FROM “TREE-THINKING” TO “CYCLE-THINKING”:
ONTogenetic systematics OF NUDibRANCH molluscs

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ABSTRACT

During the last decade traditional morphological paradigm of evolutionary biology has been challenged. Molecular systematics and morphology-based phylogenetics were considered as “advanced” fields compared to the “old-fashioned” traditional systematics. At the same time, an enormous body of the practical and theoretical methods of “traditional” biology was considered usually in a minimal degree. It is here demonstrated that the current evolutionary paradigm in the “phylogenetic era” lacks a theory of how organisms change their shape. The links between evolution, ontogeny, systematics and phylogenetics are prima facie obvious, but similarly greatly underestimated currently, though the field of “evo-devo” is continuously growing. As a synthesis (or more exactly, re-synthesis) of the still in considerable degree independently developing major biological fields, i.e. ontogeny, evolution and taxonomy, the new conception of ontogenetic systematics is therefore suggested; the practical usefulness of the new concept is illustrated by some examples from nudibranch molluscs. Such re-formulation of apparently well-known and obvious biological knowledge implies also a great challenge for current phylogenetics and systematics: an understanding of the necessity to consider not only evolutionary “lines” and “branches” of the “Tree of Life”, but also its cycle nature, since ontogenetic cycles are indispensable and active parts of the process of evolution.

FROM SYSTEMATICS TO EVOLUTION AND VICE VERSA: THE CURRENT PARADIGM

After collapse of the classical biological science following by two world wars, traditional systematics underwent rapid evolution leading to dramatic changes in this field. Major agenda of the unprecedented challenge for the systematics become the “search for objectivity”. Following this way several schools pretending on an objective systematics emerged consequently. Phenetics refused...
classical systematic hierarchy in favour of “direct” measurement of a dimension between characters (Sokal & Sneath, 1963). Initial enthusiasms of phnetists soon was declined and replaced by the next paradigm – phylogenetic systematics (Henning, 1966). Phylogenetic systematics became the most prolific and successful branch of the “objectivity-driven” taxonomy, first of all because it was actually a stricter reformulation of the classical heritage of Darwin’s (1859) and Haeckel’s (1866) texts. I.e. phylogenetic systematics, exactly in Darwinian sense, converted traditional taxonomic hierarchy into a consequence of the evolutionary events. Heated debates around theoretical foundations of taxonomy featured 1970S and 1980S and caused formation of the modern paradigm (see e.g. Wiley, 1981; Ridley, 1986; Pesenko, 1989; Wägele, 2005; and many others). Very shortly outlined, this paradigm implies tree-thinking instead of taxon-thinking.

In other words, there are no more “statical” taxa of classical systematic hierarchy, but instead any (monophyletic) taxon should be regarded as a part of an endless “Tree of Life”. To produce this, traditional hierarchy should be “ripped” and separate characters afterward need to be “extracted” and reanalyzed under various methods (e.g. Wiley et al., 1991). Then, a new, apparently objective hierarchy of characters (and taxa) is expected to appear. The breakthrough in computer technologies almost not leaved a space for critics of such an approach and “new, easy, and objective” phylogenetics celebrated their victory over all 1990S and earlier 2000S. Both modern and classical zoological periodicals then rapidly showed thousands of trees of strict dichotomic forms.

The major target of phylogenetic systematics – reconstruction of a definite “Tree of Life” apparently was so close, but real results soon demonstrated a completely different picture. A principal theme of most of the phylogenetic studies instead became “absence of resolution of phylogenetic trees” (see almost any paper that contains morphological phylogenetic analyses, e.g. Dayrat, Gosliner, 2005). Major advantages of the phylogenetic systematics – reconstructing/showing the historical sequence of the morphological apomorphies was soon almost completely disregarded by some authors (e.g. Scotland et al., 2003). Though few authors attempted to advocate importance of morphology itself as dataset for reconstructing phylogeny (e.g. Wiens, 2004), and though a so-called “bio-ontological” approach has been developed (see e.g. Ramirez et al., 2007; Vogt, 2009), modern systematics soon was transformed into “phylogenies without synapomorphies” (see Mooi & Gill, 2010).

Even as promisingly claimed often recently, that a reasonable study should include both morphology and molecules (see e.g. major topics for the planning in October 2011 a large-scale international conference Deep Metazoan Phylogeny 2011 at Ludwig-Maximilians-Universität München), this does not prevent for transforming the until quite recently extremely fashionable morphology-based phylogenetic systematics into an auxiliary discipline, in favour of the molecule-based “fourth great school of systematics” – the “It-Doesn’t-Matter-Very-Much school” (see Felsenstein, 2004, p. 145). Finally, most of the recent researchers will eagerly answer “yes” on a question whether or not “A new and general theory of molecular systematics emerged” (Edwards, 2009) (see e.g. any content of any journal where the word “evolution” is mentioned; few examples could be cited – e.g. Dunn et al., 2008; Lartillot, Philippe, 2008). Substantial revision of traditional systems (e.g. Halanych, 2004), apparently caused by the new field emergence, forces even traditional taxonomists and evolutionary morphologists, especially (still) well-established in Russia, for uncritical acceptance of the results of molecular phylogenetics and claims for a “revolution in systematics” (see e.g. Shatalkin, 2005). The general current enthusiasm about molecular phylogenetics is so overwhelming (even despite on numerous problematic issues – see e.g. Philippe et al., 2011a), that any opposite or just more balanced views could be easily interpreted as an “old-fashion” adherence of an author with old ideas. Nevertheless, one of such attempts will be performed here.
Considering the above outlined few key-points of the “modern” systematics development it is possible to conclude that several generations of “objective” approaches have substituted each other during the last 50 years. The current one is molecular phylogenetics, and it actually includes elements of all previously “eaten by each other” approaches: analysis of numerous separate characters apart from any hierarchy concept of phenetics and the cladistic approach of Hennigian phylogenetic systematics that, in contrast, is based on the at least idealistic assumption of homology of characters.

Many shortcomings of the traditional systematics leave of course a possibility for some kind of “misuse” of its methods, leading e.g. to so called splitting and lumping, arbitrary- and authority-driven classificatory schemes, a potential possibility for almost “endless” split a higher taxon into subtaxa, etc., and partially provoked the XX-century race for “objective systematics”. But is the molecular phylogenetics exactly the long-expected substitution for the “fabulously arbitrary” classical systematics? As it was admitted by molecular phylogenetists themselves, “Phylogenetics is still a difficult and controversial field, because no foolproof method is yet available to avoid systematic errors” (Lartillot & Philippe, 2008, p. 1469). Special bioinformatics literature is full of debates of the usefulness of the different mathematical models of the nucleotide substitutions and alignment algorithms. All the enormously branched field of the molecular systematics is constructed on the probabilistic principles that are not “hided”, but instead, widely advertised (see Nei, Kumar, 2000; Felsenstein, 2004; Lukashov, 2009; and many others).

However, even the phylogenetic theorists and bioinformatics specialists are in doubt while attempting to distinguish “truth” and “statistics” in the molecular phylogenetics (see e.g. Wägele et al., 2009; Kumar, 2010; Philippe et al., 2011a). The exponential growth of the new publications in this field already has led to the hardly avoidable contradictions. E.g., the famous Ecdysozoa vs. Coelomata controversy: currently phylogenetists claim that the new data clearly in favour of the former (e.g. Holton, Pisani, 2010), but numerous previous contradicting studies most likely suggested that is not a final conclusion. In turn, newest nudibranch phylogenies based, for the first time, on a substantial taxon sampling, resulted, however, mostly in a conclusion, that “our results do not resolve all the relationships within the Cladobranchia” (see Pola & Gosliner, 2010, p. 931). In the meanwhile, on two main problems of the molecular phylogenetics — incompleteness and absence of a definite resolution have been pointed soon after the new field became a mainstream (see, e.g. Jenner, 2000). It is quite clear that obtaining of the large molecular data sets and developing of the sophisticated molecular tools is of much benefit for the independent checking of the evolutionary-morphological hypotheses. However, there are still so scarce data in favour of the true objectivity of such approach. Some remarkable examples of controversies, e.g. on the phylogenetic position of animals with extremely simple morphology, like Acoela, where molecular phylogenetic methods prima facie unquestionably superior over traditional approaches, revealed however, that the range of discussions even in the newest publications (i.e. basal vs. derived simplified position of acoelomorph – Mwinyi et al., 2010 vs. Philippe et al., 2011b) is comparable with the past debates in the evolutionary morphology field (e.g. Ivanov, Mamkaev, 1973). And after 15 years of active developing of sophisticated programs for molecular phylogeny reconstructions, professional taxonomists recommend “use biology, not algorithms to make homology decisions” (see Mooi & Gill, 2010, p. 26).

Thus, as a result of more than 40 years of theoretical discussions and about 20 years of practical applications, the field of phylogenetic systematics, while performing their great quest for objectivity, have provided us with: 1. New arbitrariness, 2. Novel preconceptions, 3. Absence of the strict resolution, 4. Doubts in monophyly of every taxa. That was therefore almost entirely missed in the apparently exhaustive
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theoretical discussions, which are included perhaps thousands of papers and hundreds of monographs, and that have led to the current situation? The answer is very simple, quite disappointing, and somewhat contradicting even with the first lines of the present paper. This almost entirely forgotten field is the traditional systematics. This, quite humble and clearly endangered (even the recent great rising of “Zootaxa” could not completely prevent traditional systematics from the label of “old-fashioned”) in the modern time, scientific tribe of professional taxonomists almost 300 years already has performed their really great task – finding a way how to describe independently from our consciousness existing patterns of the organisms in a most consistent manner.

