

REVIEW: PART OF A SPECIAL ISSUE ON DEVELOPMENTAL ROBUSTNESS
AND SPECIES DIVERSITY

Species diversity vs. morphological disparity in the light of evolutionary
developmental biology

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- **Background** Two indicators of a clade's success are its diversity (number of included species) and its disparity (extent of morphospace occupied by its members). Many large genera show high diversity with low disparity, while others such as *Euphorbia* and *Drosophila* are highly diverse but also exhibit high disparity. The largest genera are often characterized by key innovations that often, but not necessarily, coincide with their diagnostic apomorphies. In terms of their contribution to speciation, apomorphies are either permissive (e.g. flightlessness) or generative (e.g. nectariferous spurs).
- **Scope** Except for *Drosophila*, virtually no genus among those with the highest diversity or disparity includes species currently studied as model species in developmental genetics or evolutionary developmental biology (evo-devo). An evo-devo approach is, however, potentially important to understand how diversity and disparity could rapidly increase in the largest genera currently accepted by taxonomists. The most promising directions for future research and a set of key questions to be addressed are presented in this review.
- **Conclusions** From an evo-devo perspective, the evolution of clades with high diversity and/or disparity can be addressed from three main perspectives: (1) evolvability, in terms of release from previous constraints and of the presence of genetic or developmental conditions favouring multiple parallel occurrences of a given evolutionary transition and its reversal; (2) phenotypic plasticity as a facilitator of speciation; and (3) modularity, heterochrony and a coupling between the complexity of the life cycle and the evolution of diversity and disparity in a clade. This simple preliminary analysis suggests a set of topics that deserve priority for scrutiny, including the possible role of saltational evolution in the origination of high diversity and/or disparity, the predictability of morphological evolution following release from a former constraint, and the extent and the possible causes of a positive correlation between diversity and disparity and the complexity of the life cycle.

Key words: Phenotypic plasticity, evolvability, generative key innovation, heteroblasty, heterochrony, large genera, life cycle complexity, modularity, permissive key innovation, species diversity, species robustness.

INTRODUCTION

Two important morphological indicators of a clade's evolutionary success are its diversity, as measured by the number of included species, and its disparity, this being an estimate of the lineage's occupancy of a suitably defined n -dimensional morphospace (Foote, 1997; McGhee, 1999; Wills, 2001; Erwin, 2007). Success in disparity does not necessarily go together with success in diversity. Arguably, developmental robustness is better mirrored in disparity than in diversity, but this expectation must be tested against the actual patterns of diversity and disparity of a number of plant and animal taxa. Unfortunately, the actual robustness of the developmental processes responsible for the production of relevant morphological traits is seldom available for representatives of otherwise interesting clades and must be tentatively extrapolated from evidence about other, in particular model, taxa.

HOT SPOTS OF EVOLUTION

Very large genera

Taxonomic ranks are arbitrary. Therefore, the fact that two taxa have been traditionally assigned the same rank is a poor justification for regarding them as comparable (e.g. Stevens,

1994; Minelli, 2000). On the other hand, convincing evidence in favour of their monophyly is all we need to fix our attention on those lower (say, genus) level taxa to each of which hundreds of species are currently assigned. Is there a way to explain their unusual diversity and, occasionally, disparity? The question has been traditionally addressed in terms of population genetics, geography and ecology, and much less in terms of evolutionary developmental biology (evolvability, plasticity, modularity, heterochrony). The latter perspective (about which see also Minelli and Fusco, 2012) is the focus of this review.

Examples will be taken from a diversity of large genera, animal and plant alike. All of the genera I will discuss are large or very large; additionally, some of them also exhibit unusually high degrees of disparity. Let us briefly introduce a gallery of taxa, before discussing them as actors in the evolutionary play.

The number of species given in this article for select plant and animal genera is mostly in accordance with the current version of the *Catalogue of Life* (indicated by this database's acronym appended to the species number, e.g. 2043_{CoL} for *Carex*); alternative sources are individually specified.

The meaning of 'large' is quite indeterminate. *Crocidura* (Mammalia Soricomorpha), with 172_{CoL} species, is enormous

if compared with the other mammalian genera. On the other hand, a genus like *Berberis* (including *Mahonia*: Laferrière, 1997a, b; Marroquín and Laferrière, 1997) (Berberidaceae), with some 531_{CoL} species, does not figure among the 40 largest genera of flowering plants listed by Frodin (2004).

Comparisons are difficult, not simply because of different traditions – along the splitter–lumper continuum – among taxonomists dealing with different groups, but also because of intrinsic differences in what just looks equivalent because of the universal use of Linnaean binomials (Minelli, 2000). Indeed, the 1599_{CoL} species recognized in *Senecio* (Asteraceae) or the 1565 species recognized in *Solanum* (Solanaceae) (solanaceae-source.org) are the taxonomic expression of a larger diversity than the numerically comparable, or even larger, numbers of agamospecies (or microspecies, or apomictic lines; cf. Mabberley, 2008) some taxonomists recognize as species in *Taraxacum* (Asteraceae, with 2285_{CoL}), *Hieracium* (Asteraceae, with 2202_{CoL}) or *Rubus* (Rosaceae, with 1557_{CoL}).

It is also problematic to compare species in vertebrates or in sexually reproducing flowering plants with species recognized in diatoms. Diatom diversity cannot be ignored, however, especially the very large genera *Navicula* and *Nitzschia*, with 1268 and 728 species, respectively (www.algaebase.org). At any rate, if these numbers are off mark, this is probably by defect rather than by excess. In a critical assessment of diatom taxonomy, Mann (1999) expressed the view that species boundaries in this group have been traditionally drawn too broadly; many nominal species probably include a number of reproductively isolated entities that may deserve recognition at the species level. However, recent application of barcoding methods to the identification of diatoms has found a good agreement between ‘species’ recognized by sequence gaps and taxa delimited according to the traditional criteria (Moniz and Kaczmarska, 2010).

Of course, genus size depends to some extent on the subjective choice of taxonomists. In most groups there has been little sympathy for large genera, for practical reasons at least. As a consequence, genera that have grown to include more than 1000 species have been sub-divided, sometimes pulverized. In the case of *Aphodius* (Coleoptera Scarabaeidae), the fragmentation into >100 genus-level taxa was mostly the result of the subjective choice to elevate former subgenera to the level of genera (Dellacasa *et al.*, 2001), without the support of a phylogenetic analysis. However, in the case of *Atheta* (Coleoptera Staphylinidae), the fragmentation of a formerly huge genus, a taxonomic choice accepted by some specialists but not by others [843 species are still listed under *Atheta* by Smetana (2004) for the Palaearctic species only, and representatives of this ‘genus’ abound in other biogeographic regions too], is now supported by a cladistic analysis (Elven *et al.*, 2010) that demonstrates the polyphyly of *Atheta* as traditionally intended. A trend towards the fragmentation of large genera was also visible in botany before the advent of cladistics; witness the fate of *Eupatorium* (Asteraceae) (King and Robinson, 1987). Following Linnaeus’ footsteps, botanists have frequently attempted to keep the number of genera sufficiently small so as to help in keeping their names (and, possibly, their diagnostic traits) in mind, a trend that has to some extent contributed to keep their average (and maximum) size fairly large (e.g. Cain,

1958; Humphreys and Linder, 2009). I agree with Humphreys and Linder (2009) in acknowledging that ‘[g]enera are groups of species . . . that in some respect may ‘exist’ in nature and in others exist simply by means of definition.’ However, my choice to use genera as the taxonomic units with which to discuss diversity and disparity does not imply that genera other than sister taxa are in any sense comparable; this is not a problem, as virtually no genus-to-genus comparison is necessary to articulate the arguments below. However, it is certainly desirable to restrict attention to taxa whose monophyly is supported by cladistic analysis, a test to which not all the genera discussed here have been subjected to date. In the only case of direct comparison (clades of flowering plants with nectariferous spur vs. clades without), an attempt has been made to restrict the comparisons to pairs of sister clades.

