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Saltational evolution: hopeful monsters are here to stay

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Abstract Since 150 years it is hypothesized now that evolution always proceeds in a countless number of very small steps (Darwin in On the origin of species by means of natural selection or the preservation of favoured races in the struggle of life, Murray, London, 1859), a view termed "gradualism". Few contemporary biologists will doubt that gradualism reflects the most frequent mode of evolution, but whether it is the only one remains controversial. It has been suggested that in some cases profound ("saltational") changes may have occurred within one or a few generations of organisms. Organisms with a profound mutant phenotype that have the potential to establish a new evolutionary lineage have been termed "hopeful monsters". Recently I have reviewed the concept of hopeful monsters in this journal mainly from a historical perspective, and provided some evidence for their past and present existence. Here I provide a brief update on data and discussions supporting the view that hopeful monsters and saltational evolution are valuable biological concepts. I suggest that far from being mutually exclusive scenarios, both gradual and saltational evolution are required to explain the complexity and diversity of life on earth. In my view, gradual changes represent the usual mode of evolution, but are unlikely to be able to explain all key innovations and changes in body plans. Saltational changes involving hopeful monsters are probably very exceptional events, but since they have the potential to establish profound novelties sometimes facilitating adaptive radiations, they are of quite some importance, even if they would occur in any evolutionary lineage less than once in a million years.

From that point of view saltational changes are not more bizarre scenarios of evolutionary change than whole genome duplications, endosymbiosis or impacts of meteorites. In conclusion I argue that the complete dismissal of saltational evolution is a major historical error of evolutionary biology tracing back to Darwin that needs to be rectified.

Introduction: the limitations of Darwin's gradualism

> "*If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down.*" (Darwin 1859, p. 189)

This year many scientists around the world celebrate the 200th anniversary of the birth of Charles Darwin and the 150th anniversary of the publication of his most influential book "On the origin of species" (Darwin 1859). They do so for good reasons, because Darwin provided biology with the arguably first and so far the only unifying theory. Darwin's probably most important contribution to science is the insight that biological evolution is a two-stage process, in which heritable random variation provides the raw material, while natural selection acts as the (only) directing force that leads to the adaptation of organisms to the environment. Even though one and a half centuries have passed, these insights have largely stood the test of time (not many bold statements from the nineteenth century can reasonably make this claim). This does not mean, however, that Darwin provided us with a comprehensive and

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complete theory of evolution. Given the limited knowledge of his time (especially concerning the mechanisms of heredity), he did not have much to say about the mechanisms that generate diversity in the first place, and whether the heritable random variation he had in mind provides sufficient diversity for natural selection to bring about the complexity and diversity of the living organisms we know. These remain valid questions until today (Kirschner and Gerhart 2005). For example, while we already have a quite good understanding of how organisms adapt to the environment, much less is known about the mechanisms behind the origin of evolutionary novelties, a process that is arguably different from adaptation (Wagner 2000). Despite Darwin's undeniable merits, explaining how the enormous complexity and diversity of living beings on our planet originated remains one of the greatest challenges of biology (Lenski et al. 2003).

Darwin argued that complex and unique structures evolve through "an almost infinite number of generations" subject to natural selection fine-tuning these traits. In time, such gradual changes accumulate and result in large differences unique to higher taxa. This view, that evolution proceeds by very small steps and so creates the unique traits at all levels of biological diversity, is termed "gradualism". It can be seen as a central tenet of Darwin (see quotation above) and mainstream Darwinism (such as the "Synthetic Theory of Evolution", "neoDarwinism" and related concepts). According to this view, the gradual process of evolution by natural selection that operates within populations and species (often termed microevolution) also creates the unique traits recognizable at higher taxonomic levels (often termed macroevolution). One reason for Darwin's belief in the unique importance of gradual changes seems quite trivial. He though that "*if selection consisted merely in separating some very distinct variety, and breeding from it, the principle would be so obvious as hardly to be worth notice; but its importance consists in the great effect produced by the accumulation in one direction, during successive generations, of differences absolutely inappreciable by an uneducated eye*". (Darwin 1859, p. 32). In other words: since there are no obvious "distinct varieties" around, they cannot be of any importance. While Darwin had no problem to imagine that almost invisible changes accumulate to major differences after a long period of time, he could obviously not imagine that distinct varieties are relatively rare at any time, but nevertheless important as the starting point of new organismic lineages. As has been outlined in more detail elsewhere (Theißen 2006) rarity does not necessarily imply unimportance, however. In natural populations successful distinct varieties might be extremely rare but yet of enormous evolutionary importance, especially if they are the starting point of adaptive radiations. For example, if the

arthropod body plan or the origin of the flowering plants involved such distinct varieties, they had an enormous impact on the biodiversity of our planet, even if such "monsters" are only successful once in many million years (Theißen 2006).

