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Convergence and divergence in lizard colour polymorphisms

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ABSTRACT

Colour polymorphic species are model systems that can be used to examine the evolutionary processes generating and maintaining discrete phenotypic variation in natural populations. Lizards have repeatedly evolved strikingly similar polymorphic sexual signals in distantly related lineages, providing an opportunity to examine convergence and divergence in colour polymorphism, correlated traits and associated evolutionary processes. Herein, we synthesise the extensive literature on lizard colour polymorphisms in both sexes, including recent advances in understanding of the underlying biochemical, cellular and genetic mechanisms, and correlated behavioural, physiological and life-history traits. Male throat, head or ventral

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colour morphs generally consist of red/orange, yellow and white/blue morphs, and sometimes mixed morphs with combinations of two colours. Despite these convergent phenotypes, there is marked divergence in correlated behavioural, physiological and life-history traits. We discuss the need for coherence in morph classification, particularly in relation to 'mixed' morphs. We highlight future research directions such as the genetic basis of convergent phenotypes and the role of environmental variation in the maintenance of polymorphism. Research in this very active field promises to continue to provide novel insights with broad significance to evolutionary biologists.

Key words: correlational selection, convergence, genetic architecture, mating strategies, sexual signal, Squamata.

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I. INTRODUCTION

Colour polymorphic species are frequent model systems in evolutionary biology because discrete colour variants are an easily scored phenotypic marker that can be used to track changes in allele frequencies in the wild. For this reason, colour polymorphic species have provided significant insights into evolutionary processes, long before the modern evolutionary synthesis or the widespread availability of genomic data, and they continue to do so (Svensson, 2017). Colour polymorphism is defined as the presence of multiple, discrete colour variants (or morphs) within a single population, the rarest of which is too common to be solely due to recurrent mutation (Ford, 1945; Gray & McKinnon, 2007). Colour polymorphism has evolved repeatedly and independently in all major taxonomic groups. In several of these groups, such as birds, lizards, fish and insects, an increasing number of colour polymorphic species have been characterised in recent years (Ahi *et al.*, 2020; Gubili *et al.*, 2016; McLean *et al.*, 2017; Saenko *et al.*, 2019), providing the opportunity to examine similarities and differences in the processes generating and maintaining discrete phenotypic variation. Such comparisons can be especially powerful when polymorphism has evolved on

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multiple independent occasions within taxonomic groups, which share similarities in their basic biology (Jamie & Meier, 2020; Roulin, 2004).

Lizards are one group in which colour polymorphism has evolved independently multiple times and has been well characterised in numerous species, both within and among different families, from across the world. In most cases, the polymorphism involves coloration on the throat, head or ventral body regions, and one or both sexes may be polymorphic. There appears to be remarkable convergence in throat/head/ventral colour polymorphism with either males or both sexes exhibiting a red/orange morph, a yellow morph, and a white/blue morph. For example, the suborder Iguania, consisting of Old World agamids and chameleons (subclade Acrodonta) and New World iguanids (Pleurodonta; Blankers *et al.*, 2013), separated by ~120 million years of evolution, contain multiple species exhibiting notably similar male morph combinations (Fig. 1). Despite apparent convergence in the colour polymorphism, there are important differences in the nature of the colour variation, underlying genetic, biochemical and cellular mechanisms, and the behavioural, physiological and life-history traits associated with colour morphs. Unlike most other taxonomic groups, a number of geographically and phylogenetically distant colour polymorphic lizard systems have been extensively studied, providing a valuable opportunity to examine convergence and divergence in colour polymorphism, the underlying mechanisms and correlated traits.

Here, we synthesise the literature on colour polymorphism in lizards, focusing on throat/head/ventral colour polymorphism, which is prominently displayed during social interactions and likely functions as an intraspecific signal. Although some lizards exhibit polymorphism in dorsal or lateral coloration (e.g. polymorphism in the white lateral stripe in

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some skinks; Chapple, 2005; Chapple *et al.*, 2008), these polymorphisms could have multiple functions (e.g. protection against predators *via* cryptic or disruptive coloration, signalling, thermoregulation) which remain poorly understood. We refer to polymorphism in throat/head/ventral intraspecific colour signals as 'polymorphism' henceforth for brevity. We begin by describing variation in polymorphism, including its taxonomic distribution, and variation in polymorphism within and between the sexes. We then summarise current knowledge of the biochemical, cellular and genetic mechanisms underlying the polymorphisms, before turning our attention to function and evolution. Specifically, we discuss how colour morphs within each sex differ in associated behavioural, physiological and life-history traits and how strategies associated with the polymorphism may be influenced by environmental variation. Then, we discuss implications for the evolution and maintenance of polymorphism in lizards, including frequency-dependent selection, spatiotemporal variation in environmental conditions and geographic variation in morph composition. Lastly, we identify key research gaps and evaluate how insights drawn from colour polymorphism in lizards have shaped our understanding of evolutionary processes relating to the generation and maintenance of phenotypic variation.