In many other instances, however, the trend is the opposite. Following recognition of the paraphyletic character of a large genus, formerly segregate genera are often merged within it.

Discussing the causes of changes in size of plant genera registered in the last few decades, Humphreys and Linder (2009) interpreted the current trend toward recognizing larger genera as a result of a return to study on a broad scale, rather than of incorporation of molecular data, and argued that conceptual change has a greater impact than change in data.

The sample of very large genera listed in Table 1, some from the animal, some from the plant kingdom, plus one from the Fungi, shows a nearly total absence of the model species hitherto popular in evolutionary developmental biology (evo-devo), or in developmental genetics.

Indeed, compared with the size of the genera in the table, the diversity of the genera to which most of the model species of developmental biology, genetics, genomics and evolutionary developmental biology belong is vanishingly small, the only exception being *Drosophila*, with 1529_{CoL} species, several of which are popular subjects of investigation in these disciplines; marginal in the latter is the presence of *Solanum* species, essentially restricted to *S. lycopersicum*.

Catalogue of Life lists only four species in *Caenorhabditis*, 38 in *Mus*, four in *Gallus*, 18 in *Xenopus*, 20 in *Danio*, nine in *Ciona*, six in *Heliocidaris*, 12 in *Arabidopsis*, 30 in *Antirrhinum*, and 22 in *Neurospora*; sensibly larger, however, is *Phalaenopsis*, with 71 species. Moreover, even this very limited amount of diversity has been poorly explored, if at all, from a comparative, or phylo-evo-devo (Minelli, 2009), point of view: the major exception is the species pair *Heliocidaris tuberculata* and *H. erythrogramma* (e.g. Henry and Raff, 1990; Wray and Raff, 1991; Henry *et al.*, 1992). In the case of *Arabidopsis*, relevant information for species other than *A. thaliana* (Koch *et al.*, 2008) is essentially limited to the sequence of *A. lyrata* (Hu *et al.*, 2011), but it is sensible to consider also the rapidly growing evidence concerning its close relative *Cardamine hirsuta* (e.g. Hay and Tsiantis, 2006; Barkoulas *et al.*, 2008). It will be interesting to see if the availability of the genome sequence for *Selaginella moellendorffii* (Banks *et al.*, 2011) will eventually help in understanding evolutionary mechanisms or opportunities involved in the radiation of the very large lycophyte genus *Selaginella* (684_{CoL} species).

To close this gallery of large taxa, a few huge genera of Diptera deserve a few more words, because they suggest very different ecological and biogeographic scenarios of speciation

TABLE 1. A sample of large genera from the animal, fungal and plant kingdoms

Genus	Taxonomic position	Number of species described ¹
Mollusca		
<i>Conus</i>	Gastropoda: Conidae	654 ²
Arthropoda Hexapoda		
<i>Stenus</i>	Coleoptera: Staphylinidae	Approx. 2500 ³
<i>Tipula</i>	Diptera: Tipulidae	2263
<i>Lasioglossum</i>	Hymenoptera: Halictidae	1725
<i>Cryptocephalus</i>	Coleoptera: Chrysomelidae	1700+ ⁴
<i>Onthophagus</i>	Coleoptera: Scarabaeidae	1672
<i>Otiorrhynchus</i>	Coleoptera: Curculionidae	1672
<i>Megaselia</i>	Diptera: Phoridae	1559
<i>Drosophila</i>	Diptera: Drosophilidae	1529
<i>Andrena</i>	Hymenoptera: Andrenidae	1495
<i>Anomala</i>	Coleoptera: Scarabaeidae	1229
<i>Culicoides</i>	Diptera: Ceratopogonidae	1228
<i>Eupithecia</i>	Lepidoptera: Geometridae	1171
<i>Opius</i>	Hymenoptera: Braconidae	1088
<i>Apanteles</i>	Hymenoptera: Braconidae	995
<i>Coleophora</i>	Lepidoptera: Coleophoridae	990
Vertebrata		
<i>Anolis</i>	'Reptilia' Squamata: Dactyloidae	392
<i>Haplochromis</i>	Osteichthyes: Cichlidae	229
<i>Eleutherodactylus</i>	Amphibia: Eleutherodactylidae	186
Fungi		
<i>Cortinarius</i>	Basidiomycota: Cortinariaceae	2745
Magnoliopsida		
<i>Astragalus</i>	Fabaceae	2682 ⁵
<i>Euphorbia</i>	Euphorbiaceae	2150 ⁶
<i>Carex</i>	Cyperaceae	2043
<i>Piper</i>	Piperaceae	1950
<i>Bulbophyllum</i>	Orchidaceae	1880
<i>Psychotria</i>	Rubiaceae	1856
<i>Begonia</i>	Begoniaceae	1605
<i>Senecio</i>	Asteraceae	1599
<i>Solanum</i>	Solanaceae	1565 ⁷
<i>Dendrobium</i>	Orchidaceae	1527
<i>Acacia</i>	Fabaceae	1434
<i>Croton</i>	Euphorbiaceae	1183
<i>Miconia</i>	Melastomataceae	1163
<i>Rhododendron</i>	Ericaceae	1135
<i>Peperomia</i>	Piperaceae	1350

¹According to the *Catalogue of Life*, if not specified otherwise.²Probably the largest genus of marine invertebrates (Kohn, 1991).³Putz (2008, 2010).⁴Chamorro (2014).⁵Other estimates: 3030 species (Frodin, 2004), 3270 species (Govaerts, 1995).⁶Bruyns *et al.* (2006).⁷solanaceaesource.org (accessed 4 April 2015).

in which changes in developmental mechanisms may have played a role. Unfortunately, among these genera, *Drosophila* is the only one for which extensive developmental (and evo-devo) information is available; in addition to *Drosophila*, only *Megaselia* has recently found a place in the lab, and limited to two species (*M. scalaris* and *M. abdita*).

