

Key Transitions In Animal Evolution

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Chapter 7

From Cnidaria to “Higher Metazoa” in One Step

Ferdinando Boero¹ and Stefano Piraino²

Introduction

Metazoan evolution is traditionally seen as a long road where the main steps of the increasing addition of features leading from simple to complex organisms are called milestones. This is the way zoology is treated in textbooks (see Valentine 2004 for a review). The first chapters are dedicated to the simplest animals, and the diversity of animal phyla is ordered along a series of bauplans of gradually increasing complexity.

Protozoans usually introduce the story, since it is highly reasonable that the Metazoa originated from a colonial protozoan, probably a choanoflagellate, that evolved cellular differentiation. Cellular differentiation is the initial milestone leading, from a colony of individual cells, to an individual and multicellular organism. This organizational level has been achieved by sponges, most probably from choanoflagellates. It is difficult to “see” in sponges the premises of all the astonishing features that define what we call animals, as they lack, for instance, true nervous cells, the trademark of animals. Nevertheless, some sponges do have real tissues (see Wang and Lavrov 2007 and references therein), and tissue formation is probably another sponge milestone. Recent findings also showed that sponges possess at least some of the molecular equipments associated with development of sense organs (reviewed in Jacobs et al. 2007) and synaptic connections

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(Sakarya et al. 2007). Finally, studies on sponge nuclear and mitochondrial genomes (Larroux et al. 2006, Erpenbeck et al. 2007) confirmed that Porifera are true metazoans.

Peramorphosis vs. Paedomorphosis

It is paradoxical that ecology and embryology-developmental biology, the disciplines that contributed more to Darwinian thinking, did not participate much to the neo-Darwinian synthesis. Gould (1977) replaced developmental biology into an evolutionary framework and proposed heterochrony, and especially paedomorphosis, as a key evolutionary mechanism. From Gould's seminal book, many ideas stemmed, all proposing evolutionary processes that started from complex organisms that became simpler through neoteny or progenesis and that, then, gained new complexity from the re-elaboration of the simplified states.

However, to simplify something to reach then a higher complexity, requires a certain degree of complexity that, presumably, was reached by adding complexity to a simpler organization. Peramorphosis is just this: the addition of new features to old ones. If metazoan evolution is inferred by looking at vertebrates, or insects, or molluscs, or even nematodes, it is obvious that the story runs by the re-elaboration of features that were there already. Paedomorphosis alone, at this level of complexity, makes perfect sense. But if we concentrate on "simple" organisms, the situation becomes radically different: it is difficult to subtract when no additions have been made. Sponges added multicellularity and cell differentiation, but all the other metazoan features seem to be missing. The organization of adult sponges provides no hint about the origin of the other milestones of metazoan evolution. As suggested by Maldonado (2004), the key to identify sponge relationships with the rest of the Metazoa is their larva. Some sponge larvae, in fact, are very similar to cnidarian planulae, or to acelous turbellaria, or to placozoa. They might be the beginning of subsequent Metazoan evolution. They are clearly individuals, they have a one-way movement, with a front and a rear, they move and make choices (the substrate where to settle). If we subtract most of sponge development, what remains is a planula-like organism. From there, we might hope to see the rest of the path that leads to "higher" metazoa.

No matter what techniques are used to build up the tree of metazoan evolution, the base is invariably occupied by a group of phyla: sponges, placozoans, ctenophores, and cnidaria. Molecular data about "who came first" might be controversial, according to the chosen markers or software algorithms. The reason for this might be linked to some mismatch between the pace of evolution, intended as introduction of novelties, and that of phylogeny, intended as time of divergence between two monophyletic clades.

Micro- vs. Macroevolution Through the Inverted Cone of Development

The identification of jumps in evolutionary patterns, or punctuated equilibria, derived from the analysis of the fossil record and led, for some time, to the dismissal of Darwinian gradualism. The view was that organisms remained more or less unvaried (the equilibrium) and then, all of a sudden (in geological terms), they became something else, with an evolutionary jump. These jumps "punctuate" the otherwise prevailing equilibrium. The introduction of the concept caused a healthy burst of scientific debate, linked to the coupling or uncoupling of micro- and macroevolution. For some evolutionists (especially neontologists), microevolution was the variation within species, and macroevolution was the formation of new species. For some other evolutionists (especially paleontologists), microevolution was the origin of species and macroevolution was the origin of higher taxa.