Despite of the methods of traditional systematics have slightly changed since the Linnean time, they still successfully allow to describe these independently-existed phenomena – taxa of the systematic hierarchy. Very important for the aims of the present paper is the fact that traditional systematics still acted independently from any phylogenetic study itself (does not matter, morphological or molecular), despite on repeated claims of the tree-priority over the taxa themselves. In a most paradoxical way, the traditional taxonomy in the second part of XX century became a real “keeper” of true objectivity in the study of organism diversity. No traditional systematist will ever place a dandelion into a phylum Arthropoda and to the family of the harvest mites (Trombiculidae),...

Figure 1:
New model of the dorid evolution. Ancestral notaspid and dorid ontogenetic cycles (external features). Elaboration (prolongation) of the notaspid ontogeny led to appearing of the complicated cryptobranch ontogenetic cycle, whereas it further heterochronic modifications caused appearing of the variously juvenilized phanerobranch dorid families up to strongly paedomorphic Corambidae group. The prognostic features of this model imply presence of the cryptobranch postlarval stages in the newly discovered *Onchimira cavifera*, despite that real ontogeny of this taxon is completely unknown yet. Drawing by T.A. Korshunova based on A.V. Martynov originals.
but instead into a division of the flowering plants (Angiospermae or Magnoliophyta) and to the family Asteraceae. In a similar way, it is hardly expected, that a bivalve molluscs will be considered by traditional systematist as a polychaet, or that a nudibranch mollusk will be named as a cephalaspid.

Thus, prima facie absolutely combinative and “typological” method of the taxa formation actually have led to discovery of the independent from a particular observer natural phenomena — really existing groups of organisms, united by a set of unique characters. In any country, a student, professional expert or amateur unequivocally and independently will confirm existence of such groups, e.g. bivalve mollusces, polychaet worms or mammals. The independent multiple confirmations is a base for any scientific knowledge and in this respect, paradoxically, traditional systematics comparable with exact science.

In other words, traditional systematists in course of almost 300-years of the taxonomy development have learned perfectly how to structurally attributed any, previously unknown specimen to a known taxon of the systematic hierarchy.

And if a taxonomist will find a mollusk with crawling sole, radula and also, with a spiral protoconch, but with a two-valved shell, he will definitely consider this unusual taxon as an aberrant member of the class Gastropoda, not as an aberrant member of the class Bivalvia. Moreover, several fine, complex “enough” morphological features of the two-valved snails, including radula and reproductive system unambiguously point to the subclass Opisthobranchia, and even more exactly, to the order Sacoglossa. Understanding that Julia and Berthellinia are the members of the class Gastropoda and subclass Opisthobranchia at the level of soft body morphology (Kawaguti & Baba, 1959) then helps to paleontologists recognize their initial mistake in assessing of the fossil shells of the two-valved sacoglossans to the class Bivalvia. Is it an ideal of a scientific knowledge? Professional taxonomists are of course well aware about numerous “dangers” of the traditional systematics. Nevertheless, a system generated of the knowledge of traditional systematists, even methodologically almost lacking any notions on the evolutionary process, comes much more close to a yet not existing “ideal” of the biologically-based theory of the historical transformations of the organisms, than any modern taxa and ranking-free statistics-aided study of nucleotide substitutions in the molecular phylogenetic field. This is because they are able to distinguish and define (name) any organisms structurally and use the hierarchical principle.

There are no doubts though, that structural approach itself has many restrictions – that were a driving force for the past and present challenges for the theory of systematics. Traditional systematics offers mighty methods for exactly recognizing organismal patterns, but almost do not consider causes of emerging of such patterns, i.e. evolution. Therefore, finding, for instance, some aberrant taxa within a well-established taxonomical group (e.g. opisthobranch order Doridacea), which are, similar to the apparently ancestral (for dorids) Notaspidea by gill patterns (i.e. dorid family Corambidae), traditional systematics may relatively easily be misled in assessing their relationship. However it will be too simple and premature labeled the classical systematics as a non-evolutionary and “typological” (e.g. Mayr, 1963; Hennig, 1966). Because, as it is sometimes eluding from the current thinking, one of the major evidence for the evolution itself became exactly existence of the systematical hierarchy (Darwin, 1859). In another word, the properties of the traditional systematics allow for relatively easy converting it into a sequence of the evolutionary event (Haeckel, 1866). And though it sounded so sensational in the 1970-80S, Hennigian phylogenetic systematics was actually a quite obvious and much postponed almost direct implication of the Darwin’s and Haeckel’s key texts.

Thus, we have an obvious, but still not solved in a most consistent way, contradiction: traditional systematics very well works with the recognition
of unique taxa, but almost does not include an evolutionary approach. Whereas phylogenetic systematics (including molecular), instead, built on strict evolutionary principles, but considerably disregard the fact that any living thing exists not only as a “line” or “branch”, but forms also particular, separate organisms, quite “closed” systems called species, which are able to exist millions of years just slightly changing. Moreover, all organization of the living organisms demonstrates a hardly disputable conservatism: most of the metazoan phyla have been traced already in Cambrian, that means therefore, that not only the morphological, but also physiological, molecular and ontogenetic basis of any modern animals have not changed significantly in course of the last half of the billion years!

Is it possible to suggest some set of theoretical and practical instruments that may challenge current paradigm that can be shortly named as “tree-thinking”? Because the rapidly growing field of “phylogeny reconstruction” is almost not interested in the fundamentals, on which any evolutionary study is based, and the molecular phylogenetics is not an exception. Is it therefore possible, that suggestions how to link the “immobile” traditional systematics and idea of the historical transformation of the taxa (i.e. evolution) in most consistent and natural way, from “point of view” of the real biological processes, and not the statistical probability calculation, already emerged in the history of biology, but a working method based on such ideas was not formed? And some modern reformulation, of apparently already quite well established ideas is therefore required?

**ONTOGENETIC CYCLE — THE UNIT OF SYSTEMATICS AND EVOLUTION**

Perhaps among one of such apparently obvious and self-evident ideas, that is simultaneously underestimated by both traditional systematics and modern phylogenetics, is the principle that any organism can be understood only as a part of a particular ontogenetic (or life) cycle. This was already quite evident for the Ancient Egyptians (see Hennig, 1966), and became one of the most basic elements of the continuously growing modern field of the *evolutionary developmental biology* (commonly known as “evo-devo”). Few essentially similar quotations may be included that “Morphology considers organism not only in the adult condition, but also in all preceding stages of their development” by classic of the comparative and evolutionary morphology, Carl Gegenbaur (1859, S. 1) and “Any organism does not possess an ontogenetic cycle, but instead part of it” by modern biologist John Bonner (1965). In this respect, special emphasis on the relation between ontogeny and evolution was put in Russian science by comparative and evolutionary morphologist Vladimir Beklemishev (1925, 1969), who featured his understanding of any organism not as a static structure like morphologists and systematists, but instead as the morphoprocess, e.g. continuous flow of various processes, and first of all, the ontogenetic cycle itself (see e.g. Korotkova, 1979; Ivanova-Kazas, 1995 and many others). Beklemishev specially highlighted that exactly the life cycle of any species is the unit of the comparative morphology (see Beklemishev, 1969, introduction). Benedictus Danser (1950, p. 142), Dutch plant taxonomist, quite unequivocally formulated this principle for the field of systematics: “The life-cycle with its multiformity is the smallest unit of classification”.

In this respect, major deficiency of the current phylogenetics (in any from) in “low resolution” of taxa relationship appears not due of the not enough degree of the advancements of algorithms and software, but in fundamentally incorrect basic concept regarding the most important biologically-based properties of the organisms – the ontogenetic cycle. As it was already mentioned above, modern phylogenetics it is a somewhat hybrid between evolution-free phenetics and, strictly evolutionary phylogenetic systematics. Both books of Sokal & Sneath (1963) and Hennig (1966) thus became an indispensable basis of the modern phylogenetics. And in both monographs properties of the ontogenetic cycles were either
not considered at all (Sokal & Sneath, 1963) or specifically interpreted (Hennig, 1966). Already on the first pages of Hennig’s fundamental publication, the entire ontogenetic cycle was actually “ripped” into independent stages of the “semaphoronts” (Hennig, 1966), “character bearers”, and the major problems to assign different developmental stages to one species, without direct observations, was highlighted. Such methodological approach was important for Hennig in order to find stricter bases of his theory. However, widely cited and too superficially and incorrectly interpreted, most likely, they opened a way for further consideration not only taxonomy, but also ontogenetic cycle itself as a predominantly combinative fields, lacking their own strict patterns. The Sokal & Sneath “Numerical Taxonomy” (1963), apparently built their theoretical apparatus on a completely different ground than Hennig, and just not considered almost any biological properties (including ontogenetic cycle) at all, but instead formulated an “operational taxonomical unit” (OTU), as super-formal ground for the taxa construction. However, these both so different books have produced in total very similar effect, which can be most well described as “founder effect”: the key importance of the ontogenetic cycle was almost vanished from entire field of the phylogenetics and systematics. And a modern important review on the methods of the phylogeny reconstruction easily avoided even one mention (!) of the fundamental biological term – ontogeny (see Felsenstein, 2004), thus perfectly recapitulates one of their own most important ancestor – the Sokal & Sneath’s book “Numerical Taxonomy”.