Like Darwin, most other evolutionary biologists since then viewed gradualism as a necessary corollary of natural selection. Darwin's contemporary and strong supporter Thomas Henry Huxley, however, already preferred to divide the two issues of natural selection and gradualism to avoid this link, which he considered unnecessary. Huxley warned Darwin that the strict and unwarranted adherence to gradualism might undermine his entire system (Gould 1977a).

And indeed, up to now the empirical basis of strict gradualism is weak at best. For instance, with its abrupt transitions, the fossil record provides little evidence for a gradual evolution of new forms (Gould and Eldredge 1993). Also the branching patterns of higher taxa in both animals and plants as revealed by cladistics and systematics do not support the idea that the major features of body plans and their constituent parts arose in a gradual way (Vergara-Silva 2003). It is not surprising, therefore, that alternatives to Darwin's gradualism have been considered many times during the past one and a half century.

Saltationism and mutationism

Objections against the gradualness of evolution are everything but new. On the contrary, the gradualness of evolutionary changes has been questioned immediately after Darwin's major publication, and ever since (for a review, see Levit et al. 2008). Influential "isms" denying the comprehensive explanatory power of gradual change are known as "saltationism" and "mutationism". Advocates of these views often do not completely deny gradual changes (typically during adaptation or microevolution), but consider them unable to explain the origin of phenotypic novelties, or species and higher order taxa. For the advocates of mutationism and saltationism, sudden and discontinuous changes appear to be required to explain the origin of profound phenotypic novelties or species.

The probably best known mutationist was the Dutch botanist Hugo de Vries (1848–1935), who proposed that Darwin's gradual variations are just non-heritable fluctuations, while new species arise only by means of sudden, non-adaptive, random saltations occurring without transitional forms in "single steps". According to de Vries, all natural selection can do is to eliminate "hopeless mutants" (reviewed by Levit et al. 2008).

Mutationism can be regarded as a special type of saltationism, the general view that profound evolutionary

novelties (such as new "body plans") come into being as a result of sudden, discontinuous changes rather than by a gradual mode. Saltationists included eminent geneticists such as the British scholar William Bateson (1861–1926), the German botanist Carl Correns (1864–1933), and palaeontologists such as Karl Beurlen (1901–1985) and Otto Heinrich Schindewolf (1896–1971). Beurlen, for example, was convinced that palaeontological data unambiguously show saltation (reviewed by Levit et al. 2008).

The scientist currently most well-known for his saltational ideas is Richard Goldschmidt (1878–1958). Goldschmidt (1940) saw true species separated by "bridgeless gaps" that could only be overcome by saltational changes, and not by the slow gradual changes proposed by Darwin and his close followers ("neoDarwinians"). Goldschmidt (1933, 1940) raised no objection to gradual and continuous change within species, but he argued that new species arise abruptly by discontinuous variation, or macromutation (reviewed by Dietrich 2000, 2003; Theißen 2006). Goldschmidt was well aware that the vast majority of macromutations have disastrous effects on the fitness of organisms—these he called "monsters". But Goldschmidt argued that every once in a while a "hopeful monster" is generated which is adapted to a new mode of life. According to Goldschmidt, macroevolution proceeds by the rare success of these hopeful monsters rather than by an accumulation of small changes within populations.

