

## Some palaeontological implications of putative, long-term, gene reactivation

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**Abstract:** The reactivation of dormant genes in fossil lineages after long time periods is considered a likely evolutionary mechanism. This would not violate Dollo's law on evolutionary irreversibility in a genetic sense, but the law might appear to be contradicted by certain intra- and inter-cladogenic phenotypic variations to at least the generic level. Practical effects would include potential complications for unravelling palaeontological phylogenies, and the recognition of the true status of some so-called Lazarus taxa.

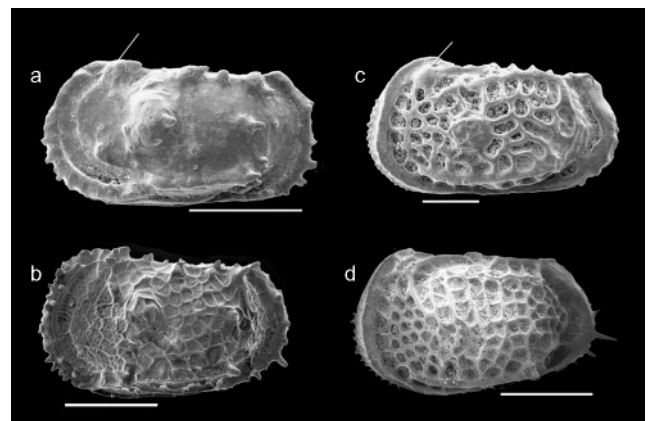
**Keywords:** Lazarus taxa, ostracodes, biological evolution, phylogeny.

Although progressive reversals for a single genetic variable during the history of a species (anagenesis) is not uncommon, reversals of morphologically complex evolutionary trends between lineages (cladogenesis) is considered by some workers as unlikely (Stanley 2001). This supposed irreversibility of evolution is enshrined as 'Dollo's law' (Louis Antoine Marie Joseph Dollo, 1857–1931), and suggests that 'degradation of genetic information is sufficiently fast that genes or developmental pathways released from selective pressure will rapidly become non-functional' (Marshall *et al.* 1994). However, in a recent publication Dingle (2002) has suggested that the occurrence of two sighted, Recent, species of marine benthic Ostracoda (Arthropoda, Crustacea) with geological histories in excess of 45 Ma, is parsimoniously explained by rejuvenation of ocular structures from functionally blind ancestors through the reactivation of dormant genes. The likelihood of such a mechanism operating, and some possible phylogenetic ramifications, are considered herein.

### Evidence of sighted descendants from blind ancestors

The two podocopid ostracodes in question (*Dutoitella lesleyae* Dingle and *Poseidonamicus whatleyi* Dingle) are found living in relatively shallow water (113–474 m and 240–355 m, respectively) on a very small, isolated, volcanic edifice (Marion Island) on the mid-ocean ridge between southern Africa and Antarctica (Dingle 2003) (Fig. 1a and c). Podocopid ostracodes have no mobile larval stages, and the oceanographical and bathymetric isolation of the archipelago suggests that ancestors of these two species actively colonized the shallow-water habitats by migrating from adjacent, relatively deep-sea areas. Typically, ostracodes living below 600–900 m are functionally blind (Benson 1984). A high rate of endemism in the relatively diverse Marion Island ostracode fauna (Dingle 2002) indicates rapid evolution since the volcanic Prince Edward Islands archipelago was formed (*c.* 450 ka; McDougall *et al.* 2001).

*Dutoitella* is first recorded in the Campanian of South Africa, and a small number of species have been found in intermediate and deep-water Maastrichtian to Eocene sediments in the SW Indian–SE Atlantic Ocean area, and New Zealand (see Dingle 2002). All these appear to have been functionally blind (i.e. lack eye tubercles), as is the cosmopolitan deep-water species *Dutoitella suhmi* (Brady), which ranges in age from Oligocene to Recent (Fig. 1b). *Poseidonamicus* is first recorded in Eocene



