

Homology and homoplasy: the retention of genetic programmes

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Abstract. Homology describes the inevitable evolutionary phenomenon that the similarity of structures among different organisms is due to the commonality of their descent. This continuity of information is maintained in evolutionary lineages in terms of genes and developmental mechanisms and will retain 'sameness' and retard, funnel and direct evolutionary diversification. Analogous 'sameness' is said to be due to independent, convergent evolution, and also involves similarity of function; the latter is not a necessary condition for structures to be identified as homologous. Here, I suggest that the biological basis for these seemingly disparate kinds of 'sameness' in evolution may in some, or even most, instances not be all that different and may be based on the same principle—the long evolutionary retention of genes, gene interactions and developmental mechanisms. Evolution might recycle and re-recruit similar mechanisms repeatedly during its course, and it often makes do with what is already available to it rather than to newly evolve or reinvent many gene interactions and developmental mechanisms repeatedly. Apparently there is no, or only a negligible, 'genomic cost' or even a selective advantage to maintaining genes and developmental mechanisms for long evolutionary periods of time, even if they are not continuously used in all members along an evolutionary line. Therefore, the biological basis of both homologous traits (those that are evolutionarily always expressed) and homoplasious traits (those that are not always 'on', but are 're-awakened' during evolution) might not be so different, and the distinction between homology and some forms of homoplasy may be somewhat artificial.

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How different are homology and homoplasy?

Why should one be interested in homology? Because it is one principle, maybe *the* unifying principle, of evolution. By understanding homology, it might be presumed, we will better understand some of the rules by which evolution proceeds, about regularity of processes in evolution, about understanding patterns and trends in evolution and, concomitantly, about diversification of form. The fact that homologous structures exist provides one of the strongest lines of evidence for evolution, but so does convergent evolution in the form of analogy, parallel evolution, reversals and atavisms (reviewed in Futuyma 1998).

Homoplasious phenotypes also attest to the strength of selection, or alternatively internal constraints, to sculpt similar phenotypes in response to similar selection pressures and to re-express ancient, retained, developmental programmes. Therefore, to improve our understanding of the predominant mechanisms by which evolution proceeds, and how biological diversity is achieved and maintained, we need to investigate the biological basis of both homology, and the various forms of homoplasy, such as convergent evolution (analogy), parallel evolution, reversals and atavisms.

Homology, as is well known, is a pre-Darwinian and pre-phylogenetic concept that is already more than 150 years old (Owen 1848, reviewed in Panchen 1994). The theory of homology continues to be debated and the concept itself has evolved over time. Today, it usually implicitly or explicitly involves the recognition of similarity of structure in organisms due to shared recent common ancestry. The recognition and definition of homology are clearly dependent on phylogenetic knowledge. But phylogenetic continuity is only a necessary, but not sufficient, criterion of homology. None the less, sometimes homology is even narrowly defined in a cladistic sense as synapomorphy — as the persistence of traits in their various transformed states (Nelson 1994). However, this is clearly an overly restrictive and somewhat circular definition because the status of a character state as synapomorphy (i.e. homology) or symplesiomorphy will depend on the set of taxa included in a phylogenetic analysis (Wake 1999, this volume).

Typically, there are four criteria by which one can recognize homology: (1) similarity of structure; (2) position (anatomical relationship); (3) phylogenetic continuity; and sometimes a fourth criterion is invoked — sameness of the underlying developmental basis of two similar structures. Note that function is not, and never has been, a defining characteristic of homology. All of these criteria have to be met, if a single one is not, the structures should not be considered homologous. Homology remains a contentious and difficult concept (Hall 1994, Wake 1994), and one might argue that it is not useful to continue to argue only about definitions, but that the underlying basis of 'sameness' in nature is what should be studied (Wake 1999, this volume).

If similar structures are not considered homologous then they are often considered to be one of several forms of homoplasy (convergence, parallelism or reversal). Lankaster (1870) coined the term 'homoplasy' as the appearance of sameness resulting from independent evolution, defined as derived similarity that is not synapomorphic. Homoplasy is usually divided into three more or less arbitrary classes.

- (1) Convergent evolution (or analogy): recognized through superficially similar features that evolved independently and arose ontogenetically by different pathways.

- (2) Parallel evolution: similar developmental modifications that reappeared independently, but were not present continuously in all members of an evolutionary lineage. Parallel evolution occurs among closely related organisms, due to parallel evolution in structures likely to be formed by identical or similar developmental mechanisms.
- (3) Reversals, atavisms and rudiments: a 'return' from an advanced character state to a more 'primitive' or ancestral state. It is not clear whether atavistic structures are formed by the same or similar developmental mechanisms as the original structures were that they resemble.