Goldschmidt (1940) presented two mechanisms for how hopeful monsters might originate. In case of one mechanism he rejected the classical gene concept, and developed an alternative model in which systemic rearrangements of chromosomes ("systemic mutations") could produce new developmental systems and potentially new species quickly. According to Dietrich (2003) it was this rejection of the classical gene concept that damaged Goldschmidt's scientific reputation and, to some extent, also the credibility of hopeful monsters. Goldschmidt's views on systemic mutations indeed did not stand the test of time. However, the second mechanism proposed by him is based on "developmental macromutations" in "rate genes" or "controlling genes" that change early development and hence cause large effects in the adult phenotype. These kinds of mutations were based on the classical gene concept, and thus were not met with the same hostility as his views on systemic mutations (Dietrich 2003). Goldschmidt's ideas about developmentally important mutants with large effects sound pretty familiar in the light of current evolutionary developmental biology (Gould 1977b; Haag and True 2001; Theißen et al. 2000, 2002; Arthur 2002; Vergara-Silva 2003). However, for a number of reasons Goldschmidt did not succeed in establishing hopeful monsters as an accepted addition to evolutionary theory (Dietrich 2000, 2003). Until today it is widely believed,

that any mutation of major effect is unlikely to be tolerated by natural selection and thus generates "hopeless monsters" rather than hopeful ones (Akam 1998).

Why are not all of us happy neoDarwinians?

It is probably not by chance that historically, besides palaeontologists, many of the biologists criticizing gradualism have been geneticists (see above). Many of their views, however, did not stand the test of time. For instance, de Vries' assumption that Darwin's gradual variations are just non-heritable fluctuations is incompatible with quantitative trait loci (QTL) analyses. So when the architects of the "Synthetic Theory" (or "Modern Synthesis") of evolutionary biology managed it during the 1930s and 1940s to unite population genetics with the classical observations of systematics, morphology, biogeography and embryology, they took evolutionary biology by storm (Dobzhansky 1937; Mayr 1942; Simpson 1944; Mayr and Provine 1980; Reif et al. 2000; Junker and Hoßfeld 2001; Junker 2004). I am pretty convinced that in contrast to those criticizing evolutionary biology mainly for non-scientific (such as religious) reasons, the vast majority of biologists would have been happy with the Synthetic Theory (including gradualism), if it only were able to fully explain the origin and diversification of life. Unfortunately, the Synthetic Theory and its contemporary derivatives have major shortcomings, for example in explaining evolutionary novelties and constraints, and the evolution of body plans (Riedl 1977; Gilbert et al. 1996; Wagner 2000; Erwin 2000; Haag and True 2001; Wagner and Müller 2002; Wagner and Laubichler 2004), which to me appear to be especially interesting aspects of the evolutionary process. As long as population genetic based evolutionary theories such as the Synthetic Theory cannot fully explain all aspects of evolution, scientists as well as lay people will, for good reasons, keep looking for better explanations.

Via evo-devo to a neoGoldschmidtian synthesis

Given the shortcomings of the Synthetic Theory and all its closely related offspring it should not come as a surprise that several attempts have been made to complement previous mainstream evolutionary biology with innovative concepts. One major approach involves a reintegration of developmental biology into evolutionary biology, giving rise to "evolutionary developmental biology" (or "evo-devo", for short). The evo-devo rationale maintains that novel morphological forms in evolution usually result from changes in developmental control genes. Thus in a typical evo-devo approach the phylogeny of developmental

control genes and their role in the evolution of morphological features are studied (for details of the evo-devo rationale, see for example Gould 1977b; Gilbert et al. 1996; Theißen et al. 2000; Carroll 2001; Arthur 2002).

In recent years evo-devo, hand in hand with QTL analyses, demonstrated that novel morphological forms in evolution can result from changes in just a few genes of large effect (Doebley et al. 1997; Wang et al. 1999, 2005; Gailing and Bachmann 2000; Moritz and Kadereit 2001), rather than many genes of small effect as implicated by gradualistic scenarios. Much progress has also been made in understanding the genetic mechanisms that bring about drastic yet coordinated changes in the adult phenotype by modification of development. Changes in both the timing (heterochrony) and the position (heterotopy) of developmental processes can occur, and quite a number of evolutionary novelties and characteristics of major clades—many of which have been used for decades as taxonomic characters—can be explained as the result of heterotopy or heterochrony (Kellogg 2000). An important subset of heterotopic changes are homeotic transitions (Baum and Donoghue 2002). "Homeosis" describes a type of variation in which "something has been changed into the likeness of something else" (Lewis 1994). Well-known examples are the *Antennapedia* mutant of the fruit fly *Drosophila melanogaster*, which has antennae replaced by leg-like organs, or the floral homeotic mutants of the angiosperms, which develop flowers that have more or less normal floral organs in places where organs of another type are typically found (Lewis 1994; Sattler 1988; Meyerowitz et al. 1989). Mutants in which the number, but not the identity of organs or segments is altered are called "meristic" mutants.