**Fig. 1.** Examples of functionally sighted and blind species of two ostracode genera. (a), (b) *Dutoitella* showing sighted (a) *D. lesleyae* Dingle from Marion Island (368 m) (NHM 2002.1060), and blind (b) *D. suhmi* (Bradley) from NW Pacific (H.M.S. *Challenger* site 241) (4206 m) (BMNH 80.38.119). (c), (d) *Poseidonamicus* showing sighted (c) *P. whatleyi* Dingle from Marion Island (355 m) (NHM 2002.1069) and blind (d) *P. major* Benson from SE Atlantic (2916 m) (SAM-PQ-MF-0495). Eye tubercles are indicated by white lines in (a) and (c). All specimens are left valves. Scale bars represent 500  $\mu$ m in (a) and 200  $\mu$ m in (b)–(d). (For additional information, see Puri & Hulings (1976), Dingle *et al.* (1990) and Dingle (2003).) Specimen reference numbers: (a)–(c) Natural History Museum, London; (d) South African Museum, Cape Town.

sediments from the SW Pacific, and numerous Tertiary and Recent species occur in deep-water sediments from the SW Atlantic, Indian and Pacific areas (see Whatley 1985; Whatley *et al.* 1998). All known species of *Poseidonamicus* are blind (e.g. Fig. 1d), except *P. panopsus* from the outer continental shelf off southwestern Africa (Recent) and *P. ocellaris*, the latter with possibly non-functioning ocular structures in instars (juveniles) from deep water on the Lord Howe Rise (Quaternary). Whatley *et al.* (1986) and Whatley & Dingle (1989) assumed that these last two species were derived from sighted Tertiary ancestors. Consequently, conventional speculative evolutionary histories, based solely on stratigraphical relationships, would place *D. lesleyae* with no known potential ancestors, and assume that

*P. whatleyi* evolved from a sighted ancestor that also gave rise to *P. panopsus*: the only potential known progenitor being *P. ocellaris*. This invokes lineages with spatially and temporally isolated, unknown, sighted ancestors, which had either persisted for long time intervals in deep-water habitats, or had populated relatively shallow environments in unrecorded and transient locations. To obviate this complex and unlikely evolutionary history, Dingle (2002) suggested that *D. lesleyae* and *P. whatleyi* acquired ocular structures by reactivation of so-called 'master control genes' (Lewis 1992). Functionally (but not genetically) blind ancestors of the two species, having colonized newly formed habitats in which eyes were again a competitive advantage, selected to activate the dormant (silent) *Pax 6* homologous gene (Quiring *et al.* 1994; Gehring & Ikeo 1999; Fernald 2000). What are the prospects of this happening?

### Dormant genes and the possibility of ocular rejuvenation

As emphasized by Marshall *et al.* (1994), the silencing of a gene does not necessitate its deletion: it can remain dormant, but for a physical feature to be rejuvenated by reactivation of the gene, the protein for which it encodes must still be functional. Theoretical models have suggested that reactivation can be successful over time scales of 0.5–6.0 Ma (maximum of 10 Ma), before significant amounts of damage accumulate in dormant genes (Marshall *et al.* 1994). Significantly, this time scale is much greater than that over which speciation proceeds in many taxa (Stanley 1979, 2001), particularly in island communities (McCune 2001), so that rejuvenation of features can theoretically occur across species boundaries. Fryer (1999) cited a possible example in anostracan branchiopods, which suggests spontaneous atavism in a lineage that may be considerably longer than 10 Ma. Marshall *et al.* (1994) considered the possibilities of rejuvenating complex morphological features high, citing the example of frequent reversals of metamorphosis in the inferred evolution of 14 living species of Mexican salamanders over a period of 10–12 Ma (Shaffer 1984). They also pointed to the potential for 'cryptic retention' of apparently dysfunctional genes over long time periods via proteins that serve multiple functions, and specifically mentioned eye lens proteins (along with numerous other examples) (Marshall *et al.* 1994). That such rejuvenations could operate rapidly is shown by population genetics models, which indicate that if only a 1% selective advantage is bestowed by the possession of a particular allele, its frequency will rise in a population from 0.01 to 0.25 in as few as 350 generations (Strickberger 1976).

