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THE DEVELOPMENTAL ORIGIN OF BIODIVERSITY : THE CASE OF THE BARNACLES (CIRRIPEDES)

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HOX GENES
CRUSTACEA
DEVELOPMENTAL GENES

ABSTRACT. – The systematic classification of Metazoa is largely based on the similarities and differences in their body plans. From a phylogenetic point of view, these similarities are inherited from a common ancestor (homologies). The data accumulated through developmental genetics during the past few decades, makes it now possible to postulate which developmental gene has had a strong influence in a given change in the body plan. Molecular biology techniques presently provide access to the developmental genes of a variety of species, almost at will. It is therefore possible to develop a 'candidate gene' approach to the genetic events that might be correlated with an evolutionary radiation of interest. This approach is here illustrated by our work on Cirripedia (Crustacea). The cirripedes (barnacles) are marine crustaceans that have a fixed or parasitic life. They are all devoid of any abdominal (pleonic) segments, at all stages of their life cycle. We searched for homeotic (*Hox*) genes in cirripedes. These genes are known to determine the identity of the various regions of the body along the anterior posterior axis in a wide variety of animals, ranging from nematodes to mammals. We report here the absence of the *abdominalA* (*abdA*) gene in three species, belonging to each one of the orders composing the Cirripedia subclass. Of the eight homeotic genes known to exist in Arthropods, only *abdA* is lacking. In contrast, *abdA* is present in *Ulophysema oerensundense*, a species presenting an abdomen, and belonging to the Ascothoracica, considered to be the sister-group to Cirripedia. It is therefore tempting to correlate the loss of *abdA* with the lack of abdomen. The 'candidate gene' approach has important implications for our knowledge of phylogeny, and hence for any project involving significant systematic research.

GÈNES HOX
CRUSTACEA
GÈNES DU DÉVELOPPEMENT

RÉSUMÉ. – La phylogénie des Métazoaires est fondée pour une grande part sur les changements de plans d'organisation. Ces plans sont établis au cours du développement des organismes. La génétique du développement nous enseigne quels peuvent être les gènes qui participent de ces changements. Les progrès de la technologie moléculaire nous ouvrent l'accès à ces gènes chez tous les organismes, et pas seulement pour le petit nombre qui constitue l'arsenal classique des généticiens. Les découvertes de ces dix dernières années ont montré que la plupart de ces gènes sont conservés au cours de l'évolution dans l'ensemble du règne animal. De manière plus étonnante, leur fonction est souvent conservée, malgré la diversité des plans d'organisation et des modes de développement. Une approche « par gènes candidats » des changements génétiques associés aux radiations évolutives est donc envisageable. Cette approche est ici illustrée par nos travaux sur les Cirripèdes. Les Cirripèdes sont des Crustacés marins fixés ou parasites, qui présentent la particularité d'être tous privés d'abdomen, quel que soit leur stade de développement. Nous avons recherché les gènes homéotiques (gènes *Hox*), connus pour déterminer l'identité des différentes parties du corps le long de l'axe antéro-postérieur, chez trois espèces de Cirripèdes, appartenant à chacun des ordres de cette sous-classe de Crustacés. Nous avons noté l'absence d'un homologue du gène *abdominalA*, alors que nous avons isolé et identifié des représentants des sept autres sur les huit gènes homéotiques connus chez les Arthropodes. En revanche, nous avons isolé un répertoire complet de huit gènes *Hox* chez *Ulophysema oeresundense*. Cette espèce, pourvue quant à elle d'un abdomen, appartient aux Ascothoraciques, un groupe considéré comme le groupe frère de l'ensemble des Cirripèdes. Il est tentant de penser que la perte

d'*abdominalA* est concomitante de la radiation des Cirripèdes. L'analyse des gènes du développement a des implications fortes pour notre connaissance de l'histoire de l'évolution, sur laquelle est fondée toute classification pertinente des organismes.

The natural system is founded on descent with modification. The characters which naturalists consider as showing true affinity between any two or more species are those which have been inherited from a common parent, and in so far, all true classification is genealogical. Community of descent is the hidden bond which naturalists have been unconsciously seeking, and not some unknown plan of creation

Charles Darwin *The Origin of Species*

THE ORIGIN OF BIODIVERSITY : GENERAL CONSIDERATIONS

According to the current theory of biological evolution, biodiversity stems from the genetic diversity of individuals in populations, caused by mutations, increased by sexuality (recombination) and screened by the processes of selection and random drift, eventually leading to speciation and to evolutionary radiations.