Homoplasy, it might be contended, is even more common in evolution than homology. One piece of evidence in favour of this tenet is that 'phylogenetic noise' is typically more prevalent than phylogenetic information in taxonomic data sets. If homoplasy is extremely common and convergence is common, then one might suggest that some of this commonality should be able to teach us something about regularity, rules and possibly processes by which these patterns of homoplasy are brought about in evolution (Sanderson & Hufford 1996). Similarly, if one sees convergence as the flipside of homology, then, almost as a by-product, one is also going to learn about homology by studying convergence and parallelism.

Therefore, it might be as important to understand non-homology as homology. Both might reveal which kinds of internal and external forces constraint shape and possibly even direct the diversity or commonality ('sameness') of shapes in evolution.

'Functional' and 'partial' homology

The debate about homology resurfaced anew since the recent publication of comparative developmental data about the expression patterns of apparently homologous genes in seemingly non-homologous structures. *Pax-6* expression in precursor cells of various kinds of light receptors in different phyla is one of the most striking examples of these kinds of results (e.g. Halder et al 1995). This gene is switched on in many light-detecting morphological structures that, based on evolutionary, structural and developmental criteria would by most biologists clearly not be considered to be homologous. These data document a surprising degree of conservation in evolution and might even necessitate a re-evaluation of the concept of homology (Abouheif et al 1997).

The compound eyes of insects and the camera eyes of vertebrates surely are not homologous structures based on the criterion of evolutionary continuity since eyes such as these evolved independently many times over in the history of animals. None the less, these eyes were categorized by some as homologues on the basis of

Pax-6 expression data. The findings show that apparently homologous genes can be expressed, possibly even in homologous networks of genes (Abouheif 1999, this volume), in phenotypically seemingly non-homologous structures. The recognition of genes as homologous requires knowledge of the phylogenetic relationships of all members of a gene family (e.g. Zardoya et al 1996). The expression of *Pax* genes in phenotypically differing kinds of light receptors raised the issues of 'levels of homology', 'partial homology' and 'functional homology' (Abouheif et al 1997).

As mentioned before, similarity of function has never been part of the definition or one of the criteria of homology, but in the developmental literature similarity of function is often erroneously used to falsely identify genes and structures as 'homologous' based solely on their similarity of expression pattern. This similarity is interpreted to imply that the structures in which these 'functionally homologous' genes are expressed are also always evolutionarily homologues. They may or may not be homologous, but expression patterns alone are insufficient evidence for homology of structures.

'Partial homology' describes a situation where genes are homologous, but the structures in which they are expressed are not. A probable example of this phenomenon is the expression of *Pax* genes and different light receptors in diverse animal phyla. It should be clear from the *Pax-6* example that homologous genes can 'make' non-homologous structures. Once a contentious concept, partial homology did, as a result of these kinds of new comparative developmental data, become relatively widely accepted (Wake 1999, this volume).

These new findings from evolutionary developmental biology raise the converse question: can partial homology exist where the structures are homologous, but the genes that are expressed in their precursors are not? The answer is probably yes; non-homologous genes, gene networks and developmental mechanisms can make structures that are typically considered to be homologues. If homology of genes were a necessary criterion of homology (the fourth criterion, see above) then all homologous structures made by non-homologous genes could not be considered to be homologues. This is clearly not the case in the opinion of many researchers.

The biological basis of 'sameness'

Biological explanations must be sought for phenomena such as stasis, modularity, preservation of design, latent homology and directionality of evolution (Wake 1999, this volume). The exciting new data from comparative developmental biology document an unexpected degree of conservation of genes and genetic programmes. Homologous genes are retained for extensively long evolutionary time spans, and they can be expressed during the development of structures that, based on phenotypic criteria, would not be considered to be homologous but

analogous. These kinds of data might shed light on the underlying basis of biological 'sameness', both in the form of homology or various forms of non-homology. If both homology and homoplasy result in 'sameness' (Wake 1999, this volume) between organisms, maybe the biological bases of both kinds of sameness might not be so different after all? One might ask, what are the biological bases for similarity of features whether they evolve independently or not? The ubiquity of homoplasy in the form of parallel and convergent evolution in nature poses the question of what can be learned from knowledge of the developmental systems about patterns in evolution and about the origin of novel features.

In this context it should be remembered that all species are mixtures (mosaics) of ancestral and derived states of characters. Mosaic evolution refers to the fact that evolution proceeds at different rates for different characters within one organisms and in evolutionary lineages. Species do not evolve as a whole but by piecemeal: many of their features evolve quasi-independently. Incidentally, this implies that because of mosaic evolution we cannot call species primitive or advanced and only particular characters are basal or derived. The fact that evolution proceeds this way can best be seen among closely related species that only differ in some but not all traits.