Evo-devo clearly paved the way for a revival of saltational evolution. The first attempt to resurrect hopeful monsters by an early "evo-devonian" (Gould 1977a), however, largely failed (reviewed by Theißen 2006). It is remarkable, therefore, that the next major attempts to bring hopeful monsters back to the stage of evolutionary biology were inspired mainly by paleobotanical evidence. Mosbrugger (1989) discussed hopeful monsters, heterochrony and homeosis, and concluded that real saltational evolution based on small mutations with large morphogenetic effects probably contributed to the origin of new body plans. I am not aware that this article, published in German in a journal typically read by students and school teachers, had a strong impact, but it encouraged at least me to think beyond hard-core neoDarwinism.

Later still, Bateman and DiMichele (1994, 2002), based on their detailed knowledge of fossil seed-ferns and extant orchids, developed their concept of "neoGoldschmidtian saltation" (reviewed by Theißen 2006). The authors defined saltational evolution as a genetic modification that

is expressed as a profound phenotypic change across a single generation and results in a potentially independent lineage that they termed "prospecies" rather than hopeful monster, however. Bateman and DiMichele (1994, 2002) discuss several putative mechanisms of saltational evolution, and how they could bring about speciation and profound phenotypic novelties. Bateman and colleagues hypothesized that vast numbers of hopeful monsters are generated continuously by heterotopy (including homeosis) and heterochrony due to mutations in key developmental genes that control morphogenesis (Bateman and DiMichele 2002; Rudall and Bateman 2002, 2003). Obviously, this is something all current saltationists agree upon.

What is a profound novelty?

The advocates of hopeful monsters all had a special interest in explaining evolutionary novelties, preferably "profound" or "fundamental" ones (Goldschmidt 1940; Gould 1977a; Mosbrugger 1989; Bateman and DiMichele 2002; Theißen 2006). So what is so special about them, what distinguishes "major innovations" and "profound novelties" from mere "modifications" of already existing phenotypic features or simple "adaptations"? There is a long discussion on that subject (see, e.g. Müller and Wagner 1991), but I am not aware that a general consensus has been achieved. In the broad zone of evolutionary changes any simple classification appears difficult and simple definitions suspicious.

The apparent "novelty" of a phenotypic feature, to begin with, often depends on how much we know about a system. Something can appear unprecedented at first glance, while a more detailed analysis may reveal many underlying similarities (or homologies) to ancestral systems (for an instructive example concerning the origin of the flower, see Theißen and Becker 2004). So there is always the hope that detailed analysis of the developmental and genetic basis of a phenotypic feature may in the end make it possible to explain its origin in a gradualistic way. This is unlikely to happen in many cases, however, where a reasonable story of continuous change is simply beyond imagination (for examples and previous discussions, see for example, Gould 1977a; Theißen 2006).

Here I suggest that profound novelties are those that cannot be unambiguously homologized to any precursor structure. This can be because such a precursor does not exist, or conflicts in homology assignments occur. Traditional criteria for recognizing homologous features include structural similarity ("special quality"), position within a comparable set of features, and the existence of transitional forms between presumptive homologous, either in development (ontogeny) or evolution (as revealed by the fossil

record) (Rutishauser and Isler 2001; Theißen 2005; and references therein). Usually, these different criteria lead to congruent homology assignments, but in case of heterotopy or merosity, this is not the case.

Homeosis is a good case in point. As outlined in more detail elsewhere (Theißen 2005), the first whorl organs of tulips and lilies are structurally very similar to the second whorl organs, and are probably specified by the same "organ identity genes" (Kanno et al. 2003), which would be compatible with homology to the petals of eudicots. They are in the position of eudicot sepals rather than petals, however, and transitional forms are not available, and typically do not exist in the case of homeotic transitions. Thus of the three tests for homology of morphological characters (Patterson 1988) homeosis passes only one ("similarity"), but fails two of them ("congruence" and "conjunction"). So either the sepals of eudicots, or the first whorl tepals of petaloid monocots (such as lilies and tulips) are profound novelties in the sense of my definition. It should be said, however, that my definition obviously has the disadvantage that in order to define a critical term, it uses another term (homology) that is also notoriously difficult to define (for a detailed discussion, see Tautz 1998; Theißen 2005). So whether it is of practical value remains to be seen.

