

Coelacanth fins and evolution

SIR — Major developmental mutations, such as the well-known homeotic mutations in the fruitfly *Drosophila*, can readily be induced in the laboratory, but are almost invariably deleterious and are widely regarded as unimportant to evolution¹. However, the median fins of coelacanth fishes seem to furnish evidence of a dramatic developmental mutation event, comparable to homeotic transformation, in the early history of the group.

The paired fins of coelacanths (such as the recent *Latimeria*), lungfishes and other lobe-finned fishes (sarcopterygii) are structurally comparable to the limbs of tetrapods and appear to develop in a similar way². The dorsal and anal fins are usually quite different, their internal skeletons taking a form similar to *a* in the figure. Phylogenetic evidence³ indicates that the primitive type of median fin skeleton in jawed fishes is a row of separate, parallel rods; *a* in the figure is essentially a 'condensed' version of this, with the rods supported by a single basal plate. Modern lungfishes have reverted to the primitive pattern⁴. The paired fins of sarcopterygians are thus of a unique, limb-like construction, whereas the median fins in most members of the group seem to be broadly similar to those of other fishes. This is not the case in coelacanths.

The posterior dorsal and anal fins of coelacanths are strongly pedunculate (*b* in the figure). The internal skeletons, musculature and innervation of these fins correspond extremely closely to those of the paired fins⁵. Further, they

are supported by complex basal plates that do not resemble those of other lobe-finned fishes but are closely comparable in structure and ossification pattern to the coelacanth pelvis (*d-f* in the figure). The anterior dorsal fin, by contrast, is of a generalized sarcopterygian type. Film of swimming *Latimeria* shows that the posterior dorsal and anal fins move in sequence with the paired fins, whereas the anterior dorsal fin does not.

The posterior dorsal and anal fins of coelacanths are fundamentally different from those of other sarcopterygians, but resemble coelacanth pelvic fins very closely. If this degree of similarity obtained between (for example) pelvic fins of two taxa, rather than between paired and median fins of the same animal, it would unquestionably be accepted as evidence of homology. The most obvious interpretation of the pattern, in the absence of direct embryological evidence, is that paired-fin structures are being expressed at the posterior dorsal and anal fin sites. This inference suggests another interesting possibility. Although coelacanths have possessed dorsal and anal fins of apparently modern pattern since the Devonian⁶, it seems clear that they are derived from fishes with 'normal' median fins. The differences between the two fin types are so great, however, that it is very difficult to imagine what structural intermediates would be like or how they could function. It is easier to envisage the replacement as a single-step event caused by a simple 'switch' in gene expression. A major aspect of coela-

canth morphology may thus have arisen quite suddenly, rather than through gradual change.

Our understanding of coelacanth development and genetics is as yet too limited to test the ideas presented here. The inferred sudden change from one median fin structure to another could be falsified by evidence from the fossil record. The Upper Devonian genus *Miguashaia*, the probable sister group of all other coelacanths⁶, appears to have 'normal' sarcopterygian median fins; further work on Devonian coelacanths may thus help to cast light on this interesting problem.

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Westhof's rule

SIR — Associations via hydrogen-bonded base pairs between different polynucleotide chains or between different segments of a polynucleotide chain lead to the various polymorphs of antiparallel DNA structures but also to unusual DNA structures such as triplexes, quadruplexes¹ or parallel helices², and also underlie the three-dimensional folding of RNA molecules. To specify a structure, one needs to indicate the nature of the hydrogen-bonding sites (Watson-Crick or Hoogsteen atomic positions); the orientation of the base with respect to the sugar (*anti* or *syn*)³; the position of the glycosyl bonds with respect to each other (*cis* or *trans*, that is, both on the same side or on different sides of the base pair); and finally, the relative orientation of the polynucleotide chains (antiparallel or parallel). Thus, the canonical antiparallel B-DNA structure possesses base pairs involving only the Watson-Crick sites with an *anti* conformation for the bases and a *cis* position of the glycosyl bonds.

I wish to suggest a general rule relating the various stereochemical constraints that apply to pairings involving at least two hydrogen bonds between any type of nucleotide of usual chirality. Less general statements have already

a, Posterior dorsal fin support of the osteolepiform *Eusthenopteron* in left lateral view (from ref. 7); *b*, sketch of *Latimeria chalumnae*; *c-f*, median fin supports of *Latimeria*, ossified parts stippled, lepidotrichia not shown. *c*, Posterior dorsal fin in left lateral view; *d*, anal fin in right lateral view, inverted; *e*, right pectoral fin in internal view, ends of shoulder girdle omitted; *f*, right pelvic fin and pelvic moiety in dorsal view (*b-f* modified from ref. 5). Note the small 'anterior cartilages' (AC) capping the anterior ends of the pelvis and median fin basal plates, and the similar ossification patterns. The 'external blades' (EB) of the dorsal and anal fin supports are double structures facing left and right, unlike the single 'lateral blade' (LB) of the pelvis. The lateral blade is deflected dorsally; if a pelvic moiety was mirrored through the sagittal plane of symmetry in the same way as the dorsal and anal fin supports, the lateral blade and its mirror image would correspond perfectly to the 'external blades'.