The introduction of the inverted cone metaphor by Arthur (1997) reconciled the role of developmental biology and of genetics in proposing a theoretical framework for macroevolution and for its coupling with microevolution, if any. The inverted cone (Fig. 1) implies that development can be seen as starting with a totipotent cell, the zygote, whose genome will be expressed in its whole potential.

Cleavage, and the consequent differentiation, reduce the potency of the new, differentiated cells that, in spite of still having the whole information, have the possibility of expressing just a part of it, exemplified by the number of other cell types that will derive from them. At the end

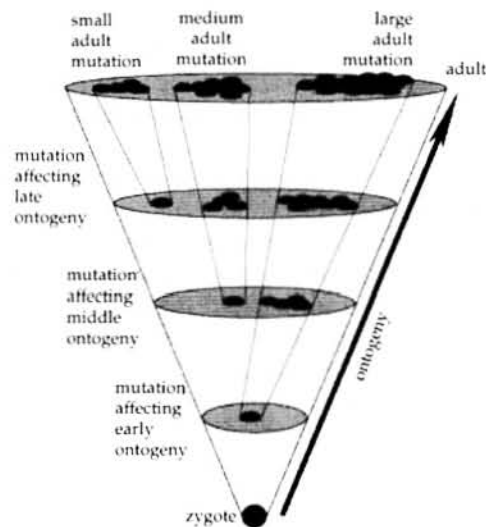


Fig. 1. The inverted cone of development (Arthur, 1977).

of development, completely differentiated cell types will lead just to a reiteration of the same cell type. A quantitatively identical genetic mutation affecting early ontogeny, then, will have a much greater impact on the final result of development than a mutation of the same size occurring at intermediate or final steps of ontogeny. With this conceptual tool at hand, it is much easier to envisage what might be the result of mutations at different ontogenetic stages.

Figure 2 shows how species 1 (S1) can give rise to species 2 (S2), the two remaining in the same genus (G1). This episode of "simple speciation" implies a mutation that becomes effective near the end of ontogeny. Species 1 and 2 share most of their ontogenetic patterns and differ for just some adult features, at the end of the inverted cone.

The founder of a monophyletic genus is a new species, but its evolution from the most proximate ancestor (referable to another genus, otherwise its descendant would not be the founder of the new one) requires a greater change than simple speciation. Species 3 (S3) does not derive from S2 due to the same evolutionary mechanism that led from S1 to S2. The mutation, even of the same size, acts earlier in ontogeny, and had a bearing on a greater part of development and of the resulting adult stage.

A new family, as depicted for the origin of species 4 (S4), requires a much earlier-in-ontogeny mutation, and even earlier are the mutations leading to a new order (from S4 to S5), a new class (from S5 to S6), or a new phylum (from S6 to S7). The first representative of a new phylum, e.g. S7 in fig. 2, is a new species that is also ascribed to a new class, a new order, a new family, a new genus. Phyla are not formed by a posteriori assemblages of the independently-formed lower taxa.

This aspect is particularly important, since genetic mutations of the same size (in terms of mutated nucleotides) might have completely different impacts on the body plan according to the ontogenetic stage in which they act. If we measure evolution according to the genetic distances obtained by

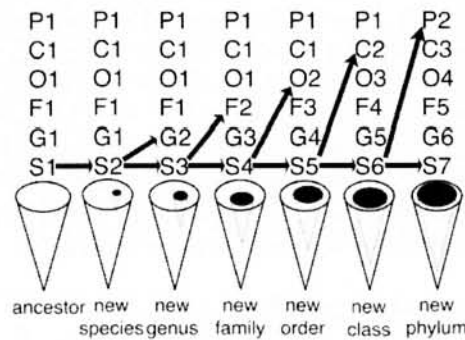


Fig. 2. Adaptation of the theory of the inverted cone of development into the formation of new taxa of different hierarchical order (redrawn from Boero et al. 2005).

comparing genomes, we obtain the overall genetic similarity among taxa, which reflects the divergence in time, measured as if evolution had a steady and gradual pace. But one thing is having diverged since some time, and another thing is to have acquired a sudden mutation, presumably irrelevant to the overall similarity of genomes, that leads to a new milestone. The gradual evolution of neutral genetic divergence might be uncoupled with the saltational evolution linked to the origin of higher taxa.