The genus *Megaselia* (Phoridae) has been described by Bickel (2009) as an 'open-ended taxon'. At present, 1559_{CoL} species have been described, but these arguably represent just the tip of an iceberg. Disney (1994) estimated that the actual diversity may well be ten times as large. Thanks to the amazing range of lifestyles and feeding habits, a huge number of

Megaselia species can coexist in a very restricted area, and even in syntopy: witness the 56 *Megaselia* species recorded from Buckingham Palace Garden (Disney, 2001). On a slightly larger geographic scale, focused collecting revealed 331 species of *Megaselia* (112 of which had never been previously recorded for Sweden) in a burnt hemiboreal forest near Stockholm (Bonet *et al.*, 2006). This genus contains about half of the world species of Phoridae, the most biologically heterogeneous family of insects (Disney, 1990), and their habits are uniquely diverse: some *Megaselia* species are predators; others are parasitoids, kleptoparasites, phytophages. Their diet spans fungi, plants, other insects at every developmental stage, carrion, and many other substrates (Disney, 1994). Another very large genus of Phoridae, still less adequately known than *Megaselia*, is *Dohrniphora*, of which up to 50–100 species commonly coexist within a small area of tropical forest (Brown and Kung, 2007, 2010; Brown *et al.*, 2015).

In both respects, i.e. species diversity and ecological disparity, only *Drosophila* (including a few large segregate genera) can probably be compared with *Megaselia*. In the latter genus, however, no local (insular) spectacular radiation is known such as that of *Drosophila* and the related genus *Scaptomyza* on the Hawaiian archipelago: altogether some 1000 species of unusual morphological disparity colonizing an astonishing number of ecological niches.

Much less popular are other very diverse genera of Diptera, such as *Mycetophila* and *Hilara*, neither of which is known to be morphologically or ecologically as diverse as either *Megaselia* or *Drosophila*. *Mycetophila*, with 735_{CoL} species, is the largest among the Mycetophiloidea or fungus gnats, particularly diverse in the Holarctic Region. A single trap operating for a year at one site in a deciduous forest in Norway yielded 315 species of fungus gnats, including 49 sympatric species of *Mycetophila* (Kjærandsen and Jordal, 2007).

Hilara belongs to the Empididae (dagger flies or balloon flies) and includes 467_{CoL} species, but a very large number of additional species await description. Moreover, the limits of this genus towards other genera are problematic, as the diagnostic characters that separate these from *Hilara* appear to be well defined in certain regional faunas, but may not hold equally well elsewhere. Bickel (2009) estimated that the *Hilara* group could easily reach some 3000–4000 morphospecies.

Diversity vs. disparity

Despite the arbitrariness of any classification of lineages in terms of diversity and, still more, disparity, examples can be given of high diversity combined with low morphological disparity [e.g. *Festuca*, 651_{CoL} (Poaceae) among the plants (e.g. Hackel, 1882; Markgraf-Dannenbergh, 1980; Lange, 1998); *Stenus* (Coleoptera Staphylinidae) (see below) among the animals], and vice versa. In plants, an example of low diversity combined with high disparity is Gnetopsida (112_{CoL} species in all, of which 41_{CoL} are in *Gnetum*, 70_{CoL} in *Ephedra* and 1_{CoL} in *Welwitschia*, three genera so distantly related that they are often segregated in as many monogeneric orders); among animals, phylum Ctenophora, with 165_{CoL} species described thus far, is classified in 45 genera, 28 of which are monotypic; of these genera, three are not firmly assigned to a family, and

the others are classified in 27 families, of which ten are monotypic.

Examples of high diversity combined with high disparity include *Euphorbia* (Euphorbiaceae) (see below) and *Lobelia* (Campanulaceae, with 417_{CoL} species) among the plants, and *Megaselia*, as already mentioned, among the animals.

Paleontologists have remarked that morphological disparity is achieved early in the history of a clade, but it is still debated how much this depends on a subsequent stabilization (increased robustness) of the developmental system, or on decreasing ecological opportunities for the evolution and fixation of new morphologies, although both causes are likely to concur (Zelditch *et al.*, 2003; Erwin, 2007; Hughes *et al.*, 2013).

Key innovations

Successful clades are often described as originating from the emergence of key adaptations that have substantially (sometimes dramatically) improved their success in comparison with their closest relatives. However, positive evidence supporting the actual role of a putative key innovation in fostering a clade's success in terms of diversity is rarely available, and the actual support for the hypothesis that a given feature is a key adaptation is just its positive correlation with a clade's larger species diversity, compared with a sister clade in which the same feature did not evolve. This critical remark is largely similar to Richardson and Chipman's (2003) definition of developmental constraint in terms of positively biased frequency of occurrence of a process, or a correlation between ontogenetic processes.

Apomorphies diagnostic of a species-rich clade may have played different roles in the evolutionary processes that culminated in the clade's current diversity. Basically, with respect to a clade's diversity, we can distinguish between permissive and generative apomorphies. A permissive apomorphy is a feature with only an indirect effect on the rate of speciation, the latter being mainly dependent on specific features of the geographic and ecological landscape in which the clade is evolving.

An example is the reduction of wings in many insect groups (and also in some clades of birds), very often associated with a life on oceanic islands (birds and insects alike) or mountain tops (insects only). In those geographic settings, a very reduced vagility is likely to be positively adaptive (e.g. Carlquist, 1965, 1974), but its effects on speciation are clearly indirect. Flightlessness involves reduced vagility, thus reduced gene flow between populations and eventually the divergence of the latter, in a classic allopatric scenario. This is the path through which wing reduction or loss may eventually emerge as responsible for the huge number of species-level taxa, e.g. in many beetle genera, especially among the ground beetles and the weevils. For example, 966_{CoL} species are recognized in *Carabus* (Carabidae), 1672_{CoL} in *Otiorrhynchus* (Curculionidae) and hundreds of microgeographically distributed taxa are found in several groups of periteline weevils, in *Trigonopterus* (also Curculionidae) (Riedel *et al.*, 2013, 2014), etc. Insular flightlessness has also evolved many times in birds; in particular, multiple times within the rails (Rallidae). In this family, 53 species (some of which have become extinct in the last four

centuries) are known only from islands, including New Guinea and Madagascar, and, of these, as many as 32 species, the vast majority of those living on remote oceanic islands, are (or were) flightless or nearly so (Taylor, 1996).

In contrast, a generative apomorphy provides a clade with the access to an environmental resource positively involved in speciation: this is often the case of plants evolving a nectariferous spur or another feature of the flower that enhances attractiveness to pollinators and opens the way to the evolution of specialized inter-relationships with the latter that may enhance the rate of speciation.

With some 2000 species (1967_{CoL}; >2150 according to Bruyns *et al.*, 2006), *Euphorbia* is the second largest genus of flowering plants, second only to *Astragalus* (2682_{CoL}). The origin of the genus has been estimated at approx. 42.5 million years ago (Mya; van Ee *et al.*, 2008). The huge species diversity within this genus is accompanied by an extraordinary morphological disparity. *Euphorbia* includes geophytes, herbs, shrubs, understorey and canopy trees, as well as succulent and xerophytic forms. The whole group is nevertheless characterized by a distinct synapomorphy, the cyathium: this is an inflorescence, somehow mimicking a typical individual flower, formed by reduced male and female flowers within a cup-shaped involucre of bracts (Hoppe and Uhlarz, 1982; Steinmann and Porter, 2002; Prenner and Rudall, 2007; Prenner *et al.*, 2008; Horn *et al.*, 2012; Dorsey *et al.*, 2013).