The retention and 're-awakening' of developmental mechanisms in convergent evolution

With more than 2000 species, fish in the cichlid family are one of the most successful groups of vertebrates. Cichlids were recently recognized to be a major example of extensive and repeated parallel evolution. In East Africa, the centre of their distribution, they form adaptive radiations with several hundred endemic species in each of the three East African great lakes: Lakes Tanganyika, Malawi and Victoria. Conspicuous parallels are found in terms of various phenotypic traits such as morphology, striking ecological specialization, colour patterns and behaviour in these three major species flocks. From molecular phylogenetic work it is now known that the relatively young and genetically rather homogeneous Lake Malawi and Lake Victoria cichlid flocks are monophyletic (or oligophyletic in the case of Lake Malawi, Meyer et al 1990). Their single ancestral lines are derived from one of the 11 lineages of cichlids that form the much older and genetically more diverse species flock from Lake Tanganyika (reviewed in Meyer 1993; Fig. 1).

Before the advent of molecular phylogenetic data, a different phylogeny of cichlids from these three lakes had been proposed that was based on phenotypic traits, namely that the often astonishing similarity of morphologies between cichlid species occurring in each of the three lakes (Fig. 2) are indicative of close evolutionary relationships. Hence, it was assumed that each of the three radiations of cichlids from East Africa had multiple ancestors that lived in the other lakes.

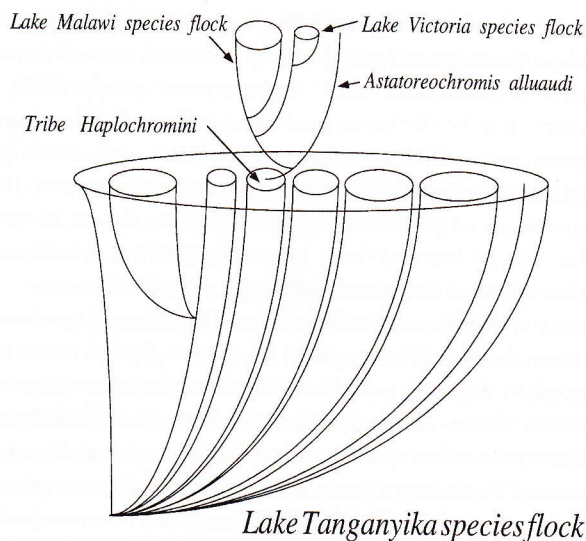


FIG. 1. Cartoon of the phylogenetic relationships of cichlid fish among the species flocks of the three great East African lakes. The species flock in Lake Tanganyika is composed of several, mostly endemic, major lineages, one of which is the tribe Haplochromini. The ancestors of the Lake Malawi and Lake Victoria adaptive radiations are derived from this lineage. The degree of genetic diversity (horizontal axis) and age (vertical axis) of the three species flocks differ significantly, indicated by the differences in the size of the vesicles that symbolize the three species flocks.

Similar morphologies and lifestyles such as mollusc crushing or algae scraping — e.g. from species such as *Tropheus* from Lake Tanganyika and *Pseudotropheus* from Lake Malawi (Fig. 2) — were seen as indications of close evolutionary relationships. The molecular phylogenetic data show that this is not the case, but rather that generalized ancestral species for each of the flocks (with the possible exception of the Lake Tanganyika radiation, which was founded by several ancestral lineages) gave rise repeatedly and independently to similar phenotypes in parallel in the three lakes either in response to similar selection pressures and/or due to retained ancestral developmental constraints or the inherit increased 'evolvability' (Kirschner & Gerhart 1998) of cichlids. Likewise, the morphologically highly specialized species from each of the younger flocks are more closely related to each other than to often phenotypically similar species in the other lakes.

The oldest of the East African cichlid lineages are probably not more than 10 million years old, yet they have attained a marvellous diversity of shapes, sizes and colours. Even more impressive is the fact that the Lake Victoria species flock of cichlids, with about 500 endemic species, might be as young as 14 000 years, yet it has the same array of ecological and behavioural diversity as the much older Lake

