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Cope's Law of the Unspecialized, Cope's Rule, and weak directionality in evolution

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ABSTRACT

Background: Edward Drinker Cope nurtured the idea that evolution moves by an inner motor towards the perfection of structures. This concept animated his major contributions to evolutionary theory, including the Law of the Unspecialized and the familiar Cope's Rule. The former states that clades start with unspecialized forms and evolve towards specialized descendants eventually bound to become extinct because of their 'overperfection'. Through time, the Law of the Unspecialized has been abandoned, probably because it is dominated by a concept of strong directionality (and the many distortions this concept entails).

Questions: Is directionality in evolution real? If so, does the evidence contradict the Law of the Unspecialized, as is now commonly assumed?

Procedure: We review the Law of the Unspecialized. Then we recast it in modern terms. We highlight the connection between Cope's Rule and the Law of the Unspecialized.

Conclusions: A form of weak directionality is real. We conclude that the concept of directionality has been unjustly deprecated. It is, in fact, a pervasive, important, and easily testable feature of evolution.

Keywords: Cope's Rule, Cope's Law of the Unspecialized, weak directionality, body size, ecological specialization.

INTRODUCTION

What we understand today as Cope's Rule is the tendency towards increasing body size in a lineage over geological time (Cope, 1887). It has been said that Cope's Rule might not really be Cope's (Polly, 1998), instead that it was attributed to Edward Drinker Cope by twentieth-century scholars such as Simpson (1953) and Rensch (1954) based on faint evidence. These authors might have been persuaded that the rule is really Cope's by passages in the great American palaeontologist's later writings, especially *The Origin of the Fittest* (1887) and *The Primary Factors of Organic Evolution* (1896), which provide ample evidence that Cope

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considered size increase to have been a regular feature in the evolutionary history of vertebrates in general, and mammals in particular. The most quotable example may be this rare and unexpected tribute to his adversary Othniel Charles Marsh:

> It is true, as observed by Marsh, that the lines of descent of Mammalia have originated or been continued through forms of small size. The same is true of all other Vertebrata.

The empirical observation, whether we refer to it as 'Cope's Rule, 'Alroy's Axiom' (as suggested by Polly, 1998) or 'Marsh's Maxim', was for Cope an almost trivial part of a larger theoretical apparatus that he referred to as the 'Law of the Unspecialized'. This 'law', which Cope nurtured during much of his career (Bowler, 1977), states that evolutionary novelties associated with new major taxa are more likely to originate from a generalized, rather than a specialized, member of an ancestral taxon:

> . . . the highly developed, or specialized types of one geologic period have not been the parents of the types of succeeding periods, but . . . the descent has been derived from the less specialized of preceding ages . . . Animals of omnivorous food-habits would survive where those which required special foods, would die. Species of small size would survive a scarcity of food, while large ones would perish . . . the lines of descent of Mammalia have originated or been continued through forms of small size. The same is true of all other Vertebrata . . . Degeneracy is a fact of evolution . . . and its character is that of an extreme specialization, which has been, like an overperfection of structure, unfavorable to survival. In general, then, it has been the 'golden mean' of character which has presented the most favorable condition of survival, in the long run. (Cope, 1896: 173–174)

Stanley (1973) perceptively recognized that Cope's Rule as it is known today is a special case of the Law of the Unspecialized. He argued that since most animal clades start at small body size, and since a lower size limit per body plan does exist (Clauset and Erwin, 2008), diversification should produce a greater number of large than small species over time. The observed directionality would then be an artifact of the increasing variance and mean in body size through time, a manifestation of a 'passive drive' rather than a result of an 'active' trend driven by the advantage of being large (Gould, 1988a). In Gould's famous words, rather than *towards* large size, evolution would proceed *away from* small size.