The cyathium has been regarded as *Euphorbia*'s key innovation because it would have facilitated a transition from wind pollination to insect pollination, thus opening up the possibility of increased speciation rates (Croizat, 1937; Webster, 1967; Horn *et al.*, 2012).

Building upon the cyathium, the *Pedilanthus* clade of *Euphorbia* has evolved a cyathial nectar spur. It would be reasonable to expect this trait to have functioned in turn as a key innovation, similar to the floral spur of other plant clades. Multiple independent origins of floral spurs throughout the angiosperms are indeed correlated with increased rates of species diversification (Hodges, 1997): compare *Aquilegia* (108_{CoL} species) vs. *Semiaquilegia* (1_{CoL}) (cf. Hodges and Arnold, 1995), *Delphinium/Aconitum* (801_{CoL}) vs. *Nigella/Actaea/Cimicifuga* (55_{CoL}), Fumarioideae (450_{CoL}) vs. *Hypecoum* (17_{CoL}), and Tropaeolaceae (95_{CoL}, all in *Tropaeolum*) vs. Akaniaceae (1_{CoL}).

Generalizations, however, are risky in this field. In the case of *Pedilanthus*, the hypothesis of a correlation between the evolution of the cyathial spur and an increased diversification rate lacks statistical support (Cacho *et al.*, 2010)

Some putative key adaptations are quite generic and have thus probably evolved independently many times, among closer or distant relatives. Such are phytophagy in insects (e.g. Mitter *et al.*, 1988) and viviparity in fishes (Slowinski and Guyer, 1993). Other putative key adaptations are much more specific and often coincide strictly with putative apomorphies of one of the large genera. Of course, complex innovations do not emerge instantly from scratch and probably derive, as a rule, from a fortuitous, but eventually winning association of novel structural and functional modules first evolved independent from one another. This is suggested, for example, by the study of Anker *et al.* (2006) on the evolution of the unique 'snapping claws' of a clade of alpheid shrimps.

Building on a morphology-based phylogeny of an extensive species sample of these crustaceans, Anker *et al.* (2006) reconstructed a three-step evolutionary scenario. In the first step, several features of the would-be snapping claw evolved independently multiple times, thus showing distinct evolutionary and developmental modularity. These features include asymmetry, folding, inverted orientation, and the evolution of adhesive plaques that enhance claw cocking, as well as tooth-cavity systems on opposing claw fingers. Eventually, these features end up as pre-adaptations for snapping. A functional snapping claw emerged in a second step, and this happened only once, in contrast to the multiple parallel emergence of the individual modules by integration of which the snapping claw resulted. Over 550 species belong to the clade [*Synalpheus* + (*Alpheus* + satellite genera)] characterized by this innovation, and its explosive radiation is attributed by the authors to this key innovation. The third step in this evolutionary reconstruction is represented by the emergence of adhesive plaques (claw cocking aids), which evolved multiple times, and within snapping alpheids characterizes the most diverse clade (*Alpheus* + derivative genera).

However, it is not necessarily the case that key innovations coincide with apomorphies characterizing successful large genera. Within the huge family Staphylinidae (rove beetles), the approx. 2500 species (Puthz, 2008, 2010) of the genus *Stenus* are characterized by their unique labium, transformed into a protrusible device for capturing prey, like the ‘mask’ of the dragonfly nymphs. Another 200 species have been traditionally grouped in a distinct genus (*Dianous*), universally regarded as the closest relative to *Stenus*, but lacking the labial apomorphy and thus potentially paraphyletic with respect to *Stenus* (Puthz, 1981). A recent molecular phylogenetic study (Koerner *et al.*, 2013), however, has reversed this picture: *Dianous* is robustly nested within *Stenus* as a clade characterized by the loss of the peculiar structure of the labium. Despite this reversal, the clade has nevertheless been able to diversify into a remarkable number of species.

The closest relatives to several very large genera are frequently small, often monotypic genera; in several instances, this translates into the recognition of families within which a very large percentage of species belong to one or a few large genera. For example, approx. 40 % of the species total in the Cyperaceae belong to the genus *Carex*, the radiation of which (2043_{CoL} species) was possibly launched by high rates of chromosome rearrangements via fission, fusion and translocation, unusual otherwise in the Cyperaceae, perhaps associated with a global cooling period between the Late Eocene and the Oligocene that fostered the genus’ adaptive radiation to temperate climates (Escudero *et al.*, 2012). Even more impressive are the overdominance of *Begonia* (1605_{CoL}) in the Begoniaceae, within which it is accompanied only by the monotypic *Hillebrandia*, and the very successful radiation of *Piper* (1950_{CoL}) and *Peperomia* (1350_{CoL}), in addition to which in the Piperaceae there are only another 22 species in four genera. In the Lepidoptera, the family Coleophoridae includes 1037_{CoL} species, of which 990_{CoL} are in *Coleophora*, whereas the 47 additional species are classified in 18 genera, nine of which are monotypic. In the Gastropoda, the family Conidae includes, besides the very large genus *Conus* (654_{CoL} species), only 39 more species in 25 genera, 16 of which are monotypic.

EVOLVABILITY

With the advent of evolutionary developmental biology, evolvability, i.e. the ability to produce heritable phenotypic variation (Pigliucci, 2008), has taken a central role in explanations of evolutionary change (Hendrikse *et al.*, 2007), together with an increasing appreciation of the complex relationships between genotype and phenotype (the so-called genotype→phenotype map), which are now largely acknowledged to be far from uniform and mostly non-linear (e.g. Alberch, 1991; West-Eberhard, 2003; Pigliucci, 2010). In other terms, rarely, if ever, does one gene correspond to one phenotypic trait, and vice versa. As a rule, a diversity of phenotypic traits are affected by the expression of one gene (pleiotropy), and different genes, or genetic cascades, may translate into indistinguishable phenotypes (convergence and/or redundancy).

Therefore, in addressing the issue of the evolution of clades with a particularly high degree of diversity or disparity, it is not sensible to ask questions uniquely in terms of available niches and diverging adaptations. The landscape of evolutionary change is distinctly anisotropic and even, to some extent, discontinuous (e.g. Theißen, 2006, 2009; Minelli *et al.*, 2009).