The importance of the ontogeny for the understanding of evolution has not disappeared from the scientific publications completely, but rather transformed into a special field. The modern founder of the field is of course famous German biologist Ernst Haeckel and his immediate predecessor, Fritz Müller. The latter suggested basic principles of the ontogenetic and evolutionary interactions (Müller, 1865) prior to the Haeckel’s first monumental monograph “Generelle Morphologie” (Haeckel, 1866). Nevertheless, we still should thank Haeckel not only for one of the most consequential defending of the evolutionary theory, but also for the formulation of the terms ontogeny and phylogeny, facts which are most likely well remembered only by a handful of modern molecular phylogenetists. It is quite hard to understand now, but in the second part of the XIX and first half of the XX centuries ontogeny was an important and actually integral part of many of the systematic and evolutionary studies. The famous Haeckel’s agenda “ontogeny recapitulates phylogeny” has received controversial acceptance, and there were many repeated attempts to challenge the biogenetic law (e.g. Sedgwick, 1909), but a comprehensive theory of the interaction of the ontogeny and evolution for the first time was suggested by the Russian morphologist and embryologist Alexei Severtsov (also spelled as Sewertzoff) (1912, 1931). Ten years prior to the well-known paper of Garstang (1922, p. 81, claimed that “no one has presented [until now] a complete theoretical scheme capable of replacing Haeckel’s as an explanation of the relations between ontogeny and phylogeny”), Severtsov exactly and unequivocally suggested such a theory that finally allowed to reformulate the biogenetic law: not phylogeny is the source for ontogeny, but instead ontogeny creates evolution (Severtsov, 1912; Garstang, 1922; Levit et al., 2004, p. 349–353).

What is the important difference in such re-formulation? The key-importance for the entire evolutionary field is due to the very clear understanding that not some obscure historical processes along the endless branches of the Tree of Life are responsible for the evolution, but instead, the routine “miracle” of each new ontogeny formation and their slight or pronounced modifications solely feature the evolution itself. This new understanding of Haeckel’s law opened new horizons in evolutionary studies and have lead to formation of a particular field of the studies of the interaction between ontogeny in evolution. For many decades, this field was developed quite independently in Russia (USSR) and in USA. In both countries independent sets of theoretical instruments
Figure 2:
Comparision of the morphological patterns of apistobranch molluscs of the group Notaspidea, ancestral to all dorids (gill, lag and anal opening, an are ventro-lateral, rhinophores, rh — without pockets, their bases united) with adult (gills, dg and anal opening, an are dorso-terminal, rhinophores, rh have pockets and are diverged) and postlarval (gills absent, anal opening ventro-terminal, rhinophores without pockets and united) morphology of the cryptobranch dorids. A, B, C — Berthellina citrina (Ruppell et Leuckart, 1828) (Notaspidea), adult specimen 23 mm length; D — Cadlina laevis (L., 1767) (Doridacea), adult specimen 25 mm length; E — C. laevis, postlarval stage ca. 590 μm length; F — C. laevis, preceding early postlarval stage ca. 400 μm length. Scale bars: B, C — 1 mm; E, F — 100 μm (on lower inset, E — 30 μm).
for the description of the phylogenetic effects of the ontogenetic shifts have been established. In Russia it became the *phylembriogenesis* concept of Severtsov (1912; 1934) and his successors (e.g., Schmalhausen, 1938, 1969 and many others). In USA, instead dominated attempts of re-formulating concepts of Haeckel’s initially auxiliary term heterochrony (De Beer, 1930; Gould, 1977; Alberch et al., 1979; McNamara, 1997 and many others). Both schools have used basically the same principle, i.e. the “ontogeny defines evolution”, but make different accents and use somewhat different methodological tools. For instance, in the Russian theory of phylembryogenesis, researchers persisted in using a quite “rigid” scheme, describing the alteration of the ontogeny leads to the evolutionary effects only at three levels: earlier ontogenetic changes (*archallaxis*), middle ontogenetic stages (*deviation*) and, finally, most recent additions to a given ontogeny (*anaboly*). The main idea referred to the wholeness of organisms and their ontogenetic cycles (e.g. Schmalhausen, 1938).

On the contrary, the approach of *dissociability* (Needham, 1933) featured the Gould (1977) version of the theory of interaction of the ontogeny and evolution and allowed to consider any organism as rather mosaic where different parts can develop relatively separate from each other. The dissociability concept also allowed to construct the much more flexible theory of *heterochronic shifts* of ontogeny, either regressive (e.g. pedomorphosis) or “progressive” (=peramorphosis) (see e.g. McNamara, 1986, 1997).

An almost one century gap between genetic and phylogenetic approaches in biology (when Wilgelm Roux has proclaimed his “developmental mechanics” instead of the Haeckel’s biogenetic law) was filled only in 1980S, when the apparently completely new field currently known under name of “evo-devo” has emerged (see e.g. Raff & Kaufmann, 1983; Hall, 1992, 1999, 2003; Gilbert et al., 1996; Minelli, 2003; Carroll, 2008; and many others) as a re-union of the *ontogeny and evolution*. In reality, “evo-devo” should be rather considered as a modern re-formulation of the Haeckel biogenetic law and Severtsov’s phylembriogenesis theory with genetic addition. The rise of “evo-devo” was mostly coincided with the declining of the previous ontogenetic-evolutionary concepts in both, Severtsov’s and Gould’s version. However, seeking for a new wide-scope biological theory and pretending to describe ontogenetic mechanisms (i.e. organisms’ shape transformation), evolutionary developmental biology almost “forgot” about true indispensable “data base”, almost three hundred years have accumulating the information about the non-random organism diversity patterns – traditional systematics, that deals not with some “theoretical” but instead with most really practical organism shape patterns. But the most responsible field for such “ontogenetic oblivion” is of course modern phylogenetics, as a discipline that claimed repeatedly to be the strict substitution of the traditional systematics. In the 1970-80S phylogenetically-orientated theorists virtually re-discovered the biogenetic law theme (see Fink, 1982; Kluge, 1985; De Queiroz, 1985; Mishler, 1988; Weston, 1988; Bryant, 1991; and others), but finally mostly concluded ontogenetic studies are just of auxiliary importance for the phylogenetic inference, except for few examples, which not became a mainstream (e.g. Nelson, 1978). Even few relatively recent attempts to refresh interactions between phylogenetics and ontogeny have met unexpected difficulties and such studies are still far from being widely accepted (e.g. Jaecks & Carlson, 2001; Wiens et al., 2005; etc.), though importance of the ontogenetic approach is not completely vanished from the most recent phylogenetic publications (e.g. Struck, 2007; Box et al., 2008; Smithwaite et al., 2009; Ji et al., 2009).

**ONTOGENETIC SYSTEMATICS**

Thus, until recently both branches of the biogenetic law developing have not led to the appearing of a general theory of the organism shape changing. The apparently promising synthesis, “evo-devo” might have become such a result of the post-Haeckelian re-thinking of the ontogeny and evolution interactions that could have integrated major branches of biology.
However, “evo-devo” remains largely a discipline applying modern technology on studying the ontogeny of organisms. In favour of such view quite clearly points the most recently suggested term “phylo-evo-devo” (see Minelli, 2009), which was suggested as an important novelty in one of the leading evolutionary journal. However, since ontogeny already implies evolution and, moreover, “evo-devo” exactly means “evolutionary development biology”, this additional emphasizing on “phylo-” also makes no sense because phylogeny itself means modifications of the ontogeny in the historical scale. In other words, this fact of interacting ontogeny and evolution that is known since Severtsov in 1912 is now eluding from the enormous recent “evo-devo” field, and the principle that “ontogeny builds evolution” continues to be re-discovered in modern times.

Thus, despite on almost 150 years of the evident scientific history of the interactions of ontogenetic and evolutionary studies, thousands of publications and hundreds of various terms (most of them are perfectly dead now), an important synthesis and a term connected with is still missing in this field. I.e., despite of the very complicated history and promising modern researches outlined above, current evolutionary developmental biology, classical systematics (the science, which maximally possesses the information on the diversity and hierarchical patterns of the morphological characters of the organisms) and phylogenetics have all developed mostly separate from each other. Their importance for each other is self-evident but still greatly underestimated in modern biology (e.g. there are no any mentioning of the systematics on the schemes explaining “evo-devo” synthesis – see e.g. Love, Raff, 2003; Olsson et al., 2010). Therefore, their new synthesis (“re-synthesis”) might become an important source for further understanding of the historical succession of the organisms’ shape changing, i.e. evolution in its original sense.

A new term that features and highlights such re-synthesis has been suggested recently as ontogenetic systematics (Martynov, 2010). Despite of the apparent easiness of creation of this term and deep sense, uniting both ontogeny and evolution, as far as I know, there was only one single previous attempt to use it (see Albert et. al., 1998). However, regardless of using identical words, the latter publication understood under the term ontogenetic systematics not systematics itself, but instead, somewhat paradoxically, a molecular pathways that can lead to formation of a structure during the ontogeny. The term ontogenetic systematics was suggested independently in the mentioned author’s publications. However, these two both apparently very different meanings of the term ontogenetic systematics point to this highly desirable, but yet very far from completeness general theory of the organisms’ shape transformation, of course implies understand of the way how the DNA information became the macromorphological characters. And it is a widespread modern illusion that such apparently grandiose task the “evo-devo” field can performed alone. Instead, an approximation to such task has already been made, during almost 300 years, while the traditional systematics was in searching for a system how in a most unequivocal way to describe organisms’ diversity. By-products of such searching became discovery of a real and not imaginable and methodologically very useful taxa hierarchy, and then, as a direct consequence of the latter, the discovery of the evolutionary process itself.