In any case it has to be clear that "novelties" are meant here as features of the phenotype. So explanations such as the hint that major morphological changes can be based on minor genetic changes are not considered as valid resurrections of gradualism. Developmental biology has shown that the relationship between genotype and phenotype is very complex, and a single point mutation may indeed have any phenotypic consequences from not recognizable to dramatic (including lethal). Interestingly, almost the same could be said about major genetic changes up to whole genome duplications. What needs to be clarified, however—not least because so many people are interested in it—is whether major morphological changes can really occur in a saltational way, and if so, how, irrespective of their genetic basis. If the saltational origin of, say, a novel organ requires only a minor change in a single developmental control gene, that does not mean that there was no saltation event. It just means that its genetic basis was simple.

On the following I discuss some profound novelties that may have originated by saltational rather than gradual evolution in order to further illustrate what the concept of hopeful monsters actually is about. Endosymbiosis and polyploidy/hybrid speciation are both means to generate hopeful monsters, and their importance for the evolution of plants and animals is obvious, but because other excellent treatments are available (e.g. Martin et al. 2001; Leitch and Leitch 2007; Mallet 2007), they will not be considered here further.

Case examples I: saltational evolution in plants

Examples of saltational evolution in plants have already been discussed in quite some detail (examples are provided by Sattler 1988; Theißen et al. 2000; Ronse de Craene 2003; Theißen 2006). In the following, therefore, I mainly point to some recent publications.

Origin of the angiosperm flower

The origin of the angiosperm flower can be considered to be a "classical" and long-standing problem in evolutionary biology (Crepet 2000; Theißen et al. 2002; Frohlich 2003; Frohlich and Parker 2000; Stuessy 2004; Theißen and Becker 2004). Since there is no fossil record that would support a gradual mode of evolution, it is tempting to assume that saltational events, and hence hopeful monsters, have been involved, even though many attempts have been made to explain the origin of the flower in a gradualistic way (Theißen 2006). Remarkably, all current hypotheses about the origin of the flower that also consider the rapidly growing molecular evidence, postulate critical changes in homeotic genes that brought about heterotopy or homeosis (Theißen et al. 2002; Theißen and Becker 2004; Frohlich and Parker 2000; Frohlich 2003 Albert et al. 2002). An especially detailed and plausible scenario was recently developed by Baum and Hileman (2006), and extended and commented by Theißen and Melzer (2007).

Ancient homeosis in floral diversification

In a nice case study Citerne et al. (2006) identified an apparent reversal in floral symmetry in the legume *Cadia* as a homeotic transformation and "cryptic innovation". Based on his earlier work Ronse de Craene (2007) discussed in detail the origin and evolution of petals in core eudicots, including sudden homeotic changes. Mondragón-Palomino and Theißen (2008, 2009) reported that duplications of class B floral homeotic genes followed by changes in expression pattern, sub- and neo-functionalization may have been crucial for the origin and diversification of the orchid flower. Homeosis is hypothesized as a minor yet important origin of orchid floral diversity.

Catching hopeful monsters: homeosis in the wild

The die-hard gradualists have always tried to reject hopeful monsters with arguments taken from population genetics, seemingly demonstrating how unlikely the establishment of any major mutant in the wild is (for a recent example considering flowering plants, see Crepet and Niklas 2009). Such approaches are often oversimplistic in that they do

not reflect the situation in natural habitats. In reality, we know almost nothing about the performance of "monsters" in natural populations and thus the ultimate difference between hopeful and hopeless. Studying the fitness of candidate hopeful monsters (suitable mutants with a profound phenotype) in natural habitats thus remains a considerable challenge for the future (Bateman and DiMichele 2002; Vergara-Silva 2003; Dietrich 2003). Therefore, we have established a floral homeotic mutant of *Capsella bursa-pastoris* as a model system to study the performance of a hopeful monster in the wild (Nutt et al. 2006; Hintz et al. 2006). The mutant variety is termed *Stamenoid petals* (*Spe*), because it has petals completely replaced by stamens, while all other organs are unchanged. In remarkable contrast to most other floral homeotic mutants known, *Spe* exists in some natural habitats at least for decades, so its fitness must be similar to that of the wild-type. Cloning of the mutated gene is well underway (P. Nutt et al., under review). Moreover, observation of floral visitors and determination of plant fitness in both common garden experiments and in a natural habitat provided us with a surprisingly complex scenario as to how a hopeful monster can establish itself in natural habitats in sympatry with wild-type plants (J. Ziermann et al., under review). So the plausible hypothesis of Bateman and DiMichele (2002) that the establishment of hopeful monsters is most likely under temporary release from selection in environments of low biotic competition for resources will possibly not remain unchallenged.