The enormous task of listing the living species is still based on the nomenclature principles defined by Linnaeus. According to Darwin (1859, *Origin of species*, chapter XIII), the meaning of the Linnean classification, called the 'natural system' by that time, is the evolutionary process, based on 'descent with modification'. Classification is therefore no more than a model of the natural history of life. In modern terms, Darwin points out that any biological classification should be phylogenetic.

The classification of metazoans is largely based on the characteristics of their body plan. Animals that share a common body pattern are assumed to derive from a common ancestor. The body plan is established during embryonic and larval development. Hence, in the same chapter, Darwin stressed the importance of developmental characters in the classification of animals.

The advances achieved through developmental genetics during the past fifty years were recently acknowledged by the awarding of the 1995 Nobel Prize of Physiology and Medicine to the *Drosophila* geneticists who initiated this field, Ed Lewis, C. Nusslein-Volhard and E. Wieschaus (see comment in Deutsch *et al.* 1995). Many genes, first discovered as playing a crucial role during the development of *Drosophila*, have been shown to be evolutionarily conserved and seem to play similar functions throughout the animal kingdom. This overall similarity of the genetic tools of development in all metazoans is surprising if one considers the net product of the developmental process: the amazing diversity of animal body plans. Paradoxically, this very similarity provides

an approach to the question of the genetic origin of this diversity directly at the molecular level. Recent progress in molecular technology enable us now to make use of genetic homology to clone and study developmental genes in a wide variety of species, an approach which was until recently feasible in only a handful of model organisms: the fly *Drosophila melanogaster*, the nematode *Caenorhabditis elegans*, the coleopteran *Tribolium castaneum*, the teleost *Danio rerio* and the mouse *Mus musculus*. It now seems conceivable to study specific developmental genes in any species, and thereby address the question as whether or not a change in either the coding sequence or the regulation of a given gene, can be correlated with a change in the body plan. This approach, 'the candidate gene approach' has been illustrated during the past few years in a variety of organisms by several research teams. We wish here to emphasize its value for our understanding of the origin of the biological diversity, by reporting some experimental results recently obtained in our laboratory, on the developmental genetics of barnacles (Cirripedia, Crustacea).

BARNACLES : WONDERFUL AND PECULIAR ANIMALS

Cirripedes, whose common name is 'Barnacles', are very peculiar animals. They were first thought to be Mollusca by Linnaeus, on the basis of their fixed life and protective calcareous shell. At the beginning of the 19th century, Thomson, whilst observing their typical nauplius larvae, recognized them as Crustaceans (see Winsor 1969). Darwin devoted several years to their study, and wrote two important monographs, which are still a reference today (for historical aspects of the study of cirripedes, see Anderson 1994, chap. 1).

Among crustaceans, Cirripedia belong to the Thecostraca. Contrary to their sister-group Ascothoracica, they all have a peculiar body plan: they are devoid of any abdominal (pleonic) segments. This absence of the third tagma is unique in crus-

taceans, at least as a characteristic of a whole subclass. It is therefore tempting to assume that this modification of body plan is directly correlated with the evolutionary events that led to the Cirripedian radiation.

All cirripedes are fixed animals. They comprise three super-orders: the Acrothoracica are modified barnacles that burrow in a mollusc shell, the Rhizocephala are endoparasites living mainly on other crustacean species, the Thoracica fix themselves to a solid support, either directly (Sessilia) or by means of a long stem (Pedonculata). Another quite interesting feature of the body plan concerns Rhizocephala. They share with the other cirripedes their early larval mode of development, passing through nauplius and cyprid stages. These larvae are clearly segmented, like any other *bona fide* crustacean. After the cyprid stage, the animal injects a few cells into its host, either after a metamorphosis that leads to a new larval stage, the kentrogon (kentrogonid Rhizocephala), or directly from the cypris (akentrogonid Rhizocephala) (Glennner and Hoeg 1995, Hoeg 1995). These cells give rise to the adult form of the animal, which is composed of internal roots that penetrate the host, and of an external part, the externa, consisting mainly of the ovaries. The externa is completely asegmented, forming a kind of sack, hence the name of the genus *Sacculina*.

