Mollecular ecology and evolution: Approaches and application. – 455–477, Basel (Birkhäuser Verlag).

TEMPLETON, A.R., 2001: Using phylogeographic analysis of gene trees to test species status and processes. – Molecular Ecology, **10**: 779–791.

TESAKOV, Y.I., 1978: Tabulata: populational, biocoenosoic and biostratigraphic analysis. – Transactions, Academy of Sciences of the USSR, Siberian Branch, Institute of Geology and Geophysics, **409**, 264 p. (in Russian).

VAUGHAN, T.W., 1901: The stony corals of the Porto Rican waters. – Bull. U. S. Fish Commission, **XX**, second part, 290–320, XXXVIII pl.

VAUGHAN, T.W., 1907: Recent Madreporaria of the Hawaiian Islands and Laysan. – U. S. Nat. Mus. Bull., **59**: IX + 427 p., XCVI pl.

VERON, J.E.N., 1995: Corals in space and time: the biogeography and evolution of the Scleractinia. – XIII + 321 p., Ithaca (Cornell University Press).

VERON, J.E.N., 2000: Corals of the World. – vol. 1: XII + 463 p.; vol. 2: VIII + 429 p.; vol. 3: VIII + 490 p., Townsville, Queensland (Australian Institute of Marine Science).

VERON, J.E.N., 2001: Reflections. – Atoll Research Bulletin Golden Issue 1951–2001, **294**: 108–117, National Museum of Natural History, Smithsonian Institution.

VERON, J.E.N., 2002: New species described in *Corals of the World*. – Australian Institute of Marine Science Monograph Series, **11**. – 206 p., Townsville, Queensland (AIMS).

WILLIS, B.L., BABCOCK, R.C., HARRISON P.L. & WALLACE, C.C., 1997: Experimental hybridization and breeding incompatibilities within the mating system of mass spawning reef corals. – Coral Reefs, **16**: S53-S65.

WINSTON, J.E., 1999: Describing species. – XX+518 p., New York (Columbia Univ. Press).

ZLATARSKI, V., 1963: Sur *Stylocoenia taurinensis* (Michelin), Madréporaire du Tertiaire méditerranéan. – Ann. Univ. Sofia, Fac. Biol., Géol., Géogr., **56** (2): 61–73, pl. I–V, Sofia.

ZLATARSKI, V., 1982: In: ZLATARSKI, V.N. & MARTINEZ ESTALELLA, N.: Les Scléractiniaires de Cuba avec des données sur les organismes associés. – 472 p., annexe I, Sofia (Editions de l'Académie bulgare des Sciences).