The Evolutionary Cone

It has often been said that higher taxa are the product of our way of thinking and that species are the only “real” evolutionary units. But if higher taxa are monophyletic, then speciation events, as seen in Fig. 2, do have different bearings on the descendants of the newly formed species, according to the developmental changes that generated them. One might say, re-evaluating Haeckel’s recapitulation principle, that higher taxa can be identified according to the shared percentage of ontogenetic patterns. The more ontogenies differ, the higher is the “higher taxon” distinction among lineages. And higher taxa represent clades deriving from these speciations of higher rank than “simple speciations” leading to the origin of new species referable to the same genus of the ancestor.

A monophyletic phylum starts with one species (Fig. 3), representing the founder of the phylum. That species will represent also a new genus, a new family, a new order, and a new class. From this, all the subsequent radiation, if any, will take place. Leading to the distinction of new lower-level taxa, each one starting, however, with a single species. Depending on the magnitude of the genetic (and phenotypic) modifications, new higher-order taxa can evolve suddenly, without the gradual pattern shown in Fig. 3. Evolution can be both gradual and saltational, even though gradual evolution, leading to simple speciation, is much more probable than saltational one, leading to speciation originating higher-order taxa, since the viability of the result of large genetic modifications might be impaired by the change. The possibility that the sum of an enormous number of little variations might lead to the emergence of higher-order taxa is not reasonable in the light of the inverted cones of both development and evolution. Simple speciation events, in fact, do not radically alter the body plan of the descendants in respect to that of the ancestors, only leading to a simple series of variations on the same theme. Higher-order taxa, to evolve, need radical changes, occurring towards the tip of the inverted cone, far from the end of ontogeny.

Alternative Morphs—Combined Cones

The theory of alternative morphs (West-Eberhard 2003) was proposed to explain how evolutionary novelties can emerge in taxa with complex life

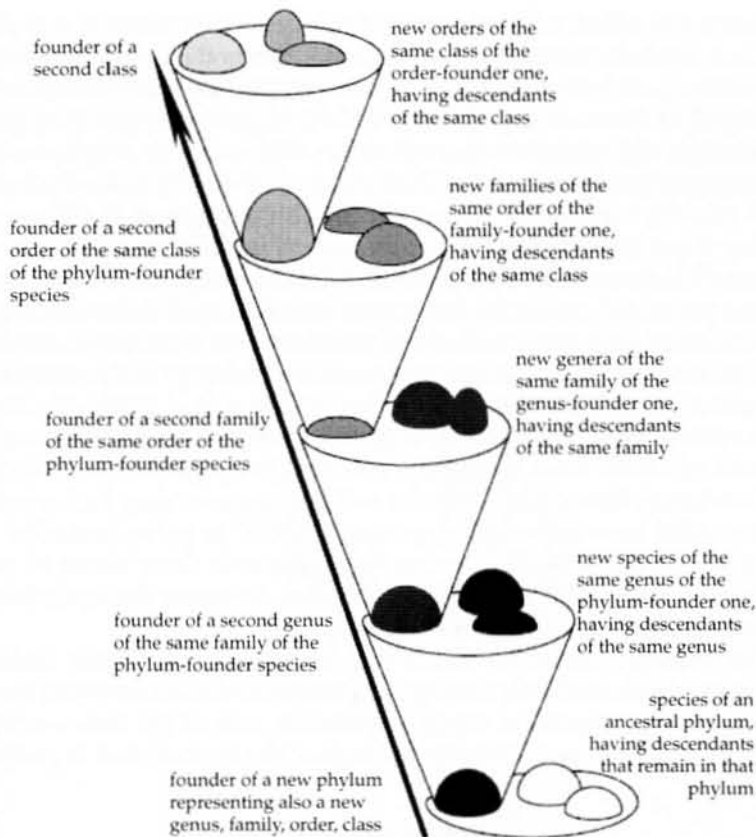


Fig. 3. Radiation of biodiversity explained by the metaphore of the inverted cone. Genetic changes of different magnitude may take place at different developmental timings, explaining both saltational and gradual radiation of taxa.

cycles. The rationale of the theory is that the strongest form of selection is stabilizing selection, with a strong tendency to conserve extant genetic and morphological states. To circumvent stabilizing selection, allowing neutral evolution only, some morphs can be temporarily reduced or suppressed (by pedomorphosis) and they can then be re-expressed in a modified form. The same idea, at a genetic level, is that of gene duplication. Important genes cannot be changed, but they can evolve by duplication, so that one copy does the "original work" and the others are free to change, leading to novelties.