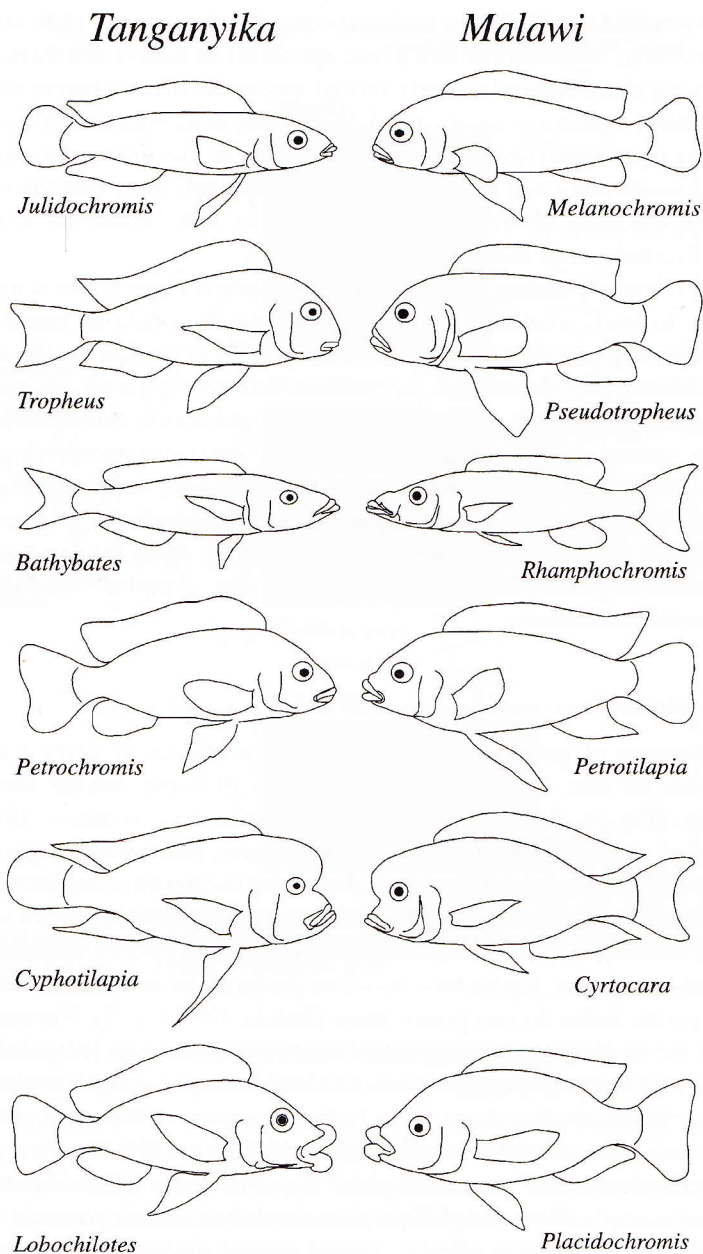


FIG. 2. Juxtaposition of endemic Lake Tanganyika and Lake Malawi cichlids to show the phenotypic similarity of the species that also perform ecologically equivalent roles in their respective species flocks.

Tanganyika cichlid flock. There are algae-scraping, fish-eating, scale-scraping, mollusc-crushing, zooplankton-eating, etc. specialists in each of the three species flocks. Among these relatively closely related species we hence observe ultra-fast speciation rates, with concomitant rapid phenotypic diversification. Yet, despite the fact that rapid speciation in cichlids appears to be the norm, the molecular data also demonstrate cases in some lineages of relatively long periods of stasis where morphological diversification appeared to have come to a relative standstill (Sturmbauer & Meyer 1992).

In terms of understanding how patterns in evolution came about it might be informative to study whether the developmental mechanisms that create almost identical phenotypes in this prominent case of parallel evolution are the same or whether different developmental mechanisms led convergently to the same morphological end in each of the three adaptive radiations. Such comparative approaches among closely related species with divergent morphologies, or among distantly related species with parallel morphologies, require phylogenetic knowledge. It might be surmised that this astonishing similarity of phenotypic traits in cichlids (Fig. 2) evolved in parallel possibly by using the same, retained developmental mechanisms, rather than by the repeated invention of developmental mechanisms.

Parallel evolution and the retention of genes in the context of sexual selection

Another example of gene retention and parallel evolution involves a sexually selected trait in fish, i.e. the 'sword' of males in some fish in the genus *Xiphophorus* (Fig. 3). Sexual selection favours coloured, ventrally elongated caudal fins, or swords in males of the fish in this genus. Males with longer swords are preferred by females over males of equal size with shorter swords (Basolo 1990). Even females of some species in which the males do not have swords seem to prefer males with artificial swords and heterospecific males with swords. Females of the basal sword-less species *Xiphophorus maculatus* prefer males with swords although their conspecific males do not possess them (Basolo 1990; Fig. 3). Viewed in the context of the traditional phenotypically based phylogeny (Fig. 3) this led to the suggestion that the evolution of swords evolved in response to an evolutionary earlier bias in females to mate with males that possess this trait, since the preference in females existed before the trait itself (Basolo 1990; Fig. 3).