Release from constraints

Within the Chilopoda (centipedes), the clade Scolopendromorpha is characterized by the presence of either 21 or 23 pairs of legs, the only exception being *Scolopendropsis duplicata*, with 39 or 43 pairs of legs, probably derived in a recent ‘leap’ from an ancestor very similar to *Sc. bahiensis*, a species whose individuals have either 21 or 23 pairs of legs (Minelli *et al.*, 2009). The number of leg pairs is thus open to change in scolopendromorph centipedes, but it is also very stable: witness the existence among the approx. 700 extant species of this single exception to the otherwise universal limitation to 21 or 23 pairs of legs, reinforced by the presence of 21 pairs of legs already in *Mazoscolopendra richardsoni* from the Upper Carboniferous (Edgecombe, 2011). However, a transition to 21 pairs of legs is an apomorphy of the Scolopendromorpha, the plesiomorphic number of leg pairs within centipedes being 15; this was probably fixed in the Devonian or earlier and has been retained, without exceptions, in Scutigermorpha, Craterostigmomorpha and Lithobiomorpha, thus showing a truly remarkable evolutionary robustness. However, within the clade that had already undergone the transition to 21 or 23 leg pairs, a lineage subsequently evolved, probably in early Mesozoic, where the previous constraints fixing leg pair number were somehow broken, thus giving rise to the Geophilomorpha, within which the leg pair number was first in the order of 41, 43 or 45, but subsequently expanded variation, with a reduction down to 27 and notably an increase up to 191 leg pairs. A remarkable constraint remained in this evolutionary diversification, in that leg pair numbers are always limited to odd numbers, it is nevertheless remarkable how diverse the geophilomorph clade became following the initial release from the former constraint on segment number.

The same trend is observed in many other cases. Eukaryotic cilia or flagella are mostly endowed with an axoneme composed of two central microtubules surrounded by a circle of nine doublets (9 + 2 arrangement). This structure is remarkably

stable among the eukaryotes, but it is far from being universal. Interestingly, departures from it have sometimes opened the way towards the evolution of an extraordinary diversity of arrangements, as in the sperm flagellum of gall midges (Diptera Cecidomyiidae), with up to 2500 doublets in the case of *Asphondylia ruebsaameni* (Lanzavecchia *et al.*, 1991; Mencarelli *et al.*, 2000).

Another example is provided by the antennal articles of the Coleoptera. Here, the plesiomorphic number of 11, widely conserved throughout the order, has been frequently reduced to lower numbers, e.g. to ten in 46 families, to nine in 31, to eight in 22, and even to three in five families and to two in two families (Minelli, 2004). Much more robust is the number of beetle antennal articles in respect to increase beyond 11, mostly limited to one extra article (as in some Anthicidae, Cerambycidae and Chrysomelidae) and very rarely extended to higher numbers, e.g. >20 in some fireflies (Lampyridae) and up to approx. 40, a deviation only found in some Cerambycidae and Rhipiceridae. More interesting in a discussion of the evolutionary effects of a release from a developmental constraint is the wide range of phenotypes evolved in some lineages: in Dermestidae, the antennae can have any number of articles between five and 11, in Chrysomelidae any number between three and 12, and in the pselaphine Staphylinidae any number between two and 11.

In many rapid radiations, the explosion of phenotypes is essentially restricted to large variation in a well circumscribed module. This is often true of the copulatory structures, especially the male ones, as shown by a large number of insect groups, and by the helminthomorph millipedes (Minelli, 2015a). Interestingly, the amazing diversity of form found in the genitalia of most representatives of a clade does not imply that the phenomenon is shared by all its members. For example, in millipede genera such as *Orthomorpha* (Jeekel, 1963; Likhitrakam *et al.*, 2011), *Coromus* (Hoffman, 1990), *Sinocallipus* (Stoeb and Enghoff, 2011) and *Anadenobolus* (Bond and Sierwald, 2002), interspecific differences in somatic features are more conspicuous than in male genital appendages.

Single modules are also involved in the spectacular radiations of cichlid fishes in the African rift lakes, especially the feeding apparatus, that can be described as an evolutionary key factor facilitating the explosive radiation, based on relatively simple morphological alterations (Cooper *et al.*, 2010; Wanek and Sturmbauer, 2015).

According to some authors (e.g. Gittenberger, 1988), another developmentally simple change such as the inversion of chirality has contributed to speciation in some gastropod genera, e.g. in *Partula* (the object of a pioneering study of speciation: Crampton, 1916), with 150_{CoL} species described from islands between New Guinea and French Polynesia.

Much of the species diversity within the huge scarab genus *Onthophagus* (1672_{CoL} species) is also concentrated in a couple of modules, the cephalic and prothoracic horns, a conspicuous morphological novelty (repeatedly evolved in the Scarabaeoidea) in the evolution of which phenotypic plasticity (see below) is also involved (e.g. Wasik and Moczek, 2011).

Parallelism and convergence

Evolutionary developmental biology has shifted the focus from the survival of the fittest to what has been dubbed as the

arrival of the fittest. In other terms, rather than focusing on the differential selective value of traits, research is centred on evolvability. It is by now very clear that phenotypes that would enjoy remarkable fitness are not found in nature because the developmental systems forbid their emergence. On the other hand, a positive bias in the landscape of evolvable forms can help explain parallelism and convergence.

In the last decades of the 20th century, a strict focus on phylogeny reconstruction has overshadowed homoplastic features, simply regarded as noise obfuscating the phylogenetic signal provided by synapomorphies, but it is time to revisit parallelism and convergence as evolutionary phenomena. Towards the turn of the century, Moore and Willmer (1997) re-opened investigations on convergent evolution by providing a detailed overview of its occurrence in invertebrates; soon thereafter, Conway Morris (e.g. 2003a, b, 2006) described convergence as a pervasive phenomenon in evolution, to the extent of allowing some degree of predictivity of long-term evolutionary trends.

In this endeavour, phylogenetic reconstruction provides the necessary scaffold, in the form of trees, against which to study character evolution, while evo-devo can provide precious insight into the evolvability of relevant traits. Studies specifically addressing this kind of question are not numerous, but it is easy to offer examples worth investigation. Specifically, in the context of this article, biased evolvability can help explain the frequent cases of multiple, parallel evolution of specific traits in species-rich and morphologically well-diversified genera. Within these taxa, sections or subgenera have often been recognized, based on these traits, but the multiple evolution of those traits has eventually been revealed by phylogenetic reconstructions based on molecular evidence.

Within *Euphorbia*, several morphological traits used in previous classifications have developed in parallel in different lineages. For example, succulence developed perhaps as many as 14 times in the genus (Steinmann and Porter, 2002; Bruyns *et al.*, 2006; Zimmermann *et al.*, 2010; Horn *et al.* 2012), and the annual life form developed independently several times from perennial ancestors in different clades of the subgenus *Esula*: nine shifts from perennials to annuals in five sections were revealed by a plastid tree, and one more by an internal transcribed spacer (ITS) tree (Frajman and Schönswetter, 2011). Multiple independent transitions from perennial to annual have also been demonstrated in other large genera, e.g. *Astragalus* (Liston and Wheeler, 1994) and *Veronica* (Albach *et al.*, 2004). Careful phylogenetic analysis is obviously needed; witness the rejection by Tank and Olmstead (2008), based on a molecular phylogeny, of Chuang and Heckard's (1991) hypothesis, based on morphology inclusive of chromosome number, of multiple perennial to annual transitions in *Castilleja* (Orobanchaceae).