Since Stanley's seminal book there has been a proliferation of studies either supporting or falsifying Cope's Rule. Conversely, Cope's original Law of the Unspecialized has been almost forgotten (Gould, 2002). This probably reflects the fact that Cope endorsed Lamarck's view of evolution as having a strong directionality, which Cope translated in his own concept of 'kinetogenesis' (Bowler, 1977). When Darwinian natural selection came to be seen as the main mechanism of adaptation, the law inevitably became unfashionable, while its nested concept of directional size increase in a lineage became disconnected and epitomized as 'Cope's Rule'. Ironically, the Darwinian twist gave a second, unintended but fatal blow to Cope's Law of the Unspecialized. Cope's understanding of directionality was akin to Lamarck's concept of linear progress up life's ladder, and ever since the many evils of social Darwinism were recognized and abandoned, evolutionary biologists have been extremely cautious about considering evolutionary progress of any sort. Indeed, we acknowledge that although the concept is firmly present and lively in our minds, it still took guts to put ink on paper and describe it. We take courage from Rosenzweig and McCord, who expressed this bold attitude over two decades ago:

> A recent symposium on progress (Nitecki, 1988) contains 14 contributions. Most of the contributors seem embarrassed by the use of the word 'progress' in evolutionary study. Only two really support it. (Rosenzweig and McCord, 1991)

In fact, progress is real, and amenable to definition. Ayala (1988) defined evolutionary progress as a 'trend that yields a *better* organism', where *better* is defined by the rules that govern the process of natural selection and provide more efficient biomechanics in design, larger distribution, and higher abundance (Gould, 1988b). We believe that the concept of progress must be now revived, precisely defined, and studied. Without it, we will continue to embrace the politically correct but scientifically naïve dogma that contingency dominates evolution. Moreover, we will also remain blind to the possibility that evolution may take a predictable direction under some circumstances. Predicting a trend is, needless to say, much better than describing a trend, for the former but not the latter yields understanding the machinery behind the pattern.

Why has Cope's Rule prevailed while its original theoretical context has foundered on these philosophical rocks? The explanation is probably its apparent simplicity, arising from a simple but easily overlooked circumstance: the fact that body size can change only along a single axis that ranges from small to large. Most traits can change in complex ways, and the underlying complexity is therefore easily recognized. Simpson (1953: 20) quoted Matthew (1915): '. . . to select a few of the great number of structural differences for measurement would be almost certainly misleading; to average them all would entail many thousands of measurements for each genus or species compared'. The simple, uniaxial nature of body size change is most probably what preserved Cope's Rule when its original context went down. The same simplicity makes it an attractive proxy for what Simpson called 'total change', and recent years have witnessed a remarkable proliferation of studies of evolutionary rates based on body size (Smith *et al*., 2010; Venditti *et al*., 2011; Raia *et al*., 2012, 2013; Lovegrove and Mowoe, 2013). Yet, there is no reason to believe that the causes of body size change should be in any way less complex than they are for more complex traits. Worse than this, increasing complexity could well be one of our best measures for evolutionary progress (Maynard Smith, 1988). By reducing trend recognition to a single axis (i.e. body size change), we thereby automatically remove any such evidence for progress.

In our view, the separation of Cope's Rule from its original context is unhelpful and unnecessary. Beyond considerations of historical accuracy and due credit, we argue that directional, active trends are a detectable and essential feature of macroevolution, and that this is the context where body size evolution, too, properly belongs. Here we refer to this feature as 'weak directionality'. Unlike Cope's strong concept of intrinsic progress, weak directionality does not entail any inner motion towards the perfection of life, but rather tight adaptation to the current circumstances. Yet, it recovers Cope's initial insight that life proceeds actively from the unspecialized towards the specialized. This implicitly entails improved complexity, and higher fitness under constant conditions. To us, the downside of progress is the same it was to Cope: increased specialization makes species less flexible, and the highly specialized are doomed to incur higher extinction risk once the conditions change.

It is important to note that the concept of weak directionality provides testable predictions, which we spell out below. By introducing weak directionality, we recast the definition of the Law of the Unspecialized in modern terms and clarify its connection with Cope's Rule in its present sense. We contend that both are valid and useful concepts, referring to different manifestations of the same evolutionary process, as Cope himself suggested.