Most generally, ontogenetic systematics may be regarded as a starting point for constructing a general theory of the evolution of ontogenies, which largely proceeded as the evolution of a limited set of basic ontogenetic cycles of metazoans that originated as early as in the Precambrian or Early Cambrian and correspond to different phyla in the classic systematics. Such re-formulation of apparently well-known and obvious biological knowledge implies also a great challenge for the current phylogenetics and systematics: an understanding of necessity of the consideration not only evolutionary “lines” and “branches” of the “Tree of Life”, but also a cycle,
since the ontogenetic cycle is an indispensable and active part of the process of evolution. I.e., it implies a gradual shifting from current merely “tree-thinking” to what could be named as the “cycle-thinking”.

At the same time, such shift does not implies consideration of evolution as a strictly cyclic process, the view that we also should thank to the Jena scientist, Ernst Haeckel. He suggested the phases of “epacme” (primary diversification), “acme” (“flourishing”) and “paracme” (declining) (see Haeckel, 1866, Bd. 2, S. 320–322), that apparently every taxon “has passed” in course of the historical development. The Haeckel’s “three-phases” evolution was then recapitulated in many of the second part of XIX and earlier XX centuries considerations; most notable became Otto Schindewolf’s (1936, 1950) “typogenesis”, “typostasis” and “typolysis”. However, it is quite obvious, that despite of many taxa have been already completely extinct, most of the basic, for instance Metazoa structural patterns, i.e. phyla, originated yet in the earlier Cambrian, and still exist in the modern biosphere. It is prevented from such simplistic representation (though, of course apparently “natural” in analogy with the ontogeny itself) of the taxa history in the three-phase model, but do not refused the possibility to consider the evolution as result of the various ontogenetic shifts (e.g., by the well established process of heterochrony). What is very important in such consideration is the possibility to predict similar, either regressive (paedomorphic) or progressive (additive) ontogenetic shifts within various descendant taxa of the same ancestral taxon, thus quite easily explaining the phenomenon of parallel evolution, especially in relatively closely related taxa. All modern phylogenetics is full of claims for the paraphyly cases, but few modern researches understand that mostly responsible for such pattern are exactly the indisputable cyclic properties of the ontogeny itself. Returning to the entire evolutionary field, considering ontogenetic cycles as a major and not just auxiliary principle thus much more increases the reliability of both morphological and molecular phylogenetics. The ontogenetic cycle thus should become a true and not only a theoretical unit of systematics and phylogenetics.

Such problematic issues are perfectly highlighted by the very practical taxonomy and phylogenetics in one of the major nudibranch groups — dorids (Doridacea or Anthobranchia), when some aberrant features of the dorid nudibranch family Corambidae, such ventral anus and gills have been considered as archaic (basal), and therefore the entire group have been placed into the beginning of the nudibranch classification (e.g. Odhner in Franc, 1968), and, what is more notable, persisted even in recent reviews (e.g. Rudman, 1998). However, as it was already evidently shown, also by careful cladistic analysis of the morphological characters (Martynov & Schrödl, in press), corambids are “just” secondary regressive descendants of the common dorid ontogenetic cycle, originated due to the progenesis (see Martynov, 1994b; Martynov et al., 2011; Martynov, Schrödl, in press). The consideration of the entire ontogenetic cycle thus helped to correctly recognize the homologies of gills and gill cavities and thus contributed to a character set with better signal for cladistic study. Few non-trivial phylogenetic studies have already come to essentially similar conclusions, most importantly, including the molecular data (see Wiens et al., 2005). It can be only guessed how many thousands or hundred of thousands particular taxa incorrect evaluation and phylogeny reconstructions will be revealed exactly due to forgetting of the ontogenetic cycle properties.

Some important (but of course not absolutely exhaustive), both theoretical and practical principles of the ontogenetic systematics are listed below:

1. The ontogeny defines evolution, and not vice versa. Therefore, — ontogeny is basis for the phylogeny.
2. Therefore, the unit of the evolution, systematics and phylogenetics — is the ontogenetic cycle and not just a “clade”.
3. The primary classificatory procedure is not connected directly with the historical or individual
succession of the origin of the classification’s objects. A systematist attributed any just discovered new specimen on the basis of sets of unique characters, evidently homologous within any given stable (well-established) taxonomic group. With only help of the classificatory scheme, any yet unknown specimen could unambiguously always incorporated (attributed) into already known higher taxa (species to genus, genus to family, etc. etc.) on the basis of the sets of unique characters. Such principle could be also named as a main principle of the systematics.

4. The evolutionary succession of the organisms’ shape transformation — it is the succession of the
formation and “disruption” of various ontogenetic cycles. From the spawn mass of a *Littorina* we expected to see a *Littorina* juvenile or larva emerging, not a nudibranch veliger or a crustacean nauplius. However, the exact shape of the newly formed molluscs or crustacean (e.g. fine details of shell or legs proportions) is hardly predictable. Thus ontogeny combines great conservatism with possibility to some shifts, which thus leave a place for evolution. Considerable, noticeable shifts of any ontogenetic cycles are e.g. paedomorphic (then juvenile features persist on the adult stages; same for progressive (“peramorphic”) shifts; then new stages are added into a given ontogeny). When the initial ancestral shape is greatly distorted, then this could be named as “disruption” of an ontogenetic cycle. This succession of the ontogeneses in the historical perspective (evolution) thus, forms own theory, significantly independent from the procedure of the attributing, describing above.

5. The biologically-based unifying theory of the historical transformations of the organisms should in a less contradicting way integrate information obtained from these both main systematic procedures: a) attributing of the *yet unclassified* specimens according to the degree of the correspondence to the already known unique sets of the characters (taxa) and b) theory of the historical transformations of these sets of characters (phylogeny in a strict sense). Such general theory which is included both listed components is therefore suggested to term as **ontogenetic systematics**.

6. Ontogeny — it is the only existing **real** keeper of the memory of the preceding historical transformations. I.e. ontogeny — it is the only single available process allowing to link these two key-components of ontogenetic systematics (history–independent taxa attribution and the theory of phylogeny itself) in a maximally objective, biologically-, and not statistically-based way.

7. The succession of the characters allows to discover various **traces** of the ancestral ontogeny (a limited memory of the heredity system), in even greatly modified secondarily ontogenetic cycles (e.g. a modified nauplius larva in the rhizocephalous crustacea allows to infer that they still belong to the in other features completely different group Cirripedia). i.e. there is a possibility to infer the phylogenetic events by the **real**, biologically-based processes. The succession of the characters also implies their “trivial”, “systematic” homology in any reasonable narrow-defined group (e.g. rhinophores and gills within dorid group are clearly homologous, but their exact degree of homology to other opisthobranch group is less defined), and also a “deep” homology between prima facie very different structure between far related taxa. The unequivocal homological correspondences manifested at the morphological level may have very complicated both molecular and ontogenetic “recording methods” in the heredity system (see e.g. Shubin *et al.*, 1997, 2009). This not yet discovered “DNA to morphology” transition mechanisms do not prevent us from assessing these unique sets as real characteristics of taxa.

8. The ontogenetic memory is maximally identical between closely related species and maximally imprecise between the very distantly related ones. These facts allow considering traditional evolution-free systematics within real, instead of only “hypothetic” historical dimension. This also implies that is senseless to search for a “succession of all ancestors” in a given ontogeny, that is often used as an evidence for a complete “failure” of the biogenetic law. Such succession can be really found, but on a restricted phylogenetic distance, between particular taxa. Thus, only converse of the systematic hierarchical principle into sequence of the ontogenetic transformations, from particular taxa to particular taxa, it is possible to construct a general theory of systematics, i.e. general theory of the organism shape transformations. These statements also imply several very important further issues: a) Recapitulations are really existing and are mighty instruments of the phylogeny inference, but should be used only on
a restricted phylogenetic distance; b) Any well-established taxon of traditional systematics is an approximation to the model of the ancestral ontogenetic cycle — i.e. such if its ancestral species had been really existed some time ago, and had particular, functional, and not some formal and abstract, properties; c) Therefore, the in the modern evolutionary and phylogenetic theory almost completely abandoned term “transitional taxon” or “missed link” is of great importance and should be restored and given full consideration as a valid and not auxiliary, “bad” term, i.e. a heritage of old, “imprecise” and “arbitrary” systematics.

9. There are firm evidences that some sets of characters (that can be called as morphogenetic networks), for instance, some “dependent” characters of one ontogenetic cycle (e.g. juvenile features) may became “dominating” characters (e.g., adult, definitive), and vice versa. This indicates that evolution does not equal freely varying characters along the endless “branches” of the “phylogenetic tree”, but instead, rather within quite limited frames of particular entire ontogenetic cycles, most basic of the have originated already in the earlier Cambrian and then became named by traditional systematics as the metazoan phyla.

10. The consideration of the evolution restricted by the particular “technological” properties of particular ontogenetic cycles lead to the possibility of considering the diagnosis of any well-established traditional systematic group (taxa) higher than species level as a minimally contradicting model of the ancestral ontogenetic cycle, that imply that all subtaxa included in this group should be therefore products of the modifications of this ancestral ontogenetic cycles.

11. Historical transformations of the ontogenetic cycles (evolution) might perform in a regressive way (for instance, paedomorphosis), a reduction development of a given character (set) compared to the ancestral condition, and in a progressive way compared to the ancestral ontogeny. Both these processes are widespread among living organisms. Any species thus is a combination of regressive and progressive features. Many groups also clearly demonstrate domination of the larval features, thus show the paedomorphosis in narrow sense.

12. A resulting model of the phylogenetic transformations of the ontogenetic cycles may include the hierarchical order of the sequence of the taxa appearing, with indications of the major succession of the morphological structures (key phylogenetic characters; it is a method to distinguish a cycle within a line), graphic model of the morphological transformations, and also a tree-like scheme.