If pedomorphosis and peramorphosis can modulate change even in species with direct development, this is even simpler for species with complex life cycles, leading to different morphs. Translated into the inverted cone metaphor (Fig. 4), the alternative morphs suggest that

mutations can affect a larval stage of the cycle (for instance the polyp stage in a medusozoan), or the adult (for instance the medusa stage of a medusozoan), or both, according to what will be the contribution of the cell altered by the mutation to the rest of development. Regulatory genes, furthermore, can modulate the expression of the various stages, a rather widespread phenomenon in the Cnidaria, and especially in the Hydrozoa, where medusa suppression occurs very easily (Bouillon et al. 2006).

The suppression of medusae does not imply the elimination of the genetic information specifying for them. Being unexpressed, this information is not subjected to natural selection and is free to change with no limits. If re-expressed, these modified genes can originate much different morphs from the original ones, as probably occurred for the medusae of *Obelia* (Boero et al. 1996, Govindarajan et al. 2006) (Fig. 5).

In spite of being the classical textbook example of the Hydrozoa, the medusae of *Obelia* have a radically different body plan from that of all other medusae: their umbrella is flat and not concave, they lack a velum, their tentacles have a chordal structure, identical to polyp tentacles. The hydroids of *Obelia*, instead, are undistinguishable from those of other members of the family, the Campanulariidae. Whereas the hydroids are highly conservative, the medusa is greatly innovative.

The probable reason for this is that the genes of the *Obelia* medusae have been re-activated after having been inactivated in an ancestral species with suppressed medusae. *Obelia* is probably one of the best examples of the origin of a new body plan through a mechanism that is perfectly

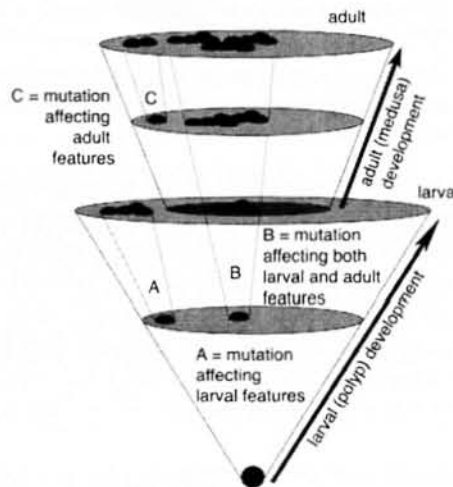


Fig. 4. The theory of alternative morphs in complex life cycles (e.g. hydrozoan life cycle) explained by the metaphor of the inverted cone. The outcome of genetic changes depends on the stage in the life cycle (larval: planula and polyp, or adult: medusa) where they take place.

explained by the theory of alternative morphs. The polyp morph, in fact, is almost indistinguishable from the polyps of other genera of the Campanulariidae, and it is for this reason that the genus is placed into this family. The medusa, however, differs in such a way from all other hydromedusae (first of all by not having a velum, the trademark of hydromedusae) that, if the polyp were unknown, it should be placed into a separate medusozoan class.

In the light of the inverted cone model (Fig. 6), the developmental cone of the hydroid remained unmodified. The medusa stage was suppressed and its genetic substrate mutated freely. When the medusa was re-expressed, its inverted cone was radically modified, resulting into a new body plan by re-elaboration of the existing genetic material.

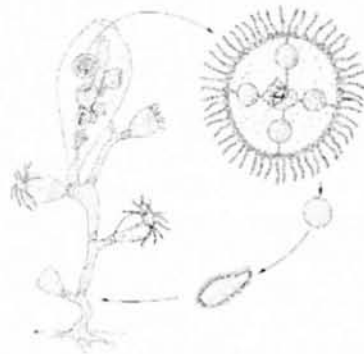


Fig. 5. The life cycle of *Obelia* sp., a classical model of hydrozoan life cycle.