We found the morphology of Barnacles sufficiently attractive to warrant a study of their homeotic (*Hox*) genes.

THE HOMEOTIC GENES

Homeosis is a term coined by the British naturalist William Bateson in 1894, from his observations *in natura* of odd animals: for instance, he found some dipterans in which one antenna, and sometimes both, were transformed into something resembling a leg, even bearing a claw. He wrote: "For the word 'Metamorphosis', I therefore propose to substitute the term 'Homoeosis', which is also more correct; for the essential phenomenon is not that there has merely been a change, but that something has been changed into the likeness of something else". He observed homeotic transformations in quite a variety of living species, crustaceans included. He entitled his book: "Materials for the study of variation, treated with especial regard to discontinuity in the origin of species". The reference to Darwin clearly shows that Bateson himself placed his work within an evolutionary perspective.

Homeosis regained some favor when Ed Lewis started, in the 1940s, to provoke homeotic trans-

formations by mutagenesis and to systematically collect homeotic mutants of *Drosophila melanogaster*. This pioneer work was at the commencement of developmental genetics (see above). In 1978, Lewis wrote an article summarizing several decades of genetic work: he showed that the homeotic genes he studied were grouped along the chromosome in a gene complex, called the Bithorax-Complex (BX-C) after the name of one of the mutants. Each homeotic gene has a specific domain of activity along the anterior to posterior (A-P) axis of the animal: the mutation of a given gene results in homeotic transformations that affect its specific domain only. Lewis drew up the rule of collinearity: the homeotic genes are arranged along the chromosome in the same order as that in which their domains of activity are arranged along the A-P axis of the animal. In addition, in this seminal paper, he hypothesized that the homeotic genes in the complex were the result of a series of gene duplications and proposed that these events might have played an important role in the evolution of insects.

Some years later, the BX-C was cloned, as well as another complex of *Drosophila* homeotic genes, the Antennapedia-Complex (ANT-C) located a little further away on the same chromosome. This led to one of the most important breakthroughs in biology of the last decades: the discovery of the homeobox (McGinnis *et al.* 1984a, b; Scott and Wiener 1984). The homeobox is a motif which bears a strong similarity in one homeotic gene to another. This motif encodes the DNA-binding domain of the protein.

Molecular genetics have also made it possible to describe the patterns of expression of the homeotic genes. Each homeotic gene is specifically expressed in a precise region of the embryo. Their specific domains of activity are derived from their specific expression domains and from the interactions between the homeogenes themselves. The homeotic genes are not involved in the segmentation process *per se*: this is the role of other developmental genes. Their function is rather to specify a precise identity to a precise region of the body along the A-P axis, comprising one or several segments. For example (with simplifications): in *Drosophila melanogaster*, the *Antennapedia* (*Antp*) gene is responsible for the identity of the mid-thoracic region, *Ultrabithorax* (*Ubx*) for the meta-thoracic and first abdominal segments, *abdominalA* (*abdA*) for the fore-abdominal and *AbdominalB* (*AbdB*), for the hind-abdominal regions. Homeotic genes can be regarded as 'master genes' (or 'selector genes') that control, within their specific domain, a specific programme of morphogenesis and differentiation, through the regulation of downstream 'effector genes'.

The homeobox confirmed Lewis' prediction of a common origin of *Drosophila* homeotic genes:

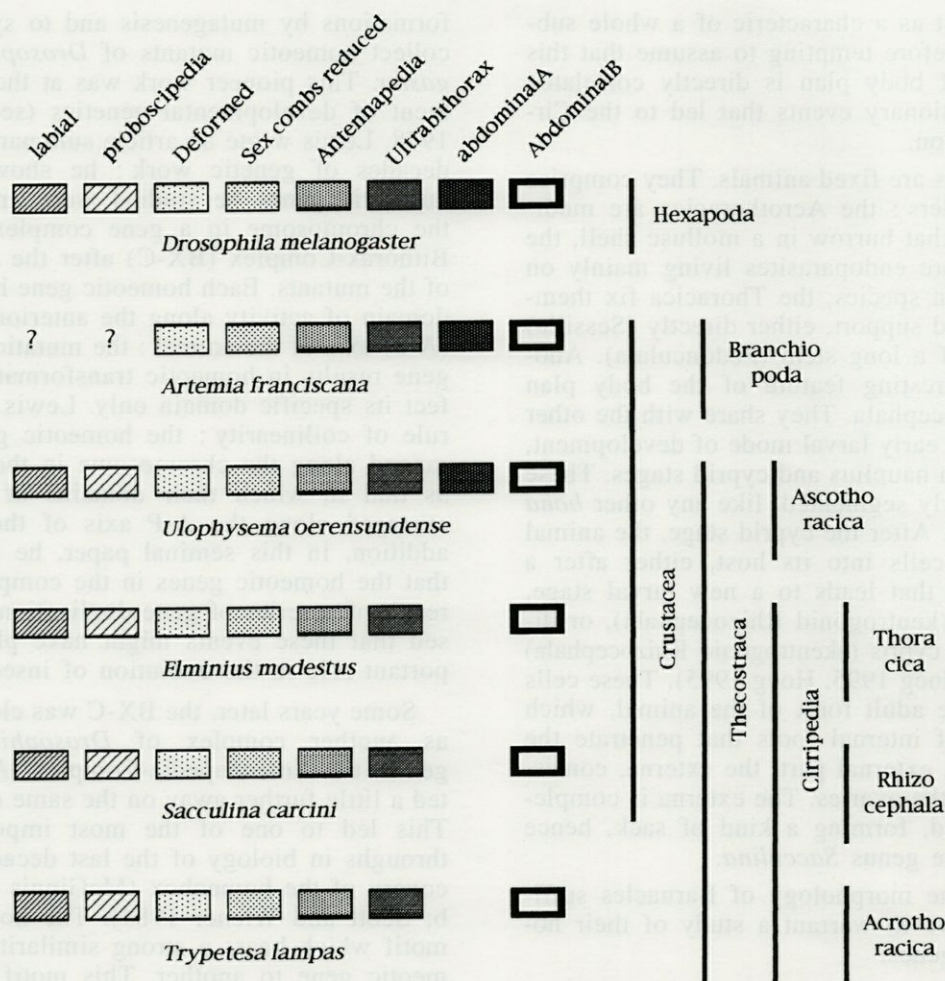


Fig. 1. – Homeotic (*Hox*) genes in arthropods. Eight homeotic (*Hox*) genes are described in *Drosophila melanogaster*. The same complement of *Hox* genes is present in all insect species tested so far. In the branchiopod crustacean *Artemia franciscana*, six *Hox* genes orthologous to the *Drosophila* ones have been described up to now (Averof & Akam 1993, 1995). From three different species of cirripedes, seven genes orthologous to seven out of the eight *Drosophila* genes have been isolated. Hence, it can be inferred that the ancestral crustacean *Hox* gene complex contained the same eight homeotic genes as the insects. We used the same methods, based on PCR amplification and cloning, as used by Averof & Akam (1993) in *Artemia*. In addition i) several sets of primers designed to be specific to particular *Hox* genes were used; ii) in *S. carcini*, PCR screening was performed on both genomic DNA and cDNA derived from all developmental stages, including embryonic, larval and adult stages, and iii) a cDNA library established from *S. carcini* nauplius II larvae was screened, from which several complete cDNAs of *Hox* genes were isolated. An extensive search for *Hox* genes has thus been performed in *S. carcini*, and we are confident that *abdA* is lacking. By the same methods *abdA* was easily retrieved in two other Crustacean species, *Ulophysema oerensundense* (Ascothoracica) and *Carcinus maenas* (Malacostraca) (not shown). The lack of *abdominalA* in cirripedes can thus be interpreted as a loss.

they are paralogous genes, *i. e.* homologous genes issued from duplications of a common ancestral gene. It was also the hook that helped to fish for homologous genes in other species. It revealed the presence of numerous *Hox* genes (for homeotic homeobox-containing genes) in species as diverse as the cephalochordate amphioxus, the amphibian *Xenopus*, chicken, mouse and human, teleost fishes, ascidians, echinoderms, a number of insects, annelids, the chelicerate *Limulus*, pla-

tyhelminths, nematodes, and among diploblastic animals, hydras and corals. This list is growing daily. The presence of *Hox* genes seems to be a characteristic of Eumetazoans. This led J. Slack, P. Holland and C. Graham (1993) to propose the term 'zootype' to qualify a group of genes, comprising the *Hox* genes plus a few others, specific to the animal lineage, and involved in the determination of the animal body plan. In addition, the genomic clustering in complexes of the

Hox genes has been conserved throughout evolution, with a few exceptions. Last but not least, the homeotic function of the *Hox* genes has been demonstrated in all species in which it could be genetically assayed, such as *Drosophila*, *Bombyx* and *Tribolium* among insects, mouse among vertebrates, and the nematode *Caenorhabditis elegans*.