In a short conclusion, the “cycle-thinking” vs. “tree-thinking” lead to another important implication: we should not concentrate so much on the merging of any descendant taxon with ancestral ones, as often done by current phylogenetics, but instead on separations of “new cycles” from “old lines”. It is possible by detecting of the sets of the newly emerged morphogenetic networks as key-features of every new taxa, never existed in the previous one. Restricted recapitulations on limited phylogenetic distances became instead some obscure theoretical considerations, but a practical system of “reference points”, unambiguously indicate real, and not hypothetically constructed direction of the evolution. Thus, the ranking system of the traditional systematics does not lose their importance: it has a crucial role indicating the succession of the modifications of the ontogenetic cycles with help of the recapitulatory reference points, but not as a continual line, but as succession of sets of particular functional organizations, including particular properties of a given ontogenetic cycle. For instance, there are not any crustaceans with veliger larvae and there are not any molluscs with the nauplius larvae.

The usefulness of the consideration of any well-established, “narrow-enough” in definition
by the morphological characters and apparently monophyletic in phylogenetic terms, taxon as model of a particular ancestral ontogenetic cycle (imagined, thus as a really existed ancestral species, and not just a formal node of a tree) will be demonstrated on the example of the three taxa that are closely related from the point of view of traditional systematics (e.g. Thiele, 1931), morphological cladistics (e.g. Wägele & Willan, 2001) or molecular phylogenetic study (e.g. Jörger et al., 2010), i.e. groups of “higher” opisthobranchs, notaspids (s.str.) and nudibranchs that were considered earlier within the “supertaxa” Acoela or Nudipleura. Based on sets of unique structural characters, we recognize three potential ancestral ontogenetic cycles within this group, and thus further define them as order Notaspidea s.str (=Pleurobranchoidea), order Doridacea (=Anthobranchia) and Nudibranchia s.str. (=Cladobranchia) and then will shortly outline some basic properties and evolutionary potential of these defined ontogenetic cycles in order to conclude whether they rather represent a natural, monophyletic unit or not. This is an initial example and an experiment in an almost completely new field of the biologically-based ontogenetic systematics and can not be completely free from flaws. Further analysis in greater details and elaboration are necessary:

Model of the ancestral ontogenetic cycle of the order Notaspidea s.str. (=Pleurobranchoidea) (Fig. 1)

Systematic diagnosis: Notum present; Thin internal shell under the notum or absent; Rhinophores are well defined, enrolled and united together with oral veil into a common structure; Mantle cavity absent in all species; Single true gill is always on the right lateral side under the notum; Anal opening on the right side behind the gill and under the notum; Genital opening in front of the gill; Jaws comprising from numerous separate elements, always present; Radula possess numerous uniform hook-shaped radular rows; Central tooth absent; Digestive gland is entire, not branched; CNS with fused cerebral and pleural ganglia; Reproductive system is diaulic in most species and triaulic in two species of the genus Bathyberthella. Vas deferens is fully closed. Copulative apparatus near female genital opening on the left side in front of the gill.

Including families (alphabetic order): Pleurobranchidae and Pleurobranchaeidae.

Key newly emerged morphogenetic networks (key phylogenetic characters): Notum; Rhinophoral-oral veil common apparatus; Gill apparatus and anus free of mantle cavity on the body wall;

Model of key-transformations: Mantle transforms into the notum (progressive); Gills attached directly to the body wall (regressive); Posterior corners of the cephalic shield are bending forward and form thus enrolled rhinophores, enlarged anterior part of the cephalic shield became oral veil (progressive);

Phylogenetically important succession of the key-characters: Rhinophores remain fused with the oral veil, the feature strongly points to the cephalic shield of Cephalaspidea s.l. Lateral gill and lateral anus position strongly point to Cephalaspidea s.l. Non-cephalic copulative organ weakly points to Acteonidae.

Recapitulations: Spiral external shell of the juvenile stages points to the basal opisthobranchs like Cephalaspidea s.lato (including Acteonidae).

Ancestral group (strong or weak inference): Weak inference for Acteonidae-like group ancestry (non-head copulative apparatus).

Monophyletic status: Yes.

General model of the ancestral ontogenetic cycle: Pelagic larva with spiral shell > benthic juvenile with notum enclosed the shell, formation of free enrolled rhinophores connected with each other and with oral veil > benthic adult with internal plate-like shell, entire notum both anteriorly and posteriorly, enrolled rhinophores connected with oral veil, lateral-ventral gill and anus partially covered by notum.

Model of further ingroup evolution (major features): Shortening of the life of pelagic larva towards to the direct development; Shell reducing towards complete absence; Notum reducing (not complete); Gill reducing (not complete);
Model of the ancestral ontogenetic cycle of the order Doridacea (Anthobranchia) (Figs 1, 5)

Systematic diagnosis: Notum present or reduced; Internal shell always absent; Rhinophores are well defined, solid, completely separate from oral veil and enclosed by anterior notal margins; Oral veil small, placed under anterior notum (if it not reduced); Mantle cavity absent in all species; Single true gill is circularly bent in a secondary cavity medially on the dorsal side of notum or gill cavity absent; Few species have ventral gills or gills are completely reduced; Genital openings lateral; Jaws comprising from the numerous separate elements, or monolith, often absent; Radula possess numerous basically hook-shaped radular rows differentiated and reduced in different degree; Central tooth present or absent; Digestive gland is entire, not branched; CNS with fused or separated cerebral and pleural ganglia; Reproductive system is triaulic in most species, except for some (but not all) species of the genus Bathydoris. Vas deferens is fully closed. Copulative apparatus near female genital opening on the left side of the body.

Including families (alphabetic order): Actinocyclidae, Aegiridae, Akiodorididae, Aldisidae, Anculidae, Bathydorididae, Chromodorididae, Dendrodorididae, Discodorididae, Dorididae, Goniodorididae, Gymnodorididae, Hexabranchidae, Mandeliidae, Onchidorididae, Phyllidiidae, Polyceridae, Vayssiereidae.
Key newly emerged morphogenetic networks (key phylogenetic characters): Formation of separate rhinophores in closed rhinophoral pockets; Solid rhinophores; Formation of a highly specialized and complicated dorsal gill apparatus and gill cavity.

Model of key-transformations: Internal shell completely disappeared (regressive); Separation of the fused rhinophores into the separate pockets by the lateral shifting and anterior notal lobes including formation of the rhinophoral pockets (progressive); Formation of the solid rhinophores and their complete separation from oral veil (progressive); Single gill and anus transit from latero-ventral to dorso-terminal position with simultaneous formation of the closed gill cavity (progressive).

Phylogenetically important succession of the key-characters: Circumanal gills remain associated with the anus and nephroproct strongly point to Notaspidea s.str. and Cephalaspidea s.l. Well defined (though solid) rhinophores point to Notaspidea s.str. Triaulic reproductive system points to the pleurobranchid notaspidean of the genus Bathyberthella.

Recapitulations: Spiral shell of the juvenile stages points to basal opisthobranchs like Cephalaspidea s.lato (including Acteonidae) and Notaspidea; Fused rhinophores in earlier postlarval stages and not enclosed by the anterior notal lobes strongly point to Notaspidea s.str. (family Pleurobranchidae); Ventral anus in earlier postlarval stages strongly points to Notaspidea s.str.; Posterior entire notum of middle postlarvae without gills and gill cavity strongly points to Notaspidea s.str.

Ancestral group (strong or weak inference): Strong inference for the Notaspidea s.str.

Monophyletic status: Yes.

General model of the ancestral ontogenetic cycle: Pelagic larva with spiral shell > benthic juvenile completely loosing the shell, formation of the solid rhinophores shifted laterally from each other by the enclosing of the lobes of anterior notum, complete separation of the rhinophores and oral veil, posterior notal lobes starts to develop in earlier postlarvae and led to dorsal anus shift and formation in juveniles of the dorsal cavity where then three first gills developed > benthic adult without shell, entire notum both anteriorly and posteriorly, solid rhinophores not connected with oral veil, dorso-terminal circumanal gill within a special cavity.

Model of further ingroup evolution (major features): Shortening of the life of pelagic larva towards to the direct development; Notum reducing; Posterior notal lobes appearing; Gill cavity reducing; Gills reducing; Rhinophoral pockets reducing.

Explanatory remarks: Presence of the well-established recapitulations of the notal and rhinophoral patterns, and ventral position together with the significant structural similarity of the adult stages (presence of the notum; digestive, nervous, reproductive systems details etc.) strongly point for the notaspidean s.str. ancestry, closely similar to the recent members of the family Pleurobranchidae. Presence of the recapitulation of the juvenile gill cavity in the juveniles of completely phanerobranch genus Onchidoris, presence of the fully-functional to partially reduced gill cavity in the adult stages of some genera of so called phanerobranch group (Onchimira, Calycidoris, Diaphorodoris), presence of the juvenile gill cavity in the adult Loy meyeni, presence of the partially modified semi-open gill cavity in adult of some Corambe species strongly point to ancestral condition of the gill cavity presence and their further reduction as major feature of the ingroup evolution (see below for details).