WHAT THE LAW OF THE UNSPECIALIZED IS NOT

Some authors have rejected the Law of the Unspecialized on empirical grounds because of its failure to explain the great diversity of clades of specialized animals. As the rationale goes, if the specialized derives from the unspecialized, then diversification should be higher in the latter. For instance, Agrawal and Dorken (2001) assumed the Law of the Unspecialized is contradicted by the observation that 80% of phytophagous insects, one of the most diverse groups of organisms, are highly specialized herbivores. Similarly, Cope's idea of specialization as an evolutionary dead-end does not always hold. Clades of specialized organisms may occasionally originate unspecialized daughter clades (Kelley and Farrell, 1998; Brochu, 2001; Colles *et al.*, 2009; Hardy and Cook, 2010; Prendini *et al.*, 2010), although the opposite is far more common.

We argue that such criticisms of Cope's Law of the Unspecialized are mistaken, for two reasons. First, it is clear from Cope's own words (recast in modern terms) that the law deals with the rate of extinction, not the rate of diversification (i.e. speciation rate minus extinction rate). Second, there is a common misconception that diversification should be higher in clades of unspecialized taxa. We deal with this latter issue in a separate section below.

In the macro-evolutionary perspective of Cope, the law simply states that diversification proceeds from the unspecialized to the specialized within 'major' taxa (e.g. Cope's *lines of descent of Mammalia*, see above). Cope did not rule out that new clades could spring from specialized species – he simply stated that the opposite is more common 'in general', and this very view is largely echoed in the modern literature (Kelley and Farrell, 1998; Brochu, 2001; Hardy and Cook, 2010; Raia *et al.*, 2011).

Cope emphasized that 'overperfection of structure' (Cope's synonym for specialization) is 'unfavorable to survival'. Translated into modern terminology, this implies that extinction rates should be higher in specialized taxa. Cope's insight was correct and has been empirically confirmed over and over at all temporal scales, as we show below.

Essential to the causal connection between the Law of the Unspecialized and Cope's Rule is the specific observation that specialized morphotypes do not characterize the early history of clades, and that specialists tend to be, on average, larger than their ancestors, whether or not the ancestors were themselves specialized. This does not imply that small-bodied forms can be specialists, but rather that the opposite should be more common, thereby yielding a net trend towards increased body size.

CLADES START UNSPECIALIZED

During mass extinctions, specialist taxa are moderately more affected than generalist taxa (Jablonski, 2001). During periods of background extinction, rates are consistently higher in clades of specialized taxa (Norris, 1992; Baumiller, 1993; Van Valkenburgh *et al.*, 2004; Raia *et al.*, 2011, 2012). Finally, at the ecological scale, specialization is one of the factors jeopardizing species survival (Cardillo *et al.*, 2005; Liow *et al.*, 2009). It is thus conceivable that most clades, no matter how inclusive they are (i.e. whether they correspond to higher taxa or not), should typically start with unspecialized species (Gavrilets and Losos, 2009). Whereas this suggests that something like the Law of the Unspecialized may operate at different scales, weak directionality does not pertain to them all. Most important in our view, the Law does not operate after mass extinctions, the very events that Cope himself pointed to as pertaining to it.

Indeed, when a mass extinction takes place, surviving clades, which will eventually diversify in the recovery phase, are left with a few, mostly generalized taxa (Erwin, 1998; Jablonski, 2001). Besides being true of many marine lineages, this pattern was also famously true of dinosaurs after the demise of crurotarsan archosaurs in the late Triassic, and of mammals after the end-Cretaceous (K-Pg) event (Bininda Emonds *et al.*, 2007; Brusatte *et al.*, 2008a, 2011; Meredith *et al.*, 2011). Diversity recovery after mass extinction proceeds at an apparently predictable pace (Kirchner and Weil, 2000), together with (but not necessarily correlated with) morphological differentiation and expansion of the occupied niche space (Erwin, 2007; Sahney *et al.*, 2010), even in the simplest and most ancient ecosystems (Xiao and Laflamme, 2009). As new taxa appear, the available morphospace is thus filled up. At some point, the archetypal morphologies of specialized lineages are bound to appear and evolution can seem only to proceed from the unspecialized towards the specialized (Gavrilets and Losos, 2009; Sahney *et al.*, 2010). This dynamic does not entail any special drive towards specialization; it is, rather, to paraphrase Gould (1988a), evolution *radiating from* the unspecialized. As Jablonski put it: 'mass extinctions will not promote the long-term adaptation of the biota. In fact, mass extinction can break the hegemony of species-rich clades honed by millions of years of selection and thereby permit radiation of taxa little favored during the interval preceding the extinction event' (Jablonski, 1986; Rosenzweig and Ziv, 1999).