Given the metazoan-wide distribution of the *Hox* genes, and their function in driving the identity of various parts of the body along the A-P axis, we chose them as the first candidates for our developmental genetic approach to the peculiar body of the Cirripedes.

THE HOX GENES OF CIRRIPEDES

Eight homeotic genes have been identified in *Drosophila*, namely, from anterior to posterior: *labial (lab)*, *proboscipedia (pb)*, *Deformed (Dfd)*, *Sex combs reduced (Scr)*, *Antp*, *Ubx*, *abdA* and *AbdB* (Fig. 1). A single *Hox* complex comprising the homologues of these eight genes is probably primitive in insects. Besides our own work on cirripedes, the only crustacean to have been studied up to now in this regard is the branchiopod *Artemia franciscana* (Averof and Akam 1993; Averof and Akam 1995). Six genes, orthologous to six *Drosophila* homeotic genes, are known to be present in *Artemia* (Fig. 1). The more anterior two *Hox* genes (*lab* and *pb*) genes are missing: Averof and Akam did not intend to be comprehensive with their study, so the fact that these two genes have not been found does not mean that they are not present in *Artemia*. We have retrieved both of them from the four cirripede species studied up to now, the acrothoracican *Trypetesa lampas*, the rhizocephalan *Sacculina carcini* and the two sessile thoracicans *Elminius modestus* and *Balanus perforatus* (E. Mouchel-Vielh *et al.* 1997 submitted, and our unpublished work). Hence it is likely that their crustacean ancestor possessed the same complement of eight *Hox* genes as insects. This conclusion is furthermore supported by available data on the chelicerate *Limulus polyphemus* (Cartwright *et al.* 1993), indicating that it might be the same for all arthropods.

In our search for *Hox* genes in *Sacculina carcini*, only seven out of the eight arthropod archetypal homeotic genes were found: *abdA* was missing. Strong experimental arguments support the idea that *abdA* is not present in the *Sacculina* genome. In order to determine whether this loss could be correlated with the parasitic life of Rhizocephalans, and the associated huge modification of their body plan, the same approach was under-

taken in two sessile cirripedes, that retain a segmented body at the adult stage, *Elminius modestus* and *Balanus perforatus*. In each one, *abdA* was also lacking, whereas all the other arthropod homeotic genes were found. The same is true for a species belonging to the third super-order among barnacles, the boring barnacle *Trypetesa lampas*. By contrast, using the same methods, a complete set of eight *Hox* genes, including *abdA*, was evidenced in the genome of *Ulophysema oeresundense*, a crustacean belonging to the Ascothoracica. Ascothoracican larvae clearly develop an abdomen, whereas acrothoracican, thoracican and rhizocephalan ones do not. Hence, it is tempting to correlate the loss of *abdA* during evolution with the absence of any pleonic (abdominal) segment.

We are currently performing a walk on the chromosome of *Sacculina carcini*, in order to support our assumption of a loss of *abdA* and/or rearrangement of the *Hox* complex at the genomic level. In addition, we are currently studying the expression of the *Hox* genes during the larval development of *S. carcini*.