Model of the ancestral ontogenetic cycles of the order Nudibranchia s.str. (=Cladobranchia)

Systematic diagnosis: Notum present or reduced; Internal shell always absent; Rhinophores are well defined, solid, connected with oral veil and partially surrounded by lateral notal margins; Oral veil is large, completely substitutes anterior notum. Mantle cavity absent in all species; True gill is absent in all species; Various secondary gills or papillae present in many species; Genital openings on the lateral side; Jaws monolith, well defined; Radula possess numerous basically hook-shaped radular rows differentiated and
reduced in different degree (up to one teeth per row); Central teeth present in most species; Digestive gland is entire in few taxa, in most is branched in various degree, in many taxa branches are penetrated to the dorsal papillae; CNS with fused or separated cerebral and pleural ganglia; Reproductive system is diaulic in most species; Vas deferens is fully closed. Copulative apparatus near female genital opening on the left side of the body.

**Including families (alphabetic order):**

**Key newly emerged morphogenetic networks (key phylogenetic characters):** Strong oral veil substitute anterior part of the notum; Solid rhinophores; Solid jaws.

**Model of key-transformations:** Internal shell completely disappeared (regressive); Rhinophoral and oral apparatus accepted as direct modification of the Pleurobranchaeidae type with addition of formation of the solid rhinophores still integrated with the strongly widened oral veil substitutes the anterior part of the notum (progressive or neutral); Complete reducing of the gill (regressive); Formation of the solid jaws based on integration of the separated elements of the notaspideans (progressive).

**Phylogenetically important succession of the key-characters:** Anus and nephroproct still placed laterally strongly point to Notaspidea s.str. Well defined (though solid) rhinophores point to Notaspidea s.str. Laterally shift rhinophores and widened oral veil substitutes anterior part of the notum point to particular notaspidean s.str. family Pleurobranchaeidae. Diaulic reproductive system points to the Notaspidea.

**Recapitulations:** Spiral shell of the juvenile stages points to basal opisthobranchs like Cephalaspidea s.lato (including Acteonidae) and Notaspidea; Separated rhinophores in earlier postlarval stages of *Tritonia* species and not enclosed by the anterior notal lobes point to family Pleurobranchaeidae of Notaspidea s.str.

**Ancestral group (strong or weak inference):**
Strong inference for the Notaspidea s.str. Weak inference for the particular notaspidean family Pleurobranchaeidae.

**Monophyletic status:** Yes.

**General model of the ancestral ontogenetic cycle:** Pelagic larva with spiral shell > benthic juvenile completely loosing the shell, formation of the solid rhinophores shifted laterally from each other without enclosing of the lobes of anterior notum, integration of the rhinophores and oral veil > benthic adult without shell, with reduced notum both anteriorly and posteriorly, solid rhinophores integrated with the widened oral veil which is substitute the anterior part of notum, true gill completely absent, weakly papillated lateral and dorsal notum.

**Model of further ingroup evolution (major features):** Shortening of the life of pelagic larva towards to the direct development; Notum reducing; Rhinophoral pockets reducing; Rhinophores secondary united together.

**Explanatory remarks.** The special similarity between rhinophoral and oral apparatus of some basal Nudibranchia (*Doridoxa*, *Heterodoris*, *Tochuina*, *Tritonia*) and the particular notaspidean s.str. family Pleurobranchaeidae and ontogenetic patterns of the rhinophores development point to possible nudibranchs s.str. ancestry within the latter group (see below for details).

**ONTOGENETIC SYSTEMATICS OF THE DORID NUDIBRANCHS (ORDER DORIDACEA)**

As was defined above, the dorid group (here considered as order Doridacea) possesses a set of unique characters, including a dorsal circumanal gill corolla integrated within posterior part of the notum and elaborated rhinophores, integrated within anterior part of the notum, typically within special
pockets. The oral veil of dorids is small and reduced, *anterior end of the body is the notal edge, not the edge of the oral veil* (Figs 2 D; 3 C). Dorids include two major groups — Cryptobranchia (cryptobranch dorids) and Phanerobranchia (phanerobranch dorids). Cryptobranchia possess special cavity around the gills, where the gills are able to completely retracted (Fig. 2 D) and usually well defined notum without posterior lobes and numerous processes. Phanerobarnchia, *by definition* is completely devoid of any gill cavity, instead gills are directly attached to the dorsal notum and able to contract, notum usually reduced and often posses posterior lobes or processes. Gills morphology and digestive (except for radula) and reproductive organs are essentially similar in cryptobranchs and phanerobranchs.

Dorid systematics is deeply rooted in the classical period of taxonomy (e.g. Linnaeus, 1758; Alder & Hancock, 1864; Abrahm, 1877; Bergh, 1892; and many others), but serious evolutionary studies were started only recently. Various classificatory schemes and implied their evolutionary models, already have been suggested in old works (e.g., Bergh, 1892; Odhner, 1934, 1939), but usually without much discussion and unequivocal set of strict evidences. The same author can use different schemes of classification in different works, that is especially characteristic for the nudibranch classics Rudolph Bergh and Nils Odhner. However, Odhner’s (1939) system of the order Nudibranchia including four suborders (one of which is Doridacea — dorids), became an important base actually for all modern classification and phylogenetic reconstructions.

The only pre-1990S challenge for the classical Nudibranchia concept was presented by Yu.S. Minichev and Ya.I. Starobogatov (1979). They, however, choose similar to the classical authors the “not much discussion” strategy, and published already “completed” systems in the abstracts of Soviet malacological conferences with minimum commentaries and explanatory remarks. They suggested numerous new taxa of the order ranks (including super- and suborders) and completely disregard any classical concepts of “Opisthobranchia” and “Nudibranchia”, thus prima facie perfectly anticipated all further both morphological cladistics (e.g. Haszprunar, 1988) and molecular phylogenetics (Jörger et al., 2010) central idea of paraphyly of any traditional taxa. However, despite on this challenge, the Minichev and Starobogatov systems remained a “blind street” compare to the modern evolutionary studies first of all was extremely lapidary and actually “closed” for further discussion in persisting of “once and for all” approach. For instance, the systems were constructed only on the reproductive apparatus features, and many important external and digestive system features have been completely omitted. At the boundary of 1980S-1990S only few publications dealing with nudibranch macrosystems and evolution have been further appeared (e.g. Schmekel, 1985; Wägele, 1989a; Evolutionary Biology of Opisthobranchs, 1991) closely approach soon happen “phylogenetic explosion”.

Thus, accumulated to the end of XX century knowledge on morphology of the nudibranch molluscs was so immense, whereas number of published evolutionary works was so scarce, that “phylogenetic explosion” appeared as absolutely unavoidable. It was happen mostly at the millennium boundary and was much inspired also by statistical approach, cladistics, and somewhat later, by molecular phylogenetics (e.g., Wägele & Willan, 2000; Valdés, 2002a,b; Fahey & Gosliner, 2004; Fahey & Valdés, 2005, Pola et al., 2007 and many others), and not only consider the dorids but also any other living organisms. By current widespread opinion such combination finally will answer on the “main evolutionary question” and presented the exhaustive “Tree of Life” — from Archaea to Chordata (see e.g. Maddison et al., 2007; Philippe et al., 2011a). The challenge thus is only increasing the number of genes used for reconstruction, and improvement of the statistical algorithms, etc. (e.g., Ciccarelli et al., 2006; Dunn et al., 2008; Goloboff et al., 2009; and many others). This problematic issues especially became clear in
the nowadays, when importance of the traditional systematics have been challenged in favour of the phylogenetics. Numerous researchers, working in the field of phylogenetics usually have superficial knowledge about tasks and methods of the traditional systematics (i.e. systematics itself), and not rarely, underlined in their work by the past evolutionary-morphological concepts, without understanding scale of the past discussions. At the same time, earlier molecular phylogenists, were much more careful about phylogeny reconstructions, leaving a “last plea” for the morphology and ontogeny (e.g., Raff et al., 1989). In this respect, quite remarkable, that famous RNA (!) researcher Carl Woese in 2009 warned about importance of the biology itself in the field of molecular biology (see Woese & Goldenfeld, 2009).

All this can be applied to the modern dorid systematics and phylogenetics. A good deal of modern papers have suggested a particular consideration on a priori decisions of character polarity (Valdés, 2002a,b; Fahey & Gosliner, 2004; Fahey & Valdés, 2005 and others), but scarcely offer a discussion for such decisions. That in this case difference to the past “extremely arbitrary” implications of the traditional taxonomy and evolutionary morphology? One of such most controversy evaluation has received the key-feature of the entire dorid group — gill apparatus.
Besides the traditional dorid group Phanerobranchia, prima facie lacking any gill cavity, such feature also characteristics for another, minor Doridacea group — Bathydoridoidea. That is most important, that the latter group traditionally is always considered as an “archaic” (Minichev, 1969). This view without critical discussion have been accepted by the morphological cladistics, as a plesiomorphic character, and bathydoridids, therefore were “translated” as a “most basal group” (Valdés, 2002a,b). This concept of morphological cladistics was then accepted by molecular one (Valdés, 2004). However, by definition “cavityless” phanerobranchs have demonstrated the presence of quite well defined gill cavities (e.g. in the genera Calycidoris and Diaphorodoris). This obviously important fact has received a very scarce discussion in past (Abraham, 1876; Roginskaya, 1972; Millen, 1985) but was not considered at all by the modern phylogenetic studies (Valdés, 2002 a,b; Fahey & Valdés, 2005; see Martynov et al., 2009 for further details).