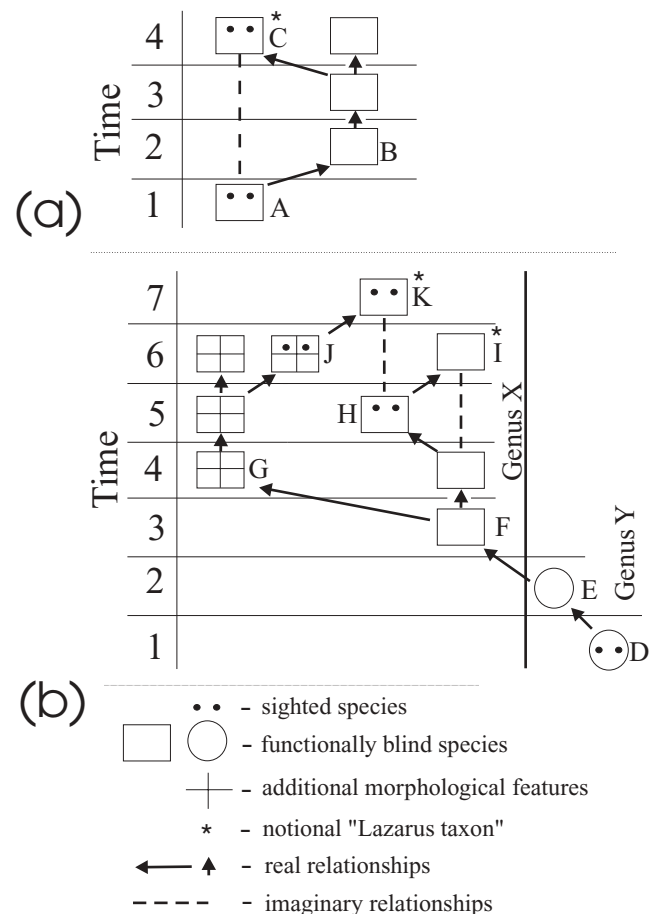
Applying these observations to the Marion Island ostracodes, it is suggested that selection for sight-promoting, dormant, alleles occurred in the shallowest ecodeemes of certain deep-living species of *Dutoitella* and *Poseidonamicus* in the vicinity of the archipelago as it rose into the photic zone during the Pleistocene. This is likely to have occurred at a maximum depth of 280 m, because although ostracode ocular structures have particularly low *f*-values (relative apertures: as low as 0.25), eyes are likely to be of little use below this depth because of the low light levels in the oceans (Myers & Kontrovitz 1988; Kontrovitz 1990; McKenzie *et al.* 1999).

In summary, although direct evidence must be lacking when dealing with fossils, genetic modelling and work on Recent material suggest that reactivation of dormant genes for complex features over periods up to 10 Ma (and possibly considerably longer) is feasible, and it is legitimate to consider some of the implications for palaeontological phylogenies.

### Discussion: some palaeontological implications

Such considerations require a fundamentally more relaxed attitude toward phylogenies and the question of 'ancestors' than that espoused, for example, by Gee in his rebuttal of Pearson on ancestor–descendant relationships (Gee 2000, 2001; Pearson 2000, 2001). Although Gee (2001) is correct in stating that in palaeontological series, ancestors can never be 'proved', the same could be said for the facts in any historical event that is recorded by indirect evidence. Degrees of probability have to be allowed to permit reasonable discussion to proceed, a concession that must follow from the acceptance by Gee (2001, p. 34) that 'the subjects of phylogenetic reconstruction are the products of evolution'. If ancestors in fossil lineages did exist, in fact (not just in theory, however tenuous the evidence), it is logical to speculate on them.

Morphological changes in fossil lineages are the cornerstone of palaeontological phylogenies, whether in 'traditional' or cladistic studies, but to allow that key features might 'reappear', perhaps many millions of years after they 'disappeared' in earlier lineages, has serious implications for the way palaeontologists view phylogenetic development. This can be illustrated by reference to Figure 2. In Figure 2a, a sighted species (A) occurs during time interval 1. It evolves into functionally blind species



**Fig. 2.** Some possible phylogenetic relationships resulting from putative reactivation of dormant genes, as discussed in the text. A, B, etc. are species, and 1, 2, etc. are successive time intervals. Arrows indicate speciation events or passage of established species into the next time interval.

B, and A becomes extinct. Only species B was extant during time intervals 2 and 3. Interval 4 contains the blind species (B) and a sighted species that has the morphological characters of species A. If the actual evolutionary relationships are that B evolved from A, and the sighted species C evolved from blind species B by gene reactivation, conventional techniques based on morphology will fail to resolve the relationships, as it is tacitly assumed that Dollo's law applies unequivocally and that once 'lost', eyes will not be reinvented. A cladistic interpretation would indicate two sister species, A (sighted) and B (blind), with no hint of true systematics, and a 'traditional' stratigraphical approach will suggest that species A continues through from intervals 1 to 4 with a 'record gap' during intervals 2 and 3 (dashed line): a so-called 'Lazarus taxon'.