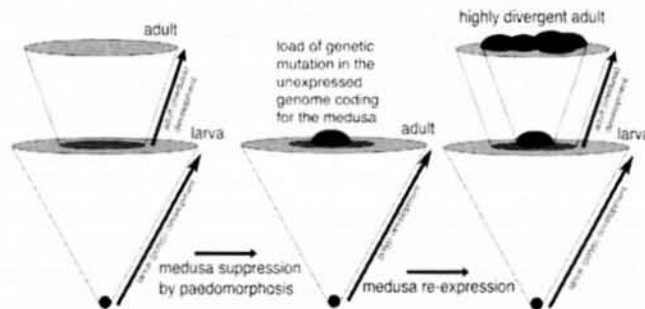


Fig. 6. High morphological divergence in the adult stage of *Obelia* sp. explained by alternation of medusa suppression, silent accumulation of genetic changes in the unexpressed part of the genome, and medusa re-expression.

The Cnidaria are the Basis of Metazoan Evolution

Boero et al. (1998, 2005, 2007) developed the idea that most of the features that are considered as the “milestones” of metazoan evolution evolved in the Cnidaria and that the so-called Cambrian explosion had the Cnidaria as its explosive, since representatives of the phylum are in the fossil record before all other present-day animals. The proposal stemmed from comparative embryology and anatomy and was later corroborated by molecular studies (see Seipel and Schmid 2005 and references therein, Matus et al. 2006), even if for some time it was not favorably accepted (e.g. Nielsen 2001). However, alternative molecular approaches can support different views, as a recent one (Dunn et al. 2008) viewing the Ctenophora as the stem group of the Metazoa, among the traditional “radial” groups.

The disparity of phylogenetic reconstructions calls for a double check of their validity, especially when molecular markers presume a more or less continuous change (i.e. gradual evolutions) that might not cope with sudden genetic changes leading to sharp evolutionary novelties by saltational events, as proposed in the first part of this chapter. Comparative morphology, under this respect, still has a lot to say. Just as molecular biology, though. The two must go together. Eye evolution, for instance, is with all probability a cnidarian affair, given the number of conserved critical genes to the regulatory developmental cascade (e.g. *Brain3*, *eyes absent*, *Six/sine oculis*) leading to eye formation throughout the metazoa. If the genetic control is the same, eyes are with all probability monophyletic, even though studies based on comparative morphology suggested analogy. A *PaxB* cubozoan gene, expressed in the rhopalia, retain combined features of Pax6- and Pax 2/5/8 types, respectively two master genes for eye and ear/gravity organs formation (Gehring 2005, O’Brien and Degnan 2003). These arguments are in favour of a shared ancestry of sense organs between cnidarians and bilaterians (Jacobs et al. 2007).

The milestones of metazoan evolution that have or might have their first appearance in the cnidaria are, according to Boero et al. (2007):

The eyes, supported by the conservation of the genetic control of eye development by PAX genes;

The statocysts, as equilibrium organs, first developed in jellyfish;

The bilateral symmetry, as documented by the finding of fundamental genetic controls for the establishment of a secondary main body axis (reviewed in Boero et al. 2007) and by some anatomical evidences, such as the dramatic polarization of nerve cells in the planula larva that, for the first time in the Metazoa, exhibits a central nervous system with an anterior, brain-like structure, and longitudinal neural projections towards the posterior pole (Piraino, unpublished data);

The mesoderm, whose homology with the mesoderm of "triploblasts" has been repeatedly demonstrated at anatomical, embryological, and molecular levels (see Seipel and Schmid 2005, 2006);

The coelom, as formed during the early ontogeny of the subumbrellar chamber of the hydromedusae, lined by a mesoderm-derived tissue, the striated muscle layer;

The chitinous exoskeleton, present in hydrozoan polyp stages;

The calcium-based skeleton, present in the Madreporaria and in some Hydrozoa;

Metamery and modularity is also a possible milestone, if the repetition of modular parts (polyps) along an axis (colony) will be demonstrated to be regulated by the same genetic controls regulating the formation of metameres or repeated modules in individual organisms.