Already in 1994 were obtained further evidences for much more complicated picture of the dorid evolution: was described an unusual corambid species Loy meyeni, possess dorsal gills within small cavity (Martynov, 1994a) — the feature not only unknown before in any corambids, but also strongly contradicts with the diagnosis of Phanerobranchia. Furthermore, pattern of the posterior notal lobes of Loy meyeni and another species L. millenae was essentially similar to the pattern known in the dorid postlarval, specimens described earlier (Thompson, 1958). Thus, as it was became obvious, that some important issues have been completely omitted in the dorid systematics and evolutionary studies because all efforts were put on understanding of the adult stages, whereas postlarval and juvenile stages of the ontogenetic cycle were not considered at all. However, quite clearly expressed implications on the paedomorphic origin of the corambids and significant corrections of the major trends of the dorid evolution (Martynov, 1994b, 1995) were positive noticed (Wägele & Willan, 2000) but not considered at all for the phylogeny reconstructions. Another important implication of the discovery of these highly aberrant corambids was unambiguous consideration about ancestral pattern of the cryptobranch mode (i.e. presence of the gill cavity). Thus, step by step, was developed an improved model of the dorid evolution (see Fig. 1), which much better explains existence real taxa being simultaneously “typical” phanerobranch by presence of the radula and buccal pump, but can be also no less better described as cryptobranch due to presence of the gill cavity, even reduced.

Thus, the new model of the dorid evolution, which considers properties of the entire ontogenetic cycle (Fig. 1) implies principally different direction of the evolution of the order Doridacea (Martynov, 1994b, 1995; Martynov et al., 2011; Martynov & Schrödl, in press) than that was “reconstructed” by the modern phylogenetic analysis with an invisible help of very old and purely evolutionary morphological concept of the “archaic” phanerobranchs (Minichev, 1969).

According to the new model, in the ancestral ontogenetic cycle of the dorid groups (order Doridacea) has emerged for the first time a key-novelty — mechanism of the transferring of the anus area (i.e. area, there then gills will be formed) from ventral to the dorsal position (see Figs 1, 2). This mechanism implies asymmetrical growth of the right notal posterior lobes and further formation on this base the gill cavity (Martynov et al., 2011). Thus, the dorid as group is clear delineated by otherwise similar to it Notaspidea s.str., by appearing in their ontogenetic cycle the gill cavity and separated rhinophores as key-novelties. This also implies that all modern cryptobranch dorids should have in their ontogenetic cycle the peculiar stage with the posterior notal lobes lead then to the gill cavity formation.

Such prognostic ability is another very important differences of the ontogenetic systematics from the current phylogenetic thinking. Taking into consideration, that about 1.500 species of cryptobranch dorid are currently known, but only 2-3 species have
been studied ontogenetically (e.g. Thompson, 1958; Usuki, 1967; Martynov et al., 2011; this study), with help of such prognostic model we can then infer, that earlier postlarval stages of yet unknown other cryptobranch also should possess such stage with the posterior lobes. A possibility to infer other ontogenetic stages used the known one (first of all, adults) has already been suggested in frames of comparative and evolutionary morphology (see e.g., Remane, 1955), but was not then used as a routine, practical methods. Such possibility to infer for any \textit{yet unknown} ontogenetic stage by already known is very important feature of the ontogenetic systematics, making the systematics itself not only purely descriptive science, as usually considered, but instead, a science of predictions, that then could be tested in different ways (e.g. by study of the ontogeny of further dorid species). Most importantly also, the such possibility to infer unknown stages is greatly contradict to the Hennig fundamental principle considering any organism as a just separate semaphoront.

The new model of the dorid evolution has also several different important implications. First of all, the essential similarity of the ontogenetic pathways in the different cryptobranchs (e.g. so different groups as Chromodorididae and Discodorididae) implies potential possibility for further independent, parallel appearing in non directly related dorid subgroups, of heterochronic regressive variants, from “moderate”, when only gill cavity not develops in adult organisms (i.e. most species of the family Onchidorididae), to “radical”, then clear earlier postlarval features (notal lobes) appeared in the adult stages. Reality of the independent heterochronic shifts underlying by the common ontogenetic cycle in dorids have been already demonstrated both structurally and phylogenetically (Martynov, 2000; Millen & Martynov, 2005; Martynov et al., 2011): corambid group (family Onchidorididae) and the genus \textit{Echinocorambe} (Akiodorididae) have reached externally very similar juvenile-like adult organization, whereas internal features still preserve unique pattern of radula and buccal pumps of onchidoridid and akiodoridid respectively.

Another very important implication of the new ontogenetic model of the dorid evolution is its possibility to find \textit{traces} (i.e. \textit{recapitulations}) of the initial cryptobranch mode of the gill formation in the earlier postlarval stages of planorbranch dorids, which are completely lacking any gill cavity at the adult stages (Martynov et al., 2011).

Finally, the new model greatly contradicts with widely accepted considerations about primary condition of the gill cavity absence in the dorid group Bathyodoridoidea (Minichev, 1969; Wägele, 1989a; Valdés, 2002b). There is no any ontogenetic information on the bathyodorid groups currently.

However, apart form the absence of the gill cavity, bathyodoridids demonstrated number of other reduced features: the notum is completely reduced in the Bathyodoridoidea, but leave a clear border between lateral body wall and dorsal side (see, e.g. Wägele, 1989b). This fact quite clearly points toward considering this feature as a secondary reduced instead of a primary one. Bathyodoridids also are completely devoid of the rhinophoral pockets — a feature that usually points to reduction in other planorbranchs.

Until recently bathyodoridids were considered as having diaulic reproductive system (Odhner, 1934; Minichev, 1969; Wägele, 1989a). It was used for further evidence of clear separation of Bathyodorididae from other dorids, and most likely also as an archaic, basal feature (e.g. Wägele, 1989a; Wägele & Willan, 2000). However, 9 years ago was described \textit{Bathydoris spiralis} Valdés, 2002 (Valdés, 2002b), the first bathyodoridid with a triaulic reproductive system, i.e. as in other dorids. The gill apparatus of \textit{B. spiralis} is very similar to the compact gill corolla of other dorids, and quite different from the “disperse” gill placement of most other species of the genus \textit{Bathydoris}. Two groups have been already recognized within bathyodoridids (Valdés, 2002b). One group of species of the genus \textit{Bathydoris} (including diaulic \textit{Bathydoris clavigera} and triaulic \textit{Bathydoris spiralis}) possesses eyes and a relatively low body, whereas
the majority of other *Bathydoris* species, like *B. abyssorum* Bergh, 1884 and, *B. ingolfiana* Bergh, 1899, do not have eyes and their body became very high, almost sphere-shaped, what is very unusual for dorids. Intriguingly, those species having eyes and low body inhabit relatively shallow depth of 40–500 m, whereas eyeless species with spherical body are known from much deeper environments, up to 4500 m (*Bathydoris abyssorum*).

In absence of an elaborated model of the dorid evolution and underlying by formal approach of phylogenetic systematics, the findings of the unique triaulic *Bathydoris spiralis* with typical for the many dorids circumanal gill corolla, the characters which are clearly connected small group Bathydoridoidea with 2000 other dorid species, did not lead, nevertheless for the consideration of which species as a transitional taxon or “missing link”. Instead main conclusion of the single available phylogenetic analysis of bathydoridid including *B. spiralis* (Valdés, 2002b) became their paraphyly. Shallow-water species turned to be a sister-group for the usual phanerobranch dorids, however these groups share only absence of the gill cavity. I.e. the resulting tree actually has showed the similarity of the bathydoridids and all other dorids, however, implicit model of the ancestral mode of the phanerobranch dorids led to their incorrect interpretation. The results were truly paradoxical and required creation within single genus *Bathydoris*, not only new genera and families, but potentially, even suborders (!), to show the tree pattern in the system of categories (Valdés, 2002b). Nevertheless, some bit of absurdity of such potential decision was clear, and in the cited paper there were not suggested any new even generic names, but the case was discussed and interpreted as failure of the traditional systematics, hardly allowed true, phylogenetic interpretation at the present stage of knowledge (Valdés, 2002b). The final conclusion to consider the genus *Bathydoris* as a paraphyletic complex s.l. not resolved any of the problematic issues and still there no any study attempting to make further solution for this remarkable case.

At the same time, if interpreting historical development of the group Bathydoridoidea according to the new model of the dorid evolution, these apparent paradoxes mostly disappeared. Ancestor of the bathydoridid, should most likely have gill cavity and free notal edge. Increasing degree of adaptations to the more and more deep water conditions led to consequential reductions of the gill cavity, notum, eyes and appearing in the most deep-water species this specific sphere-shaped body (possible a response for the pressure). According to this model, omniphagy of the genus *Bathydoris*, considered as a plesiomorphic character for all dorids (Valdés, 2002b, 2004), is only a very special adaptation of the very restricted in species number *Bathydoris* for the poverty of the food resources in the abyssal environment, when used any available benthic material. Bathydoridids, thus, judged from their many unique characters is a monophyletic group, but incorrect previous model of their evolution led to incorrect conclusion of their paraphyletic status.

Thus, one of the most important implications of both ontogenetic systematics and new model of the dorid evolution, it their prognostic ability, i.e., in the case of dorids, the possibility to predict real existence of several transitional taxa (“missing links”), combining of the presence of the gill cavity (diagnostic feature of Cryptobranchia) with various specific characters of the phanerobranch dorids (lacking any gill cavity by definition). Despite that it will be may be considered as a purely hypothetic field, many facts, instead speak in favour of such approach. One of such most remarkable case, when already constructed model of the dorid evolution has found strong support in new independent finding of *Onchimira cavifera*, having both well-defined full-functional gill cavity and simultaneously very special radular and buccal pump features, allowing unambiguously to place this truly cryptobranch taxon into the phanerobranch family Onchidorididae (see Martynov et al., 2009).
All these facts are of course intriguing but there is no any (at least explicit) prognostic in the modern systematics, both “traditional” or “phylogenetic”, though few exotic attempts to produce a “periodical systems” for taxonomy have been performed in past (e.g. Schimkewitsch, 1906, 1909). Here, therefore, will attempted to challenge this, and gave further evidence for the validity of the ontogenetic systematics by presenting a special application, that is almost completely absent in the modern systematics and phylogenetics: the prognostic table (see Table 1).