### Sanctity of Dollo's law

For the relationships in Figure 2a, a strict application of Dollo's law would be unjustified. Further, in Figure 2b, the appearance of sighted species (H and J) of genus X during two time intervals (5 and 6, respectively), from a putative non-sighted ancestor (species F), is similar to that speculated for *Poseidonamicus* (Whatley 1985). This, *a priori*, suggests intra-cladogenic ocular rejuvenation after at least 45 Ma, whereas inter-cladogenic rejuvenation, similar to that from genus Y to genus X, is implied if, as Whatley (1985) suggested, *Poseidonamicus* evolved from the sighted species *Hermanites sagitta* Bate (which is Campanian). Whether inter-familial rejuvenation is possible remains to be considered. Consequently, although at the genetic level Dollo's law has not been violated, it cannot be applied unquestioningly at the phenotypical level.

### Lazarus taxa

These are taxa with an apparent gap in their fossil record that can extend over long periods of time (see Fara 2001), and are frequently associated with 'mass extinctions' (Wignall & Benton 1999). Erwin (1996), for example, cited two gastropod genera that are recorded in the Late Permian, and not found again until the Jurassic. The phenomenon has been variously ascribed to preservational bias, 'retreat' to refugia during environmental crises, or, more likely, low abundances (see Wignall & Benton 1999; Rickards & Wright 2002), and in Figure 2, species C, I and K would be classified conventionally as Lazarus taxa of species A, F and H, respectively. Clearly, however, the younger species do not derive directly from their putative older lineages, and are not Lazarus taxa as generally understood, although it might be impossible to differentiate them morphologically. Consequently, the likelihood of gene reactivation further undermines the usefulness of the concept of 'Lazarus taxa', which has been questioned recently (for different reasons) by Rickards & Wright (2002).

### General phylogenetic considerations

The last-mentioned problem has more general implications. If fossil species A, B and C in Figure 2a differ only in their morphological expression of the on/off state of a dormant gene, then genetically they are identical and are not, in fact, different species. The same can be said for species F, H and I, and G, J and K of genus X in Figure 2b, but what of the 'Lazarus taxon' K in relation to species H? The former arrives in interval 7 via species J and G, and if the additional morphological feature of J (cross pattern) is an acquired character (in relation to species F)

that is subsequently switched off, species K is genetically different from H. However, it would be impossible to unravel its true phylogenetic status. Smith (1994, p. 137), touched on the problem in his discussion of Lazarus taxa, when he suggested that 'if the (time) gap is sizable, it is unrealistic to expect all taxa to remain morphologically unchanged' and a new name for the younger phena, which would be entirely plesiomorphic with the older, would result in a 'pseudoextinction'. But he did not, obviously, consider how such a relationship would be recognized if the new derived characters were switched off subsequent to the appearance of the younger phena.

Finally, as the lability of regulatory genes is well established (Raff 1996), and their importance in evolution as the locus of substantive morphological alteration recognized (Lowe & Wray 1997; Wray 2001), the suggestion by Budd (1999) that it is microevolutionary adaptation that drives such alteration, rather than *Hox* gene mutation, may be a key to switching on/off of various morphological expressions. The recent demonstration that, at least in some crustaceans, fundamental, progressive, ontogenetic modifications can occur to the ocular apparatus in response to changes in habitat (Jinks *et al.* 2002) suggests that such flexibility at a genetic level may be 'built in'. However, the problem of recognizing such events in the palaeontological record, and accommodating them in phylogenies could be daunting.

This work was funded by the National Science Foundation of Denmark. The author gratefully acknowledges discussions, and helpful comments on the manuscript, by R. Bromley (Copenhagen) and A. Lord (University College London). J. Whittaker, Natural History Museum, London, kindly provided the scanning electron micrograph of *Dutoitella suhmi* (Brady).

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Received 18 November 2002; revised typescript accepted 12 February 2003.

Scientific editing by Duncan Pirrie