For several reasons this 'pre-existing bias' hypothesis may not hold completely because, for example, the males of *Xiphophorus xiphidium* already possess a ventral, albeit colourless, extension of the ventral caudal fin rays. Moreover, the reconstruction of the evolution of the sword within the genus based on a molecular phylogeny of fish of this genus (Meyer et al 1994; Fig. 4) suggests that the sword evolved early in the evolution of the genus (black bar at the base of the

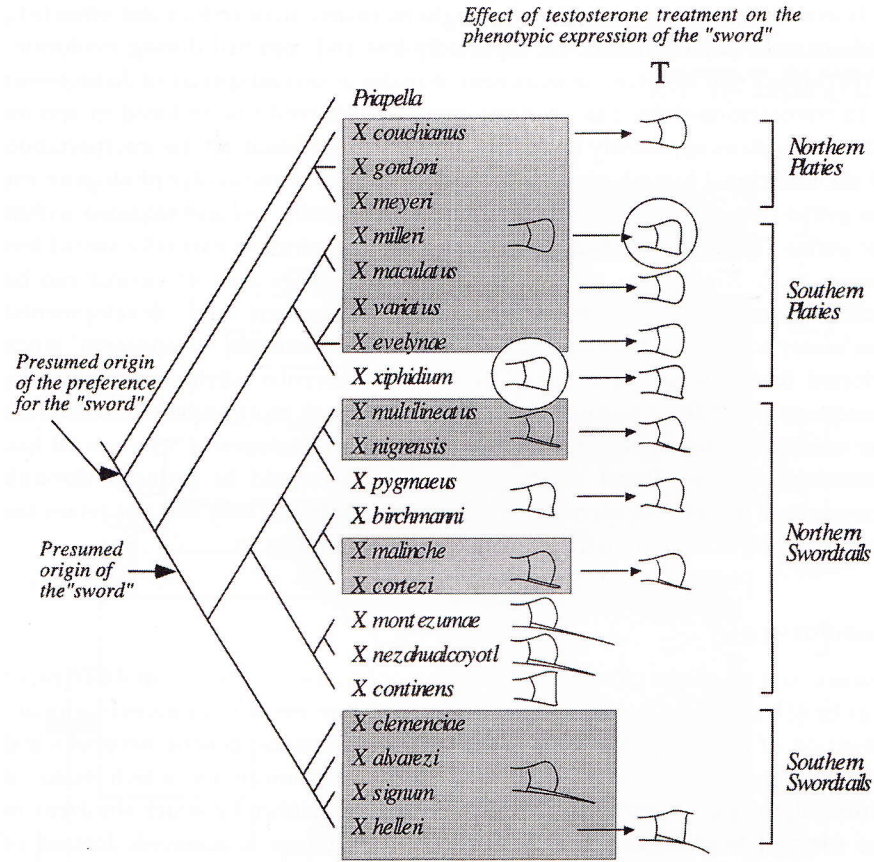


FIG. 3. Traditional (based on phenotypic traits) phylogeny of fish of the genus *Xiphophorus*. The typical size of the ventral caudal fin extension in males of each species is indicated in natural populations and after treatment with testosterone.

genus in Fig. 4), was then lost at least once (open bar in Fig. 4) and re-evolved at least twice in *Xiphophorus clemenciae* and *X. xiphidium* (Fig. 4). Furthermore, it is important to note that there are several other species of poeciliid fishes (e.g. in *Poecilia petenensis* and *Poecilia reticulata*) and many other families of fish where males have notable elongations of the most ventral rays of their caudal fins. Often, these ventral elongations can, through artificial selection, lead to extremely pronounced swords in some, naturally typically sword-less, species (e.g. *P. reticulata*). It should also be mentioned that in several species of *Xiphophorus* there is, sometimes extensive, variation in natural populations in terms of the phenotypic expression of swords (Meyer 1997).

It would appear that 'sword' genes might be ancient in poeciliids and other fish, and are variously expressed, i.e. repeatedly lost and regained during evolution. Experiments that involve the treatment of males in several species of *Xiphophorus* with testosterone show that in some cases swords could be induced in species whose ancestors apparently never had them (Fig. 3), based on the interpretation of the traditional hypothesis (Basolo 1990, 1991). The molecular phylogeny for the genus (Fig. 4) suggests that swords were repeatedly lost and regained within the genus. These observations might suggest that, since in naturally sword-less species (e.g. *Xiphophorus milleri* and *X. maculatus*, Figs 3 & 4) swords can be induced through testosterone treatment, the genetic and developmental machinery to produce swords might have been retained and 're-appeared' when selected for by sexual selection (Fig. 4). The molecular phylogeny makes the interpretation of these testosterone experiments much more consistent. Based on the traditional phylogeny it would be difficult to understand why sword-like extensions of the ventral rays in the caudal fin could be induced through testosterone if ancestral species did not have swords and they did not retain the 'sword gene', as is suggested by the molecular phylogeny.