<table>
<thead>
<tr>
<th>Gill cavity present</th>
<th>Gill cavity absent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gills present, anus ventral</td>
<td><em>Corambe</em> (Onchidorididae)</td>
</tr>
<tr>
<td>Gills absent, anus dorsal</td>
<td><em>Phyllidia, Phylidiella, Phyllidiopsis</em> etc. (Phyllidiidae)</td>
</tr>
<tr>
<td>Gills absent, anus ventral</td>
<td>Impossible combination?</td>
</tr>
</tbody>
</table>

### Table 1:
Prognostic table for the group Doridacea

**ARE THE TRADITIONAL NUDIBRANCHIA MONOPHYLETIC?**

As defined above, the traditional order Nudibranchia is here considered as two independent groups (orders): Doridacea and Nudibranchia s.str. (equal to the Cladobranchia). What was the reason for that, except for briefly outlined above in the diagnosis and the model transformations? The traditional group Nudibranchia despite of numerous attempts to challenge it (for instance, Marcus & Marcus (1967) used a system of four independent orders
corresponding to the four suborders of Nudibranchia; Minichev & Starobogatov (1979) not used the name Nudibranchia at all), nevertheless recently received status of monophyletic according to a morphological cladistic study (Wägele & Willan, 2000), and still no unambiguous molecular evidences for their paraphyly (see Jörger et al., 2010 vs. Grande et al., 2004).

In the morphological phylogenetic analysis (Wägele & Willan, 2000) indicated only 4 autapomorphies for Nudibranchia: 1. Solid rhinophores; 2. Absence (by loss) of the shell; 3. Longitudinally situated pericardium; 4. Presence of special vacuolated epithelium. However, uniqueness of most of these characters, their importance as the indicators of the monophyletic group may be questioned. First of all the loss of shell is really not possible to discuss as any key-characters since it happened many times independently within various Opisthobranchia. Formation of the solid rhinophores on the base of the enrolled chemosensory organs of the notaspideans is also not unique for the Nudibranchia, and clearly independently has taken place within the group Saccoglossa (e.g., Jensen, 1996) and acochlidians (Schrödl, Neusser, 2010). In a similar way, another listed nudibranch autapomorphy — the longitudinally situated pericardium also independently appeared within Sacoglossa and acochlidians. Finally, the vacuolated epithelium occurrence and functions remains very scarcely studied regarding its phylogenetic importance. Even, based on exclusively structural, systematical approach, traditional Nudibranchia are very heterogeneous. The group of dorids, from one side, and three other traditional suborders of the Nudibranchia (Dendronotacea, Arminacea and Aeolidacea, all three suborders also have been united under the name of Cladobranchia) have so many important differences regarding both external and internal (digestive and reproductive systems) characters, that make unification these groups under one name problematic. Is it however some promising set of structures that may be used for at least potential assessment of the para- or monophyletic status of Nudibranchia?

Interesting material for such analysis available from another external key nudibranchs feature — rhinophores. The small relic group Notaspidea s.str. is well established as ancestral or sister taxon for the Nudibranchia (Thiele, 1931; Tardy, 1970; Martynov, 1999; Wägele & Willan, 2000; Martynov & Schrödl, 2008; present work). Both adult notaspid of the family Pleurobranchidae and earlier postlarval specimens of the order Doridacea (Figs 2; 3 A, B) possess similarly constructed, united together rhinophores, without special pockets, because anterior parts of the notum yet not enclosed it, as in the adult dorids. Thus the anterior edge of the body of adult dorids is always the anterior edge of the notum, whereas the oral veil is reduced and remained under the anterior part of the notum.

In this respect quite remarkable and until recently never considered is the fact of the significant similarity in the general rhinophoral patterns between one of the notaspid family — Pleurobranchaeidae and most of the subgroups of the traditional Nudibranchia, excluding the dorids. If in Doridacea anterior notal edge enclosed the rhinophores and then separate initially common structures of the rhinophores itself and oral veil (Figs 2D; 3C), in one of the notaspid family, Pleurobranchaeidae, oral veil, instead, considerably widened, whereas anterior part of the notum is reduced. As result, rhinophores are considerably shifted laterally, and anterior edge of the oral veil (!) became anterior edge of the body instead of notum as in dorids (Compare Figs 3 A–D and 3 E).

Most remarkably, that several obviously basal in cladistics terms (see e.g. Schrödl et al., 2001), but not related directly nudibranch genera, i.e. Tochuina and Tritonia (both belong to the traditional suborder Dendronotacea), and Heterodoris and Doridoxa (traditional suborder Arminacea) have amazingly similar to the family Pleurobranchaeidae rhinophoral apparatus, including wide oral veil and reduced anterior notal edge (Compare Figs 3 E and 3 F). I.e. in the basal genera of at least two major traditional groups of Nudibranchia — Dendronotacea and Arminacea anterior edge of the
oral veil is anterior edge of the body, exactly as in the family Pleurobranchaeidae (see also Martynov & Schrödl, 2008). The difference between adult morphology of the rhinophoral apparatuses of the notaspidean families Pleurobranchidae and Pleurobranchaeidae (Compare Figs. 3 A and 3 E) has also remarkable correspondence in the ontogeny. In the postlarval specimens of Berthella californica (family Pleurobranchidae) anterior edge of the notum further grows and partially covers rhinophores and oral veil (LaForge & Page, 2007), whereas in postlarval specimens of Pleurobranchaea japonica anterior part of notum reduced, and remained notum fused with the posterior part of the oral veil (Tsubokawa & Okutani, 1991; Gibson, 2003). As already well established (Thompson, 1958; Usuki, 1967; Martynov et al., 2011; present study), earlier postlarval stages of both, cryptobranch and phanerobranch dorids have principally similar to the adult and postlarval notaspid of the family Pleurobranchidae pattern of the united rhinohores not enclosed by the anterior notum (Compare Figs 3 A and 3 B).

On the contrary, postlarval ontogeny of Tritonia hombergi (Nudibranchia: Dendronotacea), rhinophores, compare to the both dorids and notaspids do not demonstrate a stage with united rhinophores at all, but instead, they appeared initially already very separate from each other, at the lateral edges of future oral veil and lateral parts of the notum (Thompson, 1962). Thus, the only principal difference otherwise very similar rhinophoral apparatuses of Pleurobranchaeidae and non-dorid nudibranchs — presence in the latter group of solid rhinophores. However, it is not prevent for further originating of the solid rhinophores on the base of the enrolled as it was definitely took place independently in Sacoglossa. In this respect, the ontogenetic mechanism of the rhinophores development in Tritonia, without stage with the unite rhinophores, may be an important evidence that such pattern is further modification of exactly Pleurobranchaeidae-like notaspids, which have separated rhinophores at adult stage but yet united in the postlarval ontogeny. Rhinophoral development of Tritonia appeared thus as secondary modification of the ontogeny of Pleurobranchaeidae, but in which the stage with united rhinophores was further deleted. If Tritonia is a descendant of the dorid-based ontogenetic cycle, it is more likely that stage with the united rhinophores should be persists in it, which is not the case.

Thus a scenario implies that traditional Nudibranchia is heterogenous group in the terms of traditional systematics and paraphyletic in cladistics’ view (Martynov, 1999) can not be completely excluded. For further proof of above described ontogenetic patterns it is highly necessary modern studies of the postlarval ontogeny of some basal nudibranchs, and also search for additional characters that potentially can share Pleurobranchaeidae and basal Nudibranchia. At least, in non-dorid nudibranchs there is the clear pleurobranchid character — lateral position of anus. Basal nudibranch genera, such Heterodoris and Doridoxa, are without secondary respiratory structures, thus is possible to consider these taxa as modifications of the ancestral ontogenetic cycle of the Pleurobranchaeidae, in which regressive heterochronic event of the true gill reduction took place.

CONCLUDING REMARKS

Under approach of the ontogenetic systematics quite senseless to speak about just “plesiomorphic” or “apomorphic” states (two basic terms of the morphological phylogenetics). Instead much more productively to specify that was common ancestral juvenile condition (i.e. juvenile plesiomorphic state) and that was ancestral adult condition (i.e. adult plesiomorphic state) (see Figs 4, 5). Further heterochronic shifts towards juvenilization of the adult morphology might, for instance, produce similar juvenile adult morphology many times independently in different families, strongly underlined by the common ancestral ontogenetic cycle and it is well supported, e.g., in dorid nudibranchs, by unique morphological markers.
Thus, ontogenetic systematics does not disregard trees as useful representation of the evolutionary process, but instead makes phylogenetic terminology and conclusions much more precise, thus highlights the integrative interactions between the “cycle” and the “tree” (Figs 4, 5).

The “cycle-thinking” implies thus thinking in the term of newly emerged characters and particular functional organizations in any taxa, even currently completely extinct, with recapitulation on limited distance as “reference points” in the evolutionary succession of each preceding and next ontogenetic cycle-taxon. In this respect, the above demonstrated key-novelties have well characterized Notaspidea s.str., Doridacea and Nudibranchia s.str., but failed to found a reasonable ground in the purely phylogenetic conception “Nudipleura”, overwhelmingly merged all these quite well defined separate taxa and obscure potential paraphyletic status of traditional (and still accepted as monophyletic) Nudibranchia s.l.

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