Interestingly and significantly, body size evolution does not follow the same path. Although most clades develop from small ancestors (Stanley, 1973), massive extinction crises are unselective with respect to body size (Erwin, 1998; Jablonski, 2001), and large-sized taxa within major clades tend to appear only late in the evolution of clades (Brusatte *et al.*, 2010; Smith *et al.*, 2010; Young *et al.*, 2010; Raia *et al.*, 2011, 2012). As observed at the largest taxonomic and temporal scales, the Law of the Unspecialized, while valid as a pattern, is probably a passive trend, a statistical necessity brought about by diversification from the unspecialized forms that make up a large fraction of mass extinction survivors.

THE BUILD-UP OF ECOLOGICAL SPECIALIZATION WITHIN ESTABLISHED CLADES: COPE'S RULE MEETS THE LAW OF THE UNSPECIALIZED

At the intermediate temporal scale, most adaptive radiations unrelated to major extinctions seem to be linked to the appearance of a new resource, the acquisition of a key innovation (Schluter, 2000), or to the demise of a major group, which is ecologically substituted (but usually not competitively excluded) by a rising new clade (Gould and Bradford Calloway, 1980; Hallam, 1987, 1991; Vermeij, 1987; Rosenzweig and McCord, 1991; Van Valkenburgh, 1999; Brusatte *et al.*, 2008b). Benton (1987) may have been the first to apply the term 'double-wedge' to this pattern of ecological replacement of an already declining clade by a rising one (see discussion in Rosenzweig and McCord, 1991). Whatever the causal relationships in each specific case (and we do not doubt that they vary considerably), this dynamic follows a path corresponding to the Law of the Unspecialized (Stephens and Wiens, 2003; Holliday and Steppan, 2004; Brusatte *et al.*, 2008a; Young *et al.*, 2010). Within the new dominant clade, body size tends to be negatively associated with species duration (Van Valkenburgh *et al.*, 2004; Raia *et al.*, 2011, 2012) and is unrelated to either taxic (Harmon *et al.*, 2003, 2010; Holliday and Steppan, 2004; Brusatte *et al.*, 2011) or morphologic diversity (Wesley-Hunt, 2005; Barrett and Rayfield, 2006; Brusatte *et al.*, 2008b, 2010;

Meloro and Raia, 2010). Yet, body size is positively associated with ecological specialization and extinction risk (McKinney, 1997; Cardillo *et al.*, 2005, Raia *et al.*, 2012).

As evolution fine-tunes species to the environment they live in, specialized forms appear and are, on average, larger and more extinction-prone than their ancestors. This is not just the micro-evolutionary operation of adaptation, but the macro-evolutionary operation of either the long-term effects of evolutionary novelties (Schluter, 2000; Young *et al.*, 2010; Raia *et al.*, 2011) or the diversification into a newly available ecological niche space, or both. This fine-tuning entails the tendency towards higher and more effective consumption rate or resources (Brown, 1995). Such a process might also ultimately be driven by the positive scaling of body mass with production rate (the conversion of energy into offspring) that applies when new and abundant resources are exploited (Hamilton *et al.*, 2011; Meiri *et al.*, 2011), which is typical with both key innovation and invasion of a new or newly vacated portion of the niche space (Okie *et al.*, 2013). In our view, this very scale is where weak directionality applies, and Cope's Rule in its modern sense becomes a special case of the (emended) Law of the Unspecialized.