Conclusions

'Sameness' in the form of homology and homoplasy may not be all that different, or may be at least partly caused by the same mechanism: the ubiquitous evolutionary retention of genetic potentiality. The retention of genes, genetic networks and embryological pathways may be a prevalent mechanism by which stasis in morphology is attained, and it may also be one mechanism by which similarity in the form of homologous and homoplasious structures is achieved. Instead of inventing similar structures entirely anew from the genes upwards through transcription regulation, gene networks and morphogenetic mechanisms, evolution often appears to draw on 'old' genes and mechanisms that are 'recycled' and re-used for different purposes throughout evolution (Gerhart & Kirschner 1997). The idea that evolution may be haphazard and often makes do with what it has at its disposal is essentially a Jacobian idea (Jacob 1977). Evolution is a tinkerer and it will work with what it has at its disposal — it might recycle 'old' genes and genetic and embryological pathways when they are required in the same ontogenetic or ecological context to solve an ecological problem.

If developmental mechanisms (brought about by conserved developmental genes and their interactions) are retained for long evolutionary times spans (on the scale of the age of phyla in the case of *Pax-6* genes) it may be at a low or no 'genomic cost'. The evolutionary forces that maintain genes and genetic interactions will presumably have to outweigh those mechanisms (such as mutation, selection, etc.) that will lead to the deterioration of genes once they are

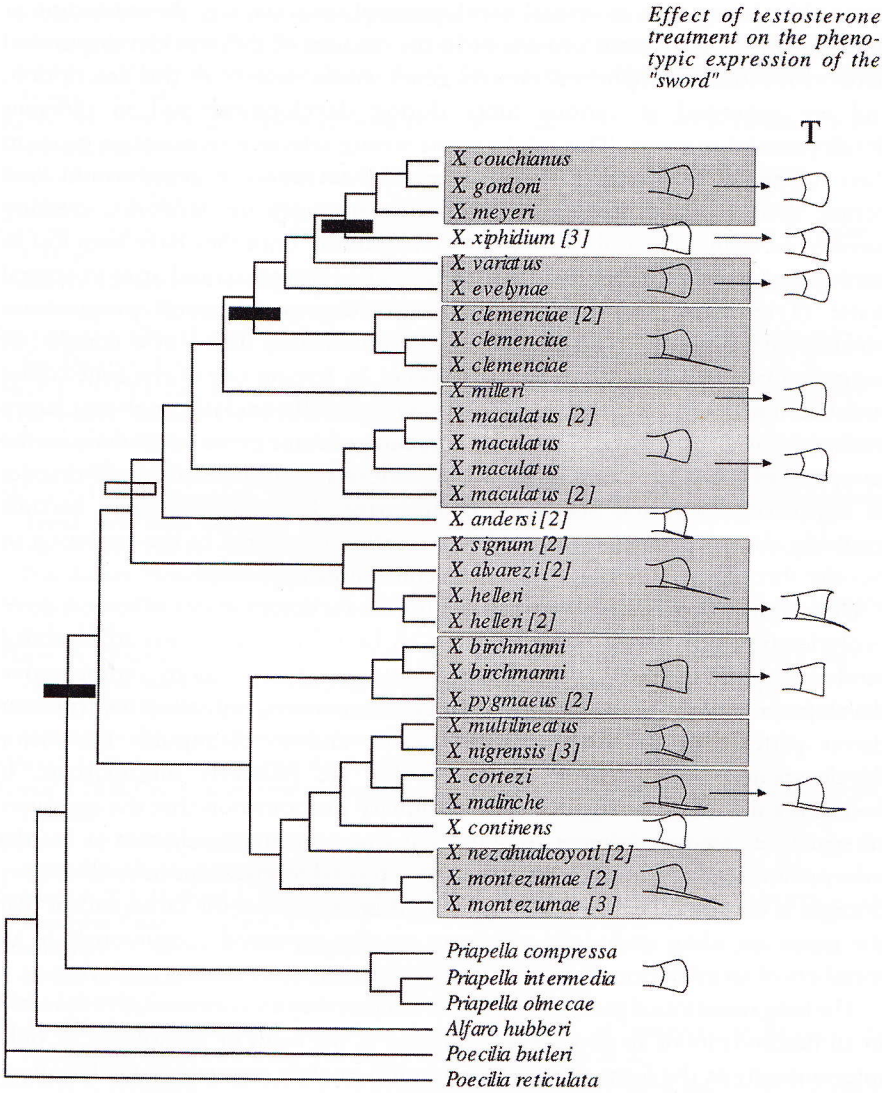


FIG. 4. Molecular (based on about 1300 bp of two mitochondrial genes and one nuclear gene) phylogeny of fishes of the genus *Xiphophorus*. The typical size of the ventral caudal fin extensions, in males of each species naturally and after treatment with testosterone, are indicated. Black bars indicate the presumed phylogenetic place of the origin, and the open bar indicates the loss of the sword within species of the genus *Xiphophorus*.