The rampant homoplasy found in many large genera suggests a strong bias in evolvability. This is a question that deserves closer scrutiny, e.g. in *Begonia*, where a number of sections were traditionally established, based on single characters that have eventually proved to be homoplasious, e.g. undivided placenta lamellae (section *Reichenheimia*) and fleshy pericarps (section *Sphenanthera*) (Thomas *et al.* 2011). Within the same genus, molecular phylogenies indicate at least eight independent transitions from herbaceous to woody, possibly based on genetic or genomic changes similar to those underlying the

corresponding transition in a diversity of plant clades (Kidner *et al.*, 2015).

In many instances, multiple evolution within a lower clade of largely similar phenotypes can be due to ‘latent homologies’, i.e. to a ‘re-awakening’ of existing but unexpressed homologous developmental mechanisms.

However, due to the complexity of the genotype→phenotype map, convergent phenotypic evolution is not necessarily associated with parallel or convergent genotypic evolution. Some studies are available, still too fragmentary to suggest any generalization, but nevertheless interesting in suggesting the frequent parallel involvement of changes in orthologous genes. Frankel *et al.* (2012) examined the genetic basis of a detailed phenotypic convergence between two species that diverged approx. 40 Mya, *Drosophila sechellia* and *D. ezoana*, and found that in both species the convergent phenotype was probably caused by *cis*-regulatory evolution of the same gene – *shavenbaby* (*svb*).

Little is known about the genetic basis of convergent traits that originate repeatedly over broad taxonomic scales, but in this case too convergent phenotypic evolution can be the visible expression of convergent genotypic evolution. Fish electric organs have evolved six times, and there are large differences between the lineages involved in the morphology of electric organ cells; nevertheless, similar transcription factors and developmental and cellular pathways are involved in the evolution of these organs, as demonstrated by the study of Gallant *et al.* (2014) involving five species representing three different orders: Gymnotiformes (*Electrophorus electricus*, *Sternopygus macrurus*, *Eigenmannia virescens*), Osteoglossiformes (*Brienomyrus brachyistius*) and Siluriformes (*Malapterurus electricus*).

Evolvability and disparity

The evolvability of major morphological traits, whose scanty robustness to developmental (and evolutionary) change translates into astounding examples of disparity within a genus, is arguably easier to study in plants than in animals. An obvious example is the evolution of insular woodiness in many lineages represented on the larger land masses only by herbaceous or at most shrubby species. Insular woodiness can precede the settlement on islands, as has been argued for the Hawaiian *Psychotria* (Rubiaceae) (Nepokroeff and Sytsma, 1996) and the Hawaiian lobelioids (Campanulaceae) (Givnish *et al.*, 1996), or follow the settlement on islands, as in the case of the Hawaiian silverswords (Asteraceae). The amazing diversification of the silversword alliance into the modern species of rosette plants, trees, shrubs, mat plants, cushion plants and lianas has occurred in a relatively short time span, i.e. within the last 6 million years, corresponding to the history of the modern high Hawaiian islands (Baldwin, 1997). Insular woodiness is no less conspicuous in an older archipelago, the Canary Islands, than in the Hawaii. Of their flora, no less than 220 native species of flowering plants are woody, as a result of at least 38 independent shifts from herbaceous growth, involving 34 genera in 15 families (Lens *et al.* 2013), but several lineages have reversed here from woodiness to herbaceousness: this transition occurred at least three times in *Echium* (Boraginaceae) (García-Maroto *et al.*, 2009) and once in *Sonchus* (Asteraceae) (Kim *et al.*, 2007).

Parallel transitions from a rosette habit to the very peculiar unifoliate growth habit characteristic of many species of this genus has occurred several times in *Streptocarpus* (Gesneriaceae), and reversals have also occurred. Noting that intermediate architectures are additionally found, Möller and Cronk (2001) remarked that a notable phenotypic plasticity seems to be a characteristic of the acaulescent clade and to underlie its great lability of form.

Instances of reversal of phenotypically conspicuous transitions are also known outside the flowering plants. An example from the lichens is provided by the Roccellaceae, a clade highly supported as monophyletic, within which the fruticose growth habit has evolved multiple times and has been also lost repeatedly (Tehler and Irestedt, 2007). Moving to animals, within the katydids (Orthoptera Tettigoniidae), the forewings evolved into leaf-like tegmina at least six times independently, and this trait was subsequently lost several times, showing the high evolvability of the level of mimicry and tegmina shape in this insect family (Mugleston *et al.*, 2013).

PHENOTYPIC PLASTICITY

One of the features of the genotype→phenotype map that probably plays an important role in generating diversity is phenotypic plasticity (or developmental plasticity: the two terms are regarded here as synonymous, in agreement with West-Eberhard, 2003), i.e. the production from the same genotype of alternative phenotypes in response to different environmental conditions (reviewed in Fusco and Minelli 2010).

A diversity of evolutionary processes are actually involved in the production and eventual fixation of phenotypic plasticity (Minelli, 2015b). We can collectively refer to them under the term of genetic accommodation, as the process by which a phenotype first produced in direct response to an environmental condition eventually becomes genetically encoded (e.g. West-Eberhard, 2003, 2005b; Moczek, 2007, 2008; Moczek *et al.*, 2011; Schlichting and Wund, 2014). This embraces a diversity of possible mechanisms. Specifically, there is genetic assimilation (Waddington, 1953) when selection progressively erodes plasticity, eventually obtaining the fixation of a genetically encoded phenotype (Robinson and Dukas, 1999; Pigliucci and Murren, 2003). Under the name of the Baldwin effect (Baldwin, 1896; see also Crispo, 2007; Badyaev, 2009) are classified instead the events in which plasticity enhances the survival of an individual in a new environment and selection subsequently favours the accumulation of heritable variation in the direction of the plastic response. Perhaps more interesting, in the context of the problems discussed in this review, are the examples of accumulation and eventual release of cryptic variation. This happens when a population is not confronted for a more or less long time with environments in which its phenotypic plasticity would have expressed some of the possible phenotypes; a part of the population’s genetic variation is thus subject to relaxed selection and eventually accumulates despite not being expressed (Gibson and Dworkin, 2004; Le Rouzic and Carlborg, 2008; Lahti *et al.*, 2009; Snell-Rood *et al.*, 2010; Van Dyken and Wade, 2010). However, an environmental change can eventually unmask this cryptic variation and expose

it again to selection, with the possible release of novel phenotypes (Barrett and Schluter, 2008; Pfennig *et al.*, 2010).

The actual role of phenotypic plasticity in phenotypic diversification is controversial (Schlichting and Pigliucci, 1998; Pigliucci, 2001; Moczek, 2010; Wund, 2012). On the one hand, plasticity hampers divergence by permitting organisms to adjust to different environmental conditions, and preventing isolation between populations as a consequence of environmental heterogeneity. Plasticity also permits the evolution of alternative phenotype expression under alternative environmental conditions, causing diversification within species, in the form of alternative morphs, without increasing species richness. However, as shown by Moczek (2010), plasticity also creates novel opportunities for diversification, including speciation, by providing novel targets for evolutionary processes, by creating novel trade-offs and by increasing genetic variation and divergence.

