

MICROPALAEONTOLOGY NOTEBOOK

Further visions of Dollo's Law through ostracods' eyes: an essay

R. V. DINGLE

Larchfield, Cambridge CB3 9LR, UK

(e-mail: Rvdingle@aol.com)

In a previous paper, Dingle (2003) considered the possibility of gene reactivation leading to the re-appearance of eyes in certain blind ostracod taxa after sightedness had been lost in lineages several million years earlier. These observations were based on two marine genera found at Marion Island in the Southern Ocean (Eocene–Recent *Poseidonamicus* Benson, and Campanian–Recent *Dutoitella* Dingle) that have evolved numerous deep-water species that were/are blind. The discovery of Recent, sighted, shallow-water forms led to the suggestion that adaptive pressure from the advantages of sightedness had resulted in the reactivation of genes that allowed an evolutionary advantage to be regained (Dingle, 2003).

While such transformations have not been enunciated in these terms by other micropalaeontologists, there have been tacit assumptions in the literature that similar processes do occur. Confrontation with the phylogenetic issues raised by these phenomena has so far been fudged by inconsistency, but, in this essay, further examples will be looked at to highlight the taxonomic swamp into which we are in danger of wading.

One of the issues is whether such processes violate Dollo's Law (Dollo, 1893) at the phenotypic, if not genetic, level. Dollo's Law has been expressed in modern terms by Marshall *et al.* (1994) as 'degradation of genetic information ... sufficiently fast that genes or developmental pathways released from selective pressure will rapidly become non-functional'. Gould (1970, p. 192) preferred to call this Dollo's 'notion of irreversibility', while recent accounts stress its relevance only to 'complex characters' (e.g. Collin & Miglietta, 2008).

Let us consider the matter from one viewpoint of conventional wisdom. While examining relatively deep-water DSDP Leg 36 Albian sediments from the Falkland Plateau, Dingle (1984) came across three new species that belonged in *Hemingwayella* Neale. However, they lacked eye tubercles and, believing that their blindness was of subgeneric significance, he placed them in *Hemingwayella* (*Parahemingwayella*) subgen. nov. (type species *H. (P.) barkeri*). For a while this criterion was accepted by other workers (e.g. Coles & Whatley, 1989), but was later discarded by Ayress *et al.* (1995) on the grounds that presence/absence of eyes is not of (sub)generic significance. Strictly applying Dollo's Law, one consequence of Ayress *et al.*'s (1995) presumption is that there has to be at least one putative sighted pre-Albian progenitor to the blind deep-water *Hemingwayella barkeri*. This ancestor gave rise not only to *H. barkeri*, but also to the earliest (currently) known sighted species (the Santonian type species *H. ornata* Neale, 1975), as well as the five modern sighted species from the Southern Ocean area.

The author is happy to concede the error of his ways and accept that the taxonomic moral of this tale is that the loss of

functionality of the genes coding for sight is not significant enough to be a criterion for indicating new genera or subgenera. The taxonomic corollary, however, must also be that any reactivation of such genes (if this is ever established as a real process) needs to be interpreted in the same light.

This brings the discussion back to the issue on which it opened and, to revisit the notion raised in Dingle (2003), readers are invited to consider two potentially less-controversial examples: *Cytheropteron* and *Bairdoppilata*.

The genus *Cytheropteron* Sars has a known stratigraphical range of the Lower Jurassic (possibly Triassic) to Recent (A. R. Lord, pers. comm. 2008), and one of its diagnostic characteristics is that it is apparently functionally blind – i.e. it does not display eye spots or tubercles. In 1972 Bate erected the genus *Oculocytheropteron* on a Santonian–Campanian species (*O. praenuntatum*) from northwestern Australia, the primary criterion distinguishing it from *Cytheropteron* being the possession of well-developed eye tubercles. A further eleven species of sighted '*Cytheropteron*' from the Cenozoic of Australasia were transferred to *Oculocytheropteron*, along with one possible northern hemisphere taxon, *O. nodosum* (Brady). Whatley & Masson (1979) re-examined the latter species during their study of *Cytheropteron* from around the British Isles and concluded that the node at the anterior cardinal angle, which had been taken for an eye tubercle by Bate (1972, p. 49), was not, in fact, such. Solely because of this, they retained *nodosum* within *Cytheropteron*.

The appearance of *Oculocytheropteron* in Australia in an environment in which it co-existed with at least five conventionally blind species of *Cytheropteron* (Bate, 1972; Neale, 1975) suggests that sightedness could well have been a local adaptive advantage, but we can only speculate on what prompted such a development at this time in this particular place.

Thus, in contrast to the perceptions surrounding *Hemingwayella*, the presence/absence of eyes in '*Cytheropteron*' clearly has been accepted by ostracod workers as a generic criterion. Curiously, no consideration seems to have been given in the literature to this phylogenetic anomaly and begs the question 'from what did *Oculocytheropteron* evolve?'. If its progenitor was a blind species of *Cytheropteron*, why should a new taxon be indicated, since sightedness is not considered a generic criterion? More critically, how did this adaptation manifest itself – has Dollo's Law been infringed in the way suggested by Dingle (2003)? The alternative to such heresy must be that *Oculocytheropteron* was a completely separate, sighted lineage within the Cytheropterinae, extending at least to the Lower Jurassic (i.e. over 100 Ma). Neither position should be maintained by workers without considering the implications – such a situation is an example of the 'fudge' that was referred to earlier.

