Coralline algae: the morphological species concept in the era of molecular genetics

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Most paleontological information is given with reference to species, as it happens in biology. Systematics delimits species and requires a species concept. Because of the importance of the definition of species, and in search of a unifying concept including uniparental and biparental groups, many species concepts have been proposed in biology (Hausdorf 2011) although the most influential one is: "*groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups*" (Mayr 1942). Reproductive isolation is the most common cause of genetic divergence, and speciation is the stage where the diverging populations will not lose their divergence upon contact, and continue to diverge. Through time, neutral mutations that do not affect phenotype can cumulate by genetic drift. In other cases, non-neutral mutations lead to increasingly divergent genotypes and phenotypes showing differential adaptation to their niche, filtered by natural selection. Coralline algae possess both a vegetative and a sexuate reproduction. The first produces clones of the parent individual, while the second implies genetic recombination.

After Woelkerling (1988) seminal work, paleobotanists strove to match the definitions and criteria of the biological systematic framework, as far as allowed by the preservation of delicate features in the fossil (Braga et al., 1993). In addition, the study of recent material by a paleontological approach was explored, as a tool to understanding the information loss due to taphonomic processes and to different techniques and preparations of fossils *vs*. modern specimens (Basso, 1994). At the same time, many efforts were devoted to critical revisions of the type material of coralline algae in historical collections, in order to re-describe live and fossil species in a modern taxonomic context. Strong emphasis was given to: 1) the large variability and morphological plasticity of coralline algae; 2) the need of a statistical treatment of biometric data; 3) the criticism of the validity of many taxa based on subtle morphological or size differences of anatomical features, poor descriptions, poorly preserved or sterile specimens, or single specimens. As a result, the fossil coralline diversity, as apparent in the early literature, started to be perceived as an artifact due to confused definitions and unclear diagnostic characters, with the caveat that the true number of different species had to be probably much lower. Waiting for a complete revision of the hundreds of living and fossil species described so far, (paleo)algologists started to give less and less importance to characters like growth-forms, biometric data, trichocyte occurrence, palisade cells occurrence, etc. in the conceptual framework of the high plasticity of coralline species.

This process had important consequences on our knowledge: for example, *Titanoderma* was merged into *Lithophyllum* (Campbell & Woelkerling 1990), and, given the difficulty to find unequivocal reference for most taxa, paleobotanists simply gave up attempting coralline identification at the species level. However, the use of an open nomenclature in coralline taxonomy, although justified by the need to avoid further nomenclatural confusion, is a frustrating exercise, since it leads to artificially simple and repetitive patterns of genera distribution. Moreover, dealing solely with supraspecific ranks leaves the coralline paleoecological (and stratigraphic?) potential and their evolutionary pattern largely unexplored.

The paleontological species is necessarily a morphological species, since neither genetics, nor interbreeding can be checked on fossils, and its recognition must be based solely on observable diagnostic characters. Other considerations, such as the coherence of species identification with its known stratigraphic or paleogeographic range should be discussed at a further stage. In other words, whenever clear diagnostic characters are identified both in living corallines and also detected in the fossil, the straightforward conclusion is that the considered entities are conspecific, no matter of age and geography. This concept was far to be accepted by the scientific community that was using "a priori" different names for live and fossil species, until the first paper synonymizing fossil species with their modern morphological counterpart appeared (Basso et al. 1996).

Molecular genetics is radically changing again our point of view. Recently, the increasing use of genetic analysis for the identification of species revealed that, in many cases, coralline specimens apparently belonging to the same morphological species are genetically different (Pardo et al., 2014). The discovery of this unexpected coralline biodiversity is accompanied by an effort to identify those combinations of morphological characters that would support species identification as from molecular genetics, in the so-called integrated taxonomy (Hebert et al., 2005; Basso et al., 2015). In particular, molecular genetics is revaluating some aspects of coralline morphological variability, unequivocally establishing that they have importance in species diagnosis. Actually, *Titanoderma* has been finally reconsidered as a distinct genus, and other believed examples of extreme morphological variability are presently considered a case of erroneous mixing up of different species under the same name (i.e. *L. margaritae*).

While twenty years ago we were convinced that an unrealistic number of coralline species existed in literature, we are now facing the fact that, based on the present-day discovery of unsuspected genetic diversity, we should expect the other way round. Accurate revisions and re-documentation of type collections is still the main tool we have to clarify coralline taxonomy, both in biology and in paleontology. Paleoalgologists shall probably go on using an open nomenclature when no better choice is available. However, this cannot be our default choice, as far as we can already refer to those species, either modern or fossil, that are presently known with adequate morphological detail (Hrabovský et al., in press).

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