Plasticity can also have a direct impact on speciation. According to West-Eberhard (1986, 1989, 2003), ecologically distinct forms can actually evolve in different environments, building onto the initial appearance of alternative morphs in a phenotypically plastic species. According to this hypothesis (see also Pfennig *et al.*, 2010; Fitzpatrick, 2012), whenever these phenotypes turn out to be positively adapted to the different environments, a way is open to rapid speciation. In a first step, environmental differences promote the fixation of the alternative phenotypes in different populations without the involvement of genetic changes, or only with minor ones. The following step involves divergent selection, often acting through a reduction of plasticity, i.e. via genetic assimilation. Eventually, adaptive divergence (or reinforcement, in the case of secondary contact between diverging populations) culminates in reproductive isolation.

West-Eberhard (2005a) and Schwander and Leimar (2011) contrasted two scenarios, ‘plasticity first’ (or ‘genes as followers’) and ‘genetic polymorphism first’ (or ‘genes as leaders’), based on whether in the evolutionary sequence plasticity or genetic polymorphism, respectively, is more important at the start. According to Schwander and Leimar (2011), both sequences are equally probable, with a possible dominance of one or the other for specific trait types. These authors have used a phylogenetic perspective to assess the prevalence of either kind of sequences in species groups traditionally used in the study of alternative phenotypes (Moran, 1992; Roff, 1996; West-Eberhard, 2003; Whitman and Ananthkrishnan, 2009), e.g. colour polymorphisms, predator-induced phenotypes, alternative mating strategies and sex determination. The best evidence for genes as leaders or followers in the evolution of alternative phenotypes was found in systems involving sex determination in tetrapod vertebrates, normal vs. reduced wing morphs in insects, and social insect castes. Transition between genetic and environmental sex determination is often easy. Among the examples given by Schwander and Leimar (2011) are instances of sex reversal following exposure to extreme temperatures, occurring in species in which sex is otherwise determined genetically (Quinn *et al.*, 2007; Radder *et al.*, 2008), and the occurrence of sex chromosomes in species with environmental sex determination (Shine *et al.*, 2002). The best investigated system, however, is probably wing polymorphism in the pea aphid *Acyrtosiphon pisum* (Brisson, 2010). In this species, adults of either sex can be either winged or wingless, but in the

male the difference is controlled by a single-gene polymorphism, whereas in the female this is an environmentally controlled polyphenism (Braendle *et al.*, 2005a). However, the protein encoded by the gene (*aphicarus*) controlling wing development in the male is also involved in the female aphid’s developmental response to the environmental stimulus involved in the production of the wings (Braendle *et al.*, 2005b).

MODULARITY AND HETEROCHRONY

Heterochrony is defined (Klingenberg 1998) as evolutionary change in rates and timing of developmental processes. This can be described from different points of view corresponding to two main alternative approaches, growth heterochrony and sequence heterochrony. The classical approach (e.g. Gould, 1977; Alberch *et al.*, 1979; McNamara, 1986, 1995; McKinney, 1988; McKinney and McNamara, 1991) refers to growth heterochrony, developmental changes in size and shape relationships. Here, a descendant is described as pedomorphic if in the adult condition it resembles a juvenile form of an ancestor or a close relative taken as reference, and as peramorphic if the descendant develops through a juvenile form similar to the adult of his ancestor or relative. In the last two decades, most of the studies on heterochrony have addressed instead sequence heterochrony, i.e. changes in the position of a developmental event relative to other events in the same ontogenetic sequence (Smith, 1996, 2002).

Diversity dependent on heterochrony

Species diversity may increase via heterochrony, but it is not clear if this effect can result in a mass increase in species numbers. Examples investigated through a careful character analysis, or suggested by sound cladistic analysis, are scattered throughout the tree of life; most of them come from small genera, but with interesting exceptions. These are probably more frequent than current taxonomy may suggest, because strongly heterochronic derivatives of a large genus can be morphologically so peculiar as to have suggested placing them in segregate genera, a taxonomic treatment from which they can be rescued only following a sound phylogenetic analysis. This is, for instance, the case of the clubmoss *Phylloglossum drummondii*, the only species in its genus, but actually shown by Wikström and Kenrick’s (1997) phylogenetic analysis to be a progenetic derivative of *Huperzia*, a genus with approx. 300 species, if circumscribed according to Øilgaard (1987).

To take instead an example from a less problematic taxon of remarkable size, heterochrony appears to have played a key role in the evolution of *Niphargus* (Fišer *et al.*, 2008), which is the most diverse genus of freshwater amphipods, with 311 species (Luštrik and Turjak, 2013).

Heterochrony reveals modularity of anatomical construction; modularity, in turn, provides scope for a multiplication of phenotypes. In *Bauhinia* (Fabaceae), a genus of 345_{CoL} species, for example, the individual petals and stamens behave as separate homologues, thus within the genus there are species like *Bauhinia blakeana*, with five petals and three fertile stamens, alongside species like *Bauhinia divaricata*, with two petals and one functional stamen only, and still others with different

numbers and numerical combinations of floral parts (Wunderlin, 1983; Chen *et al.*, 2010).

In plants, heterochrony can produce changes from the homostylous to the heterostylous condition, and vice versa. *Amsinckia* (Boraginaceae) includes both homostylous and heterostylous species. Heterostyly, probably an apomorphy of this genus, is produced by heterochrony (Li and Johnston, 2010), as shown by the growth curves for the pistil and the stamens. The growth curve of the stamen filament is identical in the homostylous and in the pin flowers of the heterostylous species, and the growth curve for the pistil is identical in the homostylous *A. vernicosa* and in the thrum flowers of the related heterostylous *A. furcata*. A few *Amsinckia* are homostylous, as a consequence of character reversal. The homostylous *A. vernicosa* has evolved from a heterostylous ancestor comparable with *Amsinckia furcata*, and the homostylous *A. gloriosa* has evolved from a heterostylous ancestor comparable with *A. douglasiana*.

Speciation by heterochrony can occur multiple times within a genus, in parallel (i.e. always by pedomorphosis or always by peramorphosis), or in the opposite direction, as in a group of scincid lizards of the genus *Plestiodon* (formerly in *Eumeces*), where *P. gilberti* and *P. lagunensis* are regarded by Richmond and Reeder (2002) as peramorphic and pedomorphic members, respectively, of the *P. skiltonianus* clade.

It would be interesting to know to what extent heterochrony is involved in the diversification of other large genera, plant and animal alike. An attractive candidate for experimental studies is *Megaselia*. The embryonic development in *M. scalaris* is amazingly short, <24 h, i.e. significantly faster than in the model species *M. abdita* and *Drosophila melanogaster*. Comparison with these species reveals that heterochronic shifts, together with simultaneous morphogenetic movements and compression of individual stages, contribute to the very rapid embryogenesis of *M. scalaris* (Wotton, 2014). It is sensible to speculate that scrambling of developmental modules in this dipteran genus are probable, and possibly involved in generating its amazing diversity (and, perhaps, disparity too).