PERSPECTIVES AND IMPLICATIONS FOR THE SYSTEMATICS OF CIRRIPEIDIA

Phylogeny of cirripedes is still a matter of debate: almost all possible nodes have been proposed to account for the radiation of Rhizocephala (see Hoeg 1992), although the most recent cladistic (Jensen *et al.* 1994) and molecular (Spears *et al.* 1994) analyses place the Rhizocephala close to the Thoracica. In addition, it has been proposed (Anderson 1994) that the Cirripede ancestor resembled a pedunculate thoracican, thus raising the question as to whether the Thoracica are monophyletic. Together with Ascothoracica, Cirripedia are thought to belong to a monophyletic Thecostraca class of crustacea. The relationships among this group have to be clarified: in particular, the Ascothoracica, which possess an abdomen, are sometimes classified within the Cirripedia. It is clear that the type of comparative genetic material presented here is decisive in resolving at least some of these phylogenetic problems. From our results on the number of *Hox* genes in the crustacean species studied, their sequences as well as the phylogenetic analysis of the sequences of another family of developmental genes, the *engrailed* family (Gibert *et al.* 1997, and unpublished data), we propose the phylogeny drawn up in fig. 2, which is in agreement with phylogenies based on morphologic criteria proposed by some authors.

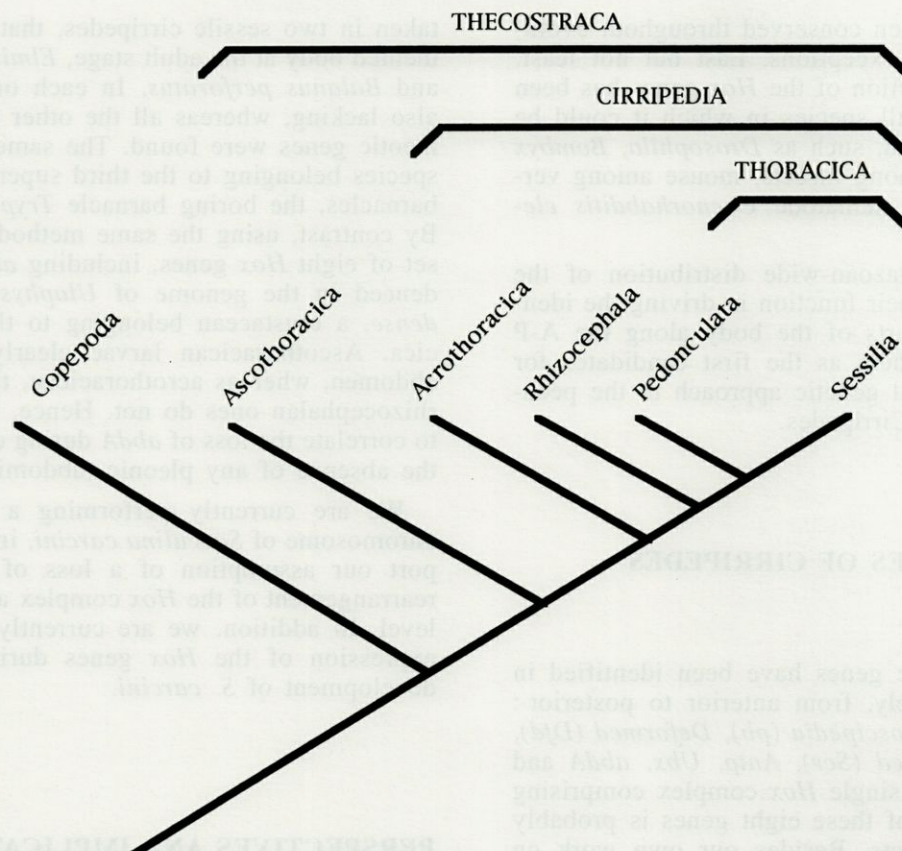


Fig. 2. – Phylogeny of the Cirripedia. The results concerning the complement of *Hox* genes present in each taxon lead us to propose a sub-class Cirripedia *sensu stricto* comprising only the three super-orders Thoracica, Ascothoracica and Rhizocephala. Cirripedia are thought to be a monophyletic group including Rhizocephala and excluding Ascothoracica. The phylogenetic relationships between Cirripedia *sensu stricto* are supported by the analysis of the sequences of the *engrailed* genes (J.-M. Gibert *et al.* 1997, and unpublished data).

As stressed above, any classification has to reflect the phylogeny as much as possible. In other words, systematics is based on the natural history of living beings, evolution. The study of biodiversity, and the necessary construction of comprehensive repertoires of the living species, is dependent on good systematic approach. Systematics is thus a prerequisite of the construction of the biodiversity repertoires. Conversely, the development of species data bases by the biodiversity programmes will help to solve (and sometimes to ask!) many yet unsolved questions on systematics and phylogenetics.

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