no longer expressed. It is conceivable that genes and gene networks might be retained by being used in several developmental contexts, e.g. the expression at different times, in different organs, or in the nexuses of different developmental networks. Most developmental control genes would seem to fit this description, and are expressed at various times during development and in different developmental contexts. This might create strong selection to maintain genes in their functional roles and in the genome. This retention of genes would then permit their recurrent co-option into new structures or networks, creating novelty, or similarly permit them to be 're-awakened' once they have been lost in the form of parallel or convergent morphologies. Novelty could arise in several ways: (1) retention and 're-awakening' of 'forgotten' genetic programmes possibly also through incorporation of this potentiality into a new context, as suggested here; (2) through gene duplications, by freeing one of the gene copies such that it may take on new functions (e.g. Ohno 1970); or (3) through regulatory evolution, by changing the control of expression of some genes or similarly by the co-option of genes into a new nexus of interactions among genes, through changes in regulatory elements. As more comparative developmental data become available, the relative importance of the retention compared to the evolution of novelty through gene duplication may become more apparent.

Developmental mechanisms are clearly important determinants of some macro-evolutionary phenomena, and they need to be incorporated into an extended modern synthesis of evolutionary biology. Only more comparative developmental data, analysed in a phylogenetic context, will allow us to better detect patterns in the diversification of life and to distinguish the major developmental mechanisms from those that are relatively unimportant. If homology describes the inevitable evolutionary phenomenon that the similarity of structures among different organisms is due to common descent—i.e. the information required for genetic and developmental mechanisms in evolutionary lineages is continuous—then analogy might be somewhat the same, except that the genes encoding analogous structures are not expressed continuously in all members of an evolutionary lineage, but are 're-awakened' during evolution.

The long retention of genetic systems—whether they are continuously expressed in all descendants of an evolutionary lineage in the form of homology, or only intermittently in the form of parallel evolution or even convergent evolution—may hence be caused by similar biological bases and may be due to similar evolutionary principles. Homology and non-homology might thus be extremes along a continuum rather than two completely different kinds of mechanisms.

Acknowledgements

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DISCUSSION

Tautz: How do we know that the genes were retained? Any gene in the genome acquires mutations continuously and can only be maintained if there is positive

selection on it. Thus, genes that have no function would inevitably be lost from the genome, at least in the long run.

Meyer: It's probably a matter of the relative frequency of mutations compared to the strength of selection.

Wilkins: One explanation is the multiple developmental functions of genes and that it is possible to select for the retention of a gene by using it in a different developmental context.

Meyer: Yes, it may have multiple functions. Almost all genes are switched on in different places and at different times in development.

Roth: You mentioned the 'sword-making genes', but it remains to be shown that what was present in the ancestor and then retained is actually a mechanism for making a sword. If the mechanism has other functions, it may just be coincidental that it can produce a sword. To call it a sword-making apparatus may belie what its function is in lineages in which it has actively been maintained by selection without the sword being expressed. Is this conceivable?

Meyer: Females prefer to mate with males that have swords, and this female preference has been hypothesized to retain swords, even though there is a cost because males with swords are more visible to predators and less able to escape. Presumably, in some cases this cost outweighed the female preference benefit, and so swords disappeared.

Roth: Is it possible that the sword-making apparatus did not originate in conjunction with sexual display, or even with production of a sword on the tail?

Meyer: Yes, it's possible that it was co-opted for that function.

Roth: So the swords themselves may not be homologous, but rather the apparatus is homologous, in the sense of phylogenetic continuity.

Meyer: For argument's sake, if we assume that swords were lost and re-evolved twice, so that they evolved by parallel evolution since within the genus there were sword-less ancestors, are those swords not homologous to the swords that existed originally?

Wagner: A question in this context is whether the character was indeed lost. Since there are sword-less forms in this genus, the question is whether the ventral fin rays remain differentiated in the sword-less forms. If so, one would again face a question of character delineation. What is described as a loss and regain of sword may just be different states of a character that consists of the developmentally individualized ventral fin rays.

Meyer: Yes and no. In some of these species there is large amount of population variation. Both sword length and pigmentation have a normal distribution.

Rudolf Raff: Part of the problem is that you're looking at the sword as an isolated item, which isn't necessarily the case. It is likely that there are regionalized differences in the rays of the fin, for example. When you're talking about a sword gene, you're not necessarily talking about a gene that directly makes the fin, but

rather a gene that affects hormonal control, or some other aspect of development, and it is this that has been selected for and against. In this sense, the entire process is homologous.

Meyer: I agree to some extent, but I don't necessarily see a difference in terms of whether selection acts on testosterone receptor genes or on other genes in the cascade of gene interactions that will eventually lead to a sword in an adult male fish.

Rudolf Raff: But it's a matter of whether you see these characters as arising in development or whether you see development as having numerous interacting components. If this is the case, then the interacting components can yield complex outcomes without disassembling the machinery at all, because what is important is how the elements in the machinery are interacting. In this case it may be a set of responder cells, and somewhere else in the body it may be something that regulates hormone levels.