In plants, developmental phase transitions are controlled by microRNAs (Wu and Poethig, 2006; Poethig, 2009; Wu *et al.*, 2009; Huijser and Schmid, 2011; Yang *et al.*, 2011, 2013), and changes in this regulatory system (specifically, miR156 and miR172) have been suggested to facilitate rapid speciation (Jones *et al.*, 2014). Intraspecific divergence for heteroblasty is known in *Eucalyptus globulus* (Hamilton *et al.*, 2010; for the genetic control of heterochrony in this species, see Hudson *et al.*, 2014) and also in *Pinus canariensis* (Climent *et al.*, 2006).

Disparity dependent on heterochrony

Heterochrony can be involved in releasing a key innovation. This is arguably the case of a key innovation associated with the emergence of the Eutheria, the placental mammals. Their great evolutionary success, in terms of both diversity and disparity, compared with the Metatheria (marsupials) has perhaps been facilitated by differences in the timing and rate of differentiation of structures of the central nervous system relative to a specific sub-set of structures of the cranial skeleton and

musculature. In marsupials, the development of the central nervous system is considerably delayed in respect to certain elements of the cranium and the associated muscular system, whereas in placental mammals the morphogenesis of the central nervous system begins well before the differentiation of the head's somatic tissues (Nunn and Smith, 1997; Smith, 1997).

Diversity, disparity and the complexity of the life cycle

At a higher taxonomic level, some clades with high levels of diversity and disparity are characterized by a remarkable complexity of the life cycle. This is obvious in the case of parasites that complete their cycle through stages infesting two or more different hosts, and frequently also show a characteristic alternation between different forms of reproduction. This is the case, for example, of the flukes among the flatworms, and also of apicomplexan protozoans. Among the latter, >1000 species have been described in a single genus (*Eimeria*). Explosive diversity similarly characterizes parasitic fungi, the most diverse genus among which is *Puccinia*, of which the astronomical number of about 4000 species have been described (Kirk *et al.*, 2008). In all these instances, host specificity has certainly played an important role in fostering diversity, but life cycle complexity *per se* is likely to have contributed. This is suggested by the huge number of species evolved in the clade of holometabolous insects, where huge clusters of diversity are not limited to sub-clades with specialized feeding habits, either as parasitoids of other arthropods (the Tachinidae among the Diptera and many large families of Parasitica among the Hymenoptera), or as phytophages (e.g. most of the Lepidoptera, and the huge beetle superfamilies Chrysomeloidea and Curculionoidea). With the evolution of holometabolous development (the so-called 'complete metamorphosis'), the larva and adult of the same animal have vast opportunities to specialize in different niches, feeding modes and habitats, and the increased opportunities to specialize turn easily into increased opportunities to speciate (e.g. Jacobs and Renner, 1988; Moczek, 2010).

Control of development vs. control of form

Complex organs are often the structural modules in which is concentrated most of the morphological diversity characterizing the many species of large genera or families. The question is if, or how, morphological complexity and species-level differences are causally related. These complex and species-specific organs are often involved, more or less directly, in mate recognition and thus eventually in pre-zygotic isolation, but this does not address the question of the evolvability of these complex features.

The latter is a virtually unexplored area. Nevertheless, an interesting suggestion may come from the fact that organisms able to evolve structures more complex than their closest relatives often also have an unusually complex life cycle.

For example, among the metazoans there are remarkable examples of agreement between the complexity of post-embryonic development and the morphological complexity of the axis of the adult appendages (Minelli, 1996, 2003). The best example is probably found in the Meloidae (blister beetles),

with their different kinds of larvae developing along their unusually complex (hypermetabolous) life cycle. Interestingly, some blister beetles also have some of the most complex antennae of all Coleoptera.

In flowering plants, development is essentially articulated in a juvenile and a flowering phase, but in a number of clades, scattered through the orders and families, developmental complexity is higher due to heteroblasty, i.e. the articulation of the vegetative phase into temporal segments characterized by abrupt and substantial differences in leaf form or size, phyllotaxy, internode length, etc. (Goebel, 1889; Allsopp, 1966; Zotz *et al.*, 2011).

Interestingly, conspicuous forms of heteroblasty are present in several species-rich genera such as *Eucalyptus* and *Acacia*. These plants thus seem able to operate a fine control of their morphogenesis, and this in turn is possibly a developmental pre-condition facilitating their evolutionary diversification, as already anticipated by Goebel (1913). In *Eucalyptus occidentalis*, heteroblasty (a sudden vegetative change in leaf anatomy and function) and the onset of the reproductive phase are under separate genetic control (Jaya *et al.*, 2010). Relationships between heteroblasty and speciation have been also suggested in *Acacia* (Kaplan, 1980; Gardner *et al.*, 2008). Besides these two examples, another large plant genus with conspicuous heteroblasty is *Berberis* (Pabón-Mora and González, 2012).

CONCLUSIONS AND PROSPECTS

Despite the very meagre overlap between the set of species hitherto selected as model organisms for studies in evolutionary developmental biology and developmental genetics and those that represent the largest genera in taxonomy, we can identify three main directions along which evo-devo can contribute to a better understanding of how selected lineages emerged as clusters of unusually high diversity and disparity. These are evolvability, phenotypic plasticity and modularity.

More important, even through the simple preliminary analysis presented in this article it is possible to circumscribe a set of topics that deserve closer scrutiny as a priority.

- (1) Is there any reason to expect that key innovations coincide with the apomorphies recognized by taxonomists as diagnostic of clades with high diversity or disparity and, if so, why and when?
- (2) Is saltational evolution involved in the origination of high diversity and/or disparity?
- (3) Following a release from a former developmental constraint, does morphological evolution follow predictable paths of change and, if so, do these evolutionary trends have a consequence on the diversity and/or disparity eventually produced?
- (4) In terms of production of diversity and/or disparity, is it sensible to compare scenarios of multiple parallel change followed by reversal with the patterns of speciation and specialization shown by insular species swarms (e.g. the Hawaiian drosophilids) originated by multiple bidirectional colonization events of the individual islands within the archipelago?
- (5) Phenotypic plasticity has very probably contributed to speciation, but solid evidence is still meagre. Where should we look for better examples? Moreover, has phenotypic plasticity also contributed to increase disparity in some clades?
- (6) Diversity and disparity are often positively correlated with the complexity of the life cycle: is this merely an effect of increased opportunities for diverging adaptations? Alternatively, are developmental genetic causes also involved, i.e. are there properties or even components in common between the genetic control of a complex life cycle and the genetic control of a complex modular phenotype?

Inevitably this is just a first set of questions among those that would be worth investigation, in this hinge between evo-devo and biodiversity – these questions, however, may already keep a number of researchers busy for a long time.

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