If all or most of the metazoan evolution milestones cited above prove to be homologous, as the eyes and the mesoderm have been, it can be argued that most of the key features of metazoan groups are present in the Cnidaria and that the various metazoan phyla have simply developed some cnidarian feature while not having others. The chitinous exoskeleton, for instance, characterizes the Ecdysozoa, whereas a calcium-based skeleton characterizes the Deuterostomia.

The phylogenetic tree of the Metazoa is usually divided into three megabranches, representing groups of phyla that share the same basic features (milestones). They are united at base by being bilateral, as opposed to the stem groups, that are called Radiata. The bilateral planula-like adult or larva of these radial forms was not taken as a sign of bilaterality in these groups since the bilateral stages lacked a central nervous system. The recent discovery of a central nervous system in a Hydrozoan planula sets back the origin of both bilaterality and the central nervous system. The most ancient Metazoa with a bilateral symmetry and a central nervous system are the Cnidaria. The recent description of Cambrian jellyfish fossils almost identical to recent ones (Cartwright et al. 2007) suggests that jellyfish were present even before the Cambrian explosion.

A somehow bold statement: The era of the Bilateria was set 540 million years ago, by paedomorphosis, when a planula became sexually competent, stopping its development but retaining the genetic information of all the milestones already present in the Cnidaria. The development of a chitinous exoskeleton would have started the Ecdysozoa, whereas that of a calcium-based skeleton would have started the Deuterostomia, all with their coelom, and mesoderm, and sense organs, and metamery (already evolved by the Cnidaria).

Conclusion: Testing Hypotheses

The above hypothesis, consisting of a constellation of sub-hypotheses, stems from comparative morphology and can be tested by investigating the genetic control that leads to the formation of the milestones, forming the sub-hypotheses. The first tests already suggested homology for both eyes and mesoderm. If most of the other milestones will prove to be homologous, the Cnidaria will acquire a pivotal role in metazoan evolution, being not only the base of their tree, but also the basis of their evolutionary novelties. The mechanisms allowing for the radiation of the main metazoan lineages from the Cnidaria are the suppression by paedomorphosis of some acquired features, the retention of their genetic specification, their re-elaboration followed by their re-expression in a modified form. This mechanism is suggested by the inverted cones of development and evolution, linked to the paedomorphic and the alternative morphs models of evolution.

If these hypotheses will be validated, the evolution of the Metazoa will result as deriving from a single, major step: the evolution of Cnidaria. And zoology textbooks will require some re-writing.

Acknowledgements

This is dedicated to the memory of Volker Schmid (1939–2008). We worked together for more than ten years, searching for the secrets of the immortal jellyfish, but we were too slow in getting them. Volker started it all by stating, one day, that he was teaching his students that the subumbrellar cavity of hydromedusae is a coelom. When FB asked him why he hadn't published anything about that, he said: But it is so obvious! It was obvious for you, Volker. And also for us, one second after you simply said that sentence. Everything became clear in a single shot. But it was worth while stating it formally for the unbelieving fans of the "higher" taxa, and then you were so kind to demonstrate it also with some molecules. Thank you. The unconventional scientist refuses to die.