A similar phylogenetic anomaly-in-the-making arises in the description of a sighted genus of ‘*Bairdoppilata*’ (*Oculobairdoppilata* gen. nov. van Itterbeeck *et al.*, 2007), based on ‘*Bairdia*’ *malzi* Morsi & Speijer from Tunisia. The new genus is distinguished within the family Bairdiidae solely by possessing a ‘... well-developed eye tubercle on the anterodorsal part of both valves’. This is analogous to Bate’s concept *vis à vis* *Cytheropteron* and *Oculocytheropteron*. As far as van Itterbeeck *et al.* (2007) could ascertain, *Oculobairdoppilata* is the only genus in the Bairdiidae (extending from lower Palaeozoic to Recent times and with species occurring world-wide in both shallow- and deep-water environments) to exhibit ‘hard part’ evidence (i.e. biomineralized tubercles) for the possession of eyes. Also, this innovation is known only during Palaeogene time in the eastern Mediterranean, and the problems it poses for scientific logic are essentially similar to those for *Oculocytheropteron*. Van Itterbeeck *et al.* (2007) wrestled with such issues by arguing that because many bairdiids live(d) in the photic zone, such species are unlikely to be/have been truly blind, relying instead on a primitive ocular system only expressed in internal soft parts. The implication of this suggestion is that until the internal physiology of such modern species are examined for functioning ocular systems, their actual ‘blindness’ or otherwise cannot be established. Clearly, such a course of action is not available for extinct species, so palaeobiologists are still left with a conundrum.

Notwithstanding this possibility, *Oculobairdoppilata* certainly sported an external lens (tubercle), presumably stealing an advantage over its fellow bairdiid competitors with its ‘more advanced eye type’ (van Itterbeeck *et al.*, 2007, p. 100). According to conventional wisdom (i.e. Dollo’s Law), it must have had ancestors which were also thus endowed.

One issue highlighted here is the inconsistency that the creation of *Oculocytheropteron* threw up, and *Oculobairdoppilata* is perpetuating, given that other examples, such as *Hemingwayella* and *Parahemingwayella*, have been resolved to the satisfaction of the broad church of fossil-ostracod workers. Either the possession of eye tubercles is, or it is not, accepted as a generic criterion: we cannot have our cake, and eat it.

Dollo’s Law leads to the inescapable conclusion that neither *Oculocytheropteron* nor *Oculobairdoppilata* could have evolved from eye-tubercle-free ancestors within *Cytheropteron* or ‘*Bairdia*’. A similar inference was drawn by Hunt (2007, p. 626) on cladistic grounds from the one Recent sighted species he studied from *Poseidonamicus* (i.e. *P. panopsus* Whatley & Dingle). Hence, by this logic, all the earlier representatives of *Cytheropteron*, ‘*Bairdia*’ and *Poseidonamicus* were ‘blind’ and the ‘sighted’ taxa (i.e. those with ‘advanced eye types’) that appear suddenly in their midst must have evolved from similarly endowed common ancestors within their respective genera, which had co-existed with blind (or ‘primitively ocular’) sister taxa. In the examples cited herein, this creates putative undiscovered fossils trails across time for earlier, sighted-species ancestors of *Oculocytheropteron praenuntatum*, *Oculobairdoppilata malzi* and *Poseidonamicus panopsus* of the order of 105 Ma, 390 Ma and 50 Ma, respectively.

Because we are dealing in this essay with structures that facilitate an ‘advanced’ form of sightedness, it also follows in logic that in these three examples there has been an unbroken

continuity of habitation in shallow water. This conclusion reinforces the notion that the sighted bairdiids are ‘conservative’, rather than van Itterbeeck *et al.*’s (2007, p. 100) contrary view. A similar level of conservatism was proposed by Hunt (2007) for *P. panopsus*.

A further enigma is the question as to which genus any putative earlier species of *Oculocytheropteron* or *Oculobairdoppilata* that had taken to deep-water habitats during this time and lost its sightedness would be allocated? This may seem a moot point, as they would be morphologically indistinguishable from the blind species in the sister genera, but the effect would be the creation of further taxonomic aberrations. We may be dealing with polyphyletic groups, in which homology is the key. In this case the issues could hinge on two factors – whether the re-acquisition/or loss of ocular structures would (a) constitute a major change ‘... based upon the position of [the] phenomenon in a complexity continuum’ and (b) whether such convergences could be discerned by recognizing ‘... trace[s] of the intermediate stages through which it had passed’ (Gould, 1970, pp. 199, 196, respectively).

An alternative explanation for such phylogenies has already been outlined in Dingle (2003). Collin & Miglietta (2008) have considered this issue from several points of view using large geonomics databases and concluded that the figure of 10 Ma cited by Marshall *et al.* (1994) for the survival of unused neutral protein-coding genes can be extended to perhaps 24 Ma. Using Wagner’s (2007) work they also considered that even homology could represent re-evolved characters ‘if they utilize the same character identity gene [regulatory] networks as the ancestral character’ (Collin & Miglietta, 2008, p. 608). Further, recent work by Borowsky (2008) on blind cavefish may point to a possible scenario leading to ‘re-evolved’ ocular characters, which involves the unification of two hitherto physically separated demes of a ‘blind’ species upon the destruction of certain ecological barriers.

While Collin & Miglietta (2008, p. 608) concluded that Dollo’s ‘Law’ should be best viewed as merely making ‘explicit ... link[s] between phylogenetic patterns and underlying mechanisms’, the main thrust of this essay is that whatever evolutionary mechanisms are ultimately invoked, micropalaeontologists should not ignore their ramifications.

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