However, plants with homeotic transitions can not only coexist with wild-type plants. As can be learned from a recent study (Barabé et al. 2008) homeotic transitions can even occur regularly within one and the same inflorescence. An intriguing example is *Philodendron*, where different types of flowers with homeotic transitions involving carpels and stamens are placed along a cylinder. Thus this plant provides another example for the view that homeotic terata do not necessarily equal hopeless monsters.

Case examples II: saltational evolution in animals

Recently I argued that hopeful monsters might be more relevant for plant than for animal evolution (Theißen 2006). One major reason given was that animals have highly conserved body plans fully outlined during embryogenesis, while plants have open, additive growth that can be more dramatically changed without serious reduction in fitness. While generally still valid, my arguments may have underestimated how radically also animal body plans can change during a very short period of time.

Cirripedes as the descendants of hopeful monsters

Cirripedes (Cirripedia, barnacles) are peculiar crustaceans with a calcareous shell. Arguably the most remarkable feature of these animals is that, as adults, they have no abdomen. However, a vestigial abdomen can be detected in cirripede larvae, which disappears during the metamorphosis to the last larval stage (Géant et al. 2006; and references cited therein). More than a thousand species of cirripedes have been described, belonging to three orders that differ in morphology and life cycle. Cirripedes were already well-known to Darwin, who studied their morphology and systematics for several years.

Recently, Géant et al. (2006) have shown that the Hox gene *abdominal-A* (*abdA*) is apparently absent in several species belonging to the three orders of Cirripedes, while it is still present in the sister group of the Cirripedes, termed Ascothoracida (Géant et al. 2006). It thus appears likely that the deletion (or substitution) of a homeotic gene resulted in the saltational origin of an organism without an abdomen that established a new evolutionary lineage. Based on their data the authors raise the question as to whether Cirripedes are hopeful monsters (Géant et al. 2006). However, since Cirripedes represent an old, widely distributed and quite species rich group of animals, they are in my view neither monsters nor just hopeful, but well adapted and successful extant organisms. Therefore, it would be more appropriate to consider Cirripedes as putative descendants of hopeful monsters rather than hopeful monsters themselves.

Is not it ironic that the favourite animals of the hard-core gradualist Darwin may represent an excellent example for non-gradualistic (saltational) evolution?

Putative saltational origin of a sessile, stalkless Crinoid

The cyrtocrinids (Cyrtocrinida) are an enigmatic order of crinoid echinoderms with only three known species, including *Holopus rangii* of the Caribbean. By detailed morphological investigation, Grimmer and Holland (1990) revealed that the chambered organ and glandular axial organ unique to crinoids among echinoderms is absent in *Holopus*. The authors hypothesized that "*Holopus* could well have evolved from stalked cyrtocrinid ancestors by a saltatory loss of major body parts. Conceivably such a loss could even have taken place between one generation of crinoids and the next" (Grimmer and Holland 1990). In other words: *Holopus* possibly originated from a hopeful monster. Like in the case of *Cirripedes*, it would be interesting to apply evo-devo methodology to the system in order to determine the genetic basis of the morphological change.