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References

- Arthur, W. 1997. *The Origin of Animal Body Plans*. Cambridge University Press, Cambridge, UK.
- Boero, F. and J. Bouillon, and S. Piraino. 1996. Classification and phylogeny in the Hydroidomedusae (Hydrozoa, Cnidaria). *Sci.Mar.* 60: 7–16.
- Boero, F. and C. Gravili, P. Pagliara, S. Piraino, J. Bouillon, and V. Schmid. 1998. The cnidarian premises of metazoan evolution: from triploblasty, to coelom formation, to metamerism. *Ital. J. Zool.* 65: 5–9.
- Boero, F. and J. Bouillon, and S. Piraino. 2005. The role of Cnidaria in evolution and ecology. *Ital. J. Zool.* 72: 65–71.
- Boero, F. and B. Schierwater, and S. Piraino. 2007. Cnidarian milestones in metazoan evolution. *Integr. Comp. Biol.* 47: 693–700.
- Bouillon, J. and C. Gravili, F. Pagès, J.-M. Gili, and F. Boero. 2006. An Introduction to Hydrozoa. *Mémoires du Muséum National d'Histoire Naturelle* 194: 1–593.
- Cartwright P. and S.L. Halgedahl, J.R. Hendricks, R.D. Jarrard, A.C. Marques, A.G. Collins, and B. Lieberman. 2007. Exceptionally Preserved Jellyfishes from the Middle Cambrian. *PLoS ONE* 2(10): e1121.
- Dunn, C.W. and A. Hejnol, D.Q. Matus, K. Pang, W.E. Browne, S.A. Smith, E. Seaver, G.W. Rouse, M. Obst, G.D. Edgecombe, M.V. Sorensen, S.H. Haddock, A. Schmidt-Rhaesa, A. Okusu, R.M. Kristensen, W.C. Wheeler, M.Q. Martindale, and G. Giribet. 2008. Broad phylogenomic analysis improves the resolution of the animal tree of life. *Nature* 452: 745–749.
- Erpenbeck, D. and O. Voigt, M. Adamski, M. Adamska, J.N. Hooper, G. Worheide, and B.M. Degnan. 2007. Mitochondrial diversity of early-branching metazoa is revealed by the complete mt genome of a haplosclerid demosponge. *Mol. Biol. Evol.* 24: 19–22.
- Gehring, W. 2005. New perspectives on eye development and the evolution of eyes and photoreceptors. *J. Heredity* 96: 1–13.
- Govindarajan, A. and F. Boero, and K. Halanych. 2006. Phylogenetic analysis with multiple markers indicates repeated loss of the adult medusa stage in Campanulariidae (Hydrozoa, Cnidaria). *Mol. Phyl. Evol.* 38: 820–834.
- Jacobs, D.K. and N. Nakanishi, D. Yuan, A. Camara, S.A. Nichols, and V. Hartenstein. 2007. Evolution of sensory structures in basal metazoa. *Integr. Comp. Biol.* 47: 712–723.
- Kusserow, A. and K. Pang, C. Sturm, M. Hroudá, J. Lentfer, H.A. Schmidt, U. Technau, A. von Haeseler, B. Hobmayer, M.Q. Martindale, and T.W. Holstein. 2005. Unexpected complexity of the Wnt gene family in a sea anemone. *Nature* 433: 156–160.
- Laroux, C. and B. Fahey, D. Liubicich, V.F. Hinman, M. Gauthier, M. Gongora, K. Green, G. Würheide, S.P. Leys, and B.M. Degnan. 2006. Developmental expression of transcription factor genes in a demosponge: insights into the origin of metazoan multicellularity. *Evol. Dev.* 8: 150–173.
- Maldonado, M. 2004. Choanoflagellates, choanocytes, and animal multicellularity. *Invert. Biol.* 123: 1–22.
- Matus, D.Q. and K. Pang, H. Marlow, C.W. Dunn, G.H. Thomsen, and M.Q. Martindale. 2006. Molecular evidence for deep evolutionary roots of bilaterality in animal development. *Proc. Natl. Acad. Sci. USA* 103: 11195–11200.

- Nielsen, C. 2001. *Animal Evolution, Interrelationships of the Living Phyla*. Oxford Univ. Press, Oxford.
- O'Brien, E.K. and B.M. Degnan. 2003. Expression of *Pax2-5-8* in the gastropod statocyst: insights into the antiquity of metazoan geosensory organs. *Evol. Dev.* 5: 572-578.
- Sakarya, O. and K.A. Armstrong, M. Adamska, M. Adamski, I-F. Wang, B. Tidor, B.M. Degnan, T.H. Oakley, and K.S. Kosick. 2007. A post-synaptic scaffold at the origin of the animal kingdom. *PLoS ONE* 2: e506.
- Seipel, K. and V. Schmid. 2005. Evolution of striated muscle: jellyfish and the origin of triploblasty. *Dev. Biol.* 282: 14-26.
- Seipel, K. and V. Schmid. 2006. Mesodermal anatomies in cnidarian polyps and medusae. *Int. J. Dev. Biol.* 50: 589-599.
- Wang, X. and D.V. Lavrov. 2007. Mitochondrial genome of the homoscleromorph *Oscarella carmela* (Porifera, Demospongiae) reveals unexpected complexity in the common ancestor of sponges and other animals. *Mol. Biol. Evol.* 24: 363-373.
- West-Eberhard, M.J. 2003. *Developmental Plasticity and Evolution*. Oxford University Press, Oxford.