Meyer: The reason I chose to talk about *Xiphophorus* was to illustrate how rapidly things can appear, disappear and reappear. A student in my lab is going to look at these sword genes by analysing cDNA libraries from regenerating cells of swords that have been cut off. This may or may not be the way to find these genes.

Müller: But you're not simply saying that things can disappear and reappear. You seemed to be saying that homoplasy and homology are more or less the same thing, and I'm surprised how you can reach this conclusion, because homoplasies arise independently in different lineages again and again by the retention of some developmental potential. Whether this is genetically determined or epigenetically determined is not important. The potential is there and so these characters arise. The switch to homology occurs when they become an integrated part of a bauplan that is the basis for further diversification of lineages, and the character is fixed within that bauplan. I would say that all homologues arose, at some point, as homoplasies, but they become homologues when they assume an organizational role in morphological evolution.

Meyer: In my opinion, a sword that reappears is the same as the original sword. It is still a homologous sword even though it disappeared for a short time in evolution.

Akam: So you would have no problem if it disappears every other generation in the female line. One could even imagine a continuum if it disappears in winter and comes back in summer, i.e. a seasonal polymorphism.

Maynard Smith: I would like to issue a slight warning here. We wrote a paper in *Nature* recently, not specifically on the problem we are discussing, but on the problem of control circuit redundancy and how two genes that do only one thing can be maintained (Nowak et al 1997). This is an important problem, and we had to work quite hard to think of mechanisms and explanations for the maintenance of genes against the constant noise of mutation. I would urge people who want, in any

context, to invoke the explanation 'this genetic machinery has been there, although not expressed in a particular form, for quite a long time and it is now being recalled' to ask themselves what maintained it in the interval. In the case of the direct development of an echinoderm there probably isn't a problem, because almost all the genetic material needed to do the direct development of an echinoderm is presumably needed to turn the rudiment in a pluteus into an adult, so it has been maintained by selection because it is doing something anyway. I'm not trying to lay down the law. I'm just asking people to think carefully about the assumptions.

Meyer: My point is that there is so much parallelism that it may mean something. The sword genes, whatever their actual function is, have been maintained for 5–10 million years, and in the cichlids many life history traits and morphogenetic mechanisms have been maintained for even longer time periods. Another example is the evolution of giving birth to live animals in sharks, which re-evolved 10 times.

Galis: I'm puzzled by your statement that the possession of pharyngeal jaws is a specialized condition in cichlids because pharyngeal jaws occur in many fish families, and their possession in cichlids is certainly plesiomorphic. In cichlids only minor anatomical changes of the pharyngeal jaw apparatus are assumed to be responsible for the diversity (Galis & Drucker 1996).

Meyer: I am aware of that, but there are many other families of fish that have pharyngeal types of jaws of one kind or another, but they don't have this particular arrangement, as cichlid fish do. They are the only family in the African great lakes that do.

Aboubeif: I have always been confused about the distinction in the literature between convergence and parallelism. Is it possible to distinguish clearly between the two?

Rudolf Raff: It depends on the mechanism. It is possible to have convergence without having similarity of mechanism or of parts, e.g. my leg and a table leg, whereas parallelism is assumed to involve the same mechanism recurring in two lineages to produce a similar effect. Obviously there are grey zones, but the concepts remain useful.

Wagner: A more primitive way to distinguish them is that parallelism is repeated evolution of a character starting from the same starting point, whereas convergent characteristics have different starting points.

Elizabeth Raff: There are many examples where different molecular pathways give rise to the same phenotypic result; thus, it would be difficult or indeed impossible to unravel whether the end result (the character) is convergent or parallel.

Carroll: The cladistic viewpoint is that there is no distinction between parallel or convergent evolution. It is a question of whether the character was or wasn't present in the immediate common ancestor, which is fairly easy to live with. I

could never understand Simpson's marked distinction between parallelism and convergence; according to cladistic methodology, it's all homoplasy (Simpson 1953).

Nicholas Holland: During his career, Simpson made two distinctions. He started out with a strictly geometric model of parallelism and convergence, and then some years later he shifted into describing these terms in relation to genetic propensity.

Akam: The distinction is critical if you're concerned with mechanisms. Do you reiterate the same developmental changes in two parallel lineages to generate the same character transition, or do you do it by quite different methods? If you're thinking mechanistically this is important, but if you're thinking purely taxonomically perhaps it isn't.

Meyer: There are two grey zones: (1) does convergence start at the level of the genus or the family; and (2) how different is different, and how same is same, in terms of developmental mechanisms?

Maynard Smith: Isn't it just a question of going back to the latest common ancestor of the two groups you are comparing?

Elizabeth Raff: But you will never know what the mechanism was in the ancestor.

Wilkins: This is a probability argument. The further back you have to go to reach a common ancestor the less likely it is that the same genetic potential has been evoked. The problem is that it's difficult to put a number to that probability.

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