Duplication of segments in a centipede

Centipedes of the order Scolopendromorpha exhibit minor interspecific variability in segment numbers; until recently all known species had either 21 or 23 leg-bearing trunk segments (Chagas-Junior et al. 2008). Segment number appeared to be very conserved and was given considerable taxonomic weight, until investigations on the Brazilian *Scolopendropsis bahiensis* revealed that is has either 21 or 23 segments in different parts of its geographic range. This surprising finding was even much topped by the identification of a new species, *Scolopendropsis duplicata*, which is closely related to *S. bahiensis*, but differs from its putative sister species in that it has either 39 or 43 rather than 21 or 23 segments (Chagas-Junior et al. 2008). The authors do not speculate on the developmental genetic basis of their remarkable finding, but a gain-of-function mutation in something resembling the pair-rule genes involved in the embryogenesis of the fruit fly *D. melanogaster* comes to mind. The authors also do not discuss the evolutionary implications of their findings. However, since centipedes of the order Scolopendromorpha complete segmentation during embryogenesis, a saltational duplication of segments appears the most plausible scenario to me.

Origin of the vertebrate jaw

In a lucid review Kuratani (2005) pulled together evidence that the vertebrate jaw has arisen as an evolutionary novelty by overriding ancestral constraints, a process that led to the partial loss of morphological homologies. This change involved the heterotopic shift of tissue interactions, and changes in the expression domains of growth-factor-encoding genes during evolution. If these changes occurred in a saltational way, the affected organism would certainly have qualified as a hopeful monster, but the author is not explicit on that.

Origin of the turtle body plan

Turtles (Testudines) have the most unusual body plan of the amniotes. Their dorsal shell consists of modified ribs. Ventral ribs are not formed, instead the dermal plastron covers the ventral body. Furthermore, in contrast to the situation in other vertebrate species in which the scapula develops outside the rib cage, the shoulder girdle is found inside the rib cage in turtles (Rieppel 2001). For such a situation a plausible scenario of continuous change from any kind of possible ancestor is almost impossible to construct (Rieppel 2001). In line with this, turtles appear abruptly in the fossil record, and until recently, the oldest known turtle from the Late Triassic period had a fully formed shell that provided no clue as to its origin.

Recently, Li et al. (2008) described a 220-million-year-old turtle from China, *Odontochelys*, that is suggested to document an intermediate step in the evolution of the shell and associated structures. While its ventral plastron is fully developed, the dorsal carapace consists of neural plates only. According to the authors, the new species shows that the plastron evolved before the carapace (Li et al. 2008). This view has been challenged by Reisz and Head (2008) who argued that the absence of most of the carapace in *Odontochelys* is a secondary loss (possibly by paedomorphosis) associated with aquatic habits rather than a primitive condition. If so, we still do not have a fossil link between fully evolved turtles and other vertebrates. So from the palaeontological point of view, turtle origin remains enigmatic, despite this exciting new fossil.

Recently, also some progress in the understanding of the developmental genetic mechanisms underlying the turtle body plan was reported, but the most essential factors are still unknown (Ohya et al. 2005; Nagashima et al. 2007).

Despite all these news, the origin of the turtle body plan remains one of the greatest mysteries of vertebrate evolution, and a prime candidate for saltational changes via hopeful monsters (Rieppel 2001).

Concluding remarks: the gradual acceptance of saltational evolution

I was surprised to see that historians have classified saltationism as an "anti-Darwinian theory" (Levit et al. 2008). I am afraid that this term could be misleading, because saltationists, like Darwin and the advocates of the Synthetic Theory, want to understand the mechanisms of evolution using scientific methods. So "anti-Darwinians" should not be confused with people, such as creationists, that see Darwin as their opponent ("contra-Darwinians" sensu Levit et al. 2008).

Getting back to Darwin's quotation from the beginning (see above) it has indeed not been demonstrated rigorously for any complex organ so far that it could not possibly have been formed in a gradualistic way. Not only for this reason, Darwin's theory is still very much alive. From an epistemological point of view, however, such a "negative" demonstration would be extremely difficult, if not impossible. It would certainly be more satisfying, and more convincing for lay people who are currently challenged by non-scientific ("contra-Darwinian") hypotheses on the origin of living beings on earth (Theißen 2006; Levit et al. 2008) if, for any complex organ or body plan, evolutionary biology could demonstrate exactly how such structures can originate (i.e. to develop "positive" scenarios). Since in many cases gradualistic scenarios appear extremely implausible (see above, and Gould 1977a; Theißen 2006),

saltational alternatives should be considered and rigorously tested.

Gould (1977a) predicted that Goldschmidt's ideas about evolution will be largely vindicated in the world of evolutionary biology during the 1980s. Obviously, he was wrong—it seems that the acceptance of saltational evolution is a rather gradual process.

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