At the micro-evolutionary scale, the trade-off between ecological tolerance and dominance is crucial to the evolution of specialization and provides a link to the Law of the Unspecialized. All species do best when using a particular habitat or resource, but their ecological dominance comes at the expense of their ability to use others. The evolution of specialization provides adaptation from high to low tolerance, and from weaker to stronger competitiveness with species arrayed along the tolerance axis. A species can generalize on the axis by being rather small so that it does not require a high input of the resource. If it does not face another species, it should evolve a size that balances the scarcity of patches at the high end with the reward that they offer. But as soon as a second species enters the community, the balance will change. Sometimes, the individual that is larger will be able to oust one that is smaller from a richer patch. In so doing, it alters the balances of both species. The larger one sees (in effect) a higher incidence of rich patches and it avoids poor ones (because they cannot support it). The smaller one avoids the richer patches because, in them, it tends to be driven off by the larger species. Both specialization and body-size variance (and mean) will increase. While a micro-evolutionary mechanism like this may be simplistic and possibly less than general, we believe that there should be some contiguity between micro- and macro-evolutionary patterns of specialization. Although we here focus on and enunciate the weak directionality pattern at the macro-evolutionary scale, we recognize the crucial importance of research that links it across different scales.

We contend that the weak directionality observed from small and unspecialized towards large and specialized is not a passive trend. It is rather a necessary path that evolution takes within a clade, provided it lives long enough, diversifies, and faces a sufficiently constant environment (Futuyma and Moreno, 1988). It is therefore unsurprising that highly specialized species are particularly common in the tropics, where environmental conditions tend to be more stable (Jocque *et al.*, 2010; Salisbury *et al.*, 2012) and clades have, in fact, greater age (Wiens *et al.*, 2011). In the tropics, species had time to co-evolve with their habitats, and found new habitats by virtue of this very co-evolution (Rosenzweig, 1992).

We underscore that the mode of evolution just described is distinct from what happens after major extinction events, where superficially similar results emerge from passive trends, controlled by the preferential extinction of specialized taxa, rather than the active evolution of specialized morphotypes within a thriving lineage.

The weak but pervasive directionality from unspecialized to specialized that is emerging from increasingly sophisticated studies of the fossil record may be taken as an updated and emended version of Cope's Law of the Unspecialized. It brings about the appearance of large-bodied forms, which at least among fossil bovids turned out to be exactly those short-lived, small-ranged species that embody the specialists (Raia *et al.*, 2011, 2012). And if, as we have argued here, the association of specialist traits and large body size is not coincidental, but driven by processes that can be named and studied empirically, Cope's Rule as understood today is still best regarded as a special case of the (emended) Law of the Unspecialized, just as it was for Cope himself. It is important to emphasize that the Law of the Unspecialized does not depend on Cope's Law. As shown in the fragment cited in the introduction, Cope considered the Law a matter of departure from the 'golden mean', implying that it might just as well involve size decrease. Why size increase nevertheless seems to be the prevailing pattern is a matter that we shall not explore here, although we note in passing that differential preservation of fossils favouring large size appears an unlikely explanation at least for terrestrial vertebrates (Damuth, 1982; Western and Behrensmeyer, 2009).

This reformulated Law of the Unspecialized generates at least two testable predictions: (1) however specialization is defined, it must increase over time during expansion of a clade; and (2) the law does not apply after a mass extinction, but should be linked to the introduction of new resources, to evolutionary innovations, or to the substitution of a diverse clade by an ecologically similar new clade.

CONCLUSIONS

Cope believed that evolution follows a predictable path driven by an inner motor akin to Lamarck's perfection of life. That idea is dead. Yet in our opinion, the empirical observation that evolution proceeds from the unspecialized towards specialization is, in itself, evidence of weak directionality. The Law of the Unspecialized ought to govern diversification of a new clade that may be invading a new portion of ecological niche space (which may be a novelty or may have become accessible owing to a key innovation) or substituting for another clade in a previously occupied portion of the ecological niche space (as exemplified by the double-wedge pattern).

We hope this paper might stimulate discussion about progress in evolution, and further research into the mechanisms behind weak directionality, at both the macro- and the micro-evolutionary scales.

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