II. VARIATION IN LIZARD COLOUR POLYMORPHISMS

Polymorphism has been reported in at least seven different families of lizards (Table 1). Most of these are Iguanians, including both acrodonts in the family Agamidae, and pleurodonts in the families Dactyloidae, Liolaemidae, Phyrnosomatidae and Tropiduridae (Table 1). Polymorphism is also relatively common among wall lizards (family Lacertidae), including at

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least eight species in the genus *Podarcis*, and has been recorded in two species of gecko (family Sphaerodactylidae; Table 1). Most polymorphic species within these highly divergent groups have evolved remarkably similar colour combinations, with a red or orange, and a yellow morph, and an additional blue, white or grey morph in some populations (Fig. 1). An exception is the striped lava lizard (*Tropidurus semitaeniatus*), in which males are either black or yellow (Bruinjé, Leivas & Costa, 2018; Bruinjé *et al.*, 2019*b*). The Roze's gecko (*Gonatodes rozei*) also has strikingly different male morphs, with throats that are orange-yellow, dull yellow, grey-brown with pale yellow markings, or grey-brown with black suffusions between yellow markings (Rivero-Blanco & Schargel, 2012). Additionally, the extendable throat dewlaps of *Anolis apletophallus* are either entirely orange ('solid') or have an orange centre surrounded by a white margin ('basal'; Stapley, Wordley & Slate, 2011). Besides these exceptions, blue morphs appear least common among polymorphic species, yet have evolved in agamids (*Ctenophorus pictus*) and iguanids (*Sceloporus grammicus*, *Urosaurus ornatus*, and *Uta stansburiana*). Interestingly, even in species that have both white/grey and blue morphs, these two morphs do not seem to co-exist within a single population (Bastiaans *et al.*, 2014).

While polymorphism has been reported more commonly in male lizards, polymorphism is also exhibited by some female agamids (Tobler, Healey & Olsson, 2011), iguanids (Lattanzio, Metro & Miles, 2014; Svensson, Sinervo & Comendant, 2001*a*), lacertids (Runemark & Svensson, 2012; Sacchi *et al.*, 2007*b*; Vercken *et al.*, 2007*b*), and the Atlas day gecko (*Quedenfeldtia trachyblepharus*; Blouin-Demers *et al.*, 2013). In these species, males and females either have the same colour morphs (*Podarcis muralis*, *Podarcis gaigeae*,

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Sceloporus undulates erythrocheilus, *Quedenfeldtia trachyblepharus*), or females lack a white (*Zootoca vivipara*; formerly *Lacerta vivipara*) or blue morph (*Urosaurus ornatus* and *Uta stansburiana*; see Table 1). Males and females can also differ in number and type of polymorphic traits; in the painted dragon (*Ctenophorus pictus*), females are only polymorphic in the presence or absence of a yellow 'bib', whereas males are also polymorphic for head colour (Tobler *et al.*, 2011). To date, there have been no reports of species where females are polymorphic but males are not. However, there are many more species for which female polymorphism has never been studied, including some species for which male polymorphism has received extensive attention. Additionally, for autosomally inherited colour polymorphisms, females may carry the underlying genotype without expressing the colour polymorphism (Olsson *et al.*, 2007*b*, 2012; Rankin & Stuart-Fox, 2015; Rankin *et al.*, 2016). The evolution and maintenance of polymorphism in females is therefore an emerging area of research.

Polymorphic lizards can have anywhere from two to six different morphs, typically including up to three 'pure' colour morphs (with the exception of the painted dragon, *Ctenophorus pictus*, which has four: red, orange, yellow and blue) and up to three 'mixed' morphs (Table 1). These mixed morphs can have either a central coloured patch with different surrounding colour (some iguanids and agamids), throat stripes (some iguanids), or a mosaic of differently coloured ventral scales (lacertids). However, defining the number of mixed morphs can be challenging, and definitions are not always consistent across studies. One challenging aspect is that the amount of colour can vary continuously within morphs (Thompson & Moore, 1991*a*; Teasdale, Stevens & Stuart-Fox, 2013). For example, four morphs, including only one

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mixed morph (an orange centre surrounded by yellow), are recognised in *Ctenophorus modestus* (Teasdale *et al.*, 2013) [formerly northern lineage tawny dragon, *C. decresii* (Dong *et al.*, in press]. Mixed orange-grey and yellow-grey morphs are not recognised because the relative extent of these colours varies continuously, making it impossible visually to distinguish a mixed-morph individual (orange-grey or yellow-grey) from a pure-morph individual (orange or yellow). Importantly, categories were defined in this species objectively, based on clustering of quantified colour variation (Teasdale *et al.*, 2013); however, mixed-morph categories in other species have generally been defined subjectively, which can contribute to inconsistencies in the number of morphs described (Pérez i de Lanuza *et al.*, 2019; Pérez i de Lanuza, Font & Carazo, 2013).

Distinguishing colour morphs is further complicated by the fact that not all researchers describe coloration in the same way. For example, in tree lizards (*Urosaurus ornatus*), researchers have seemingly described the same male morph as either yellow (e.g. Thompson & Moore, 1991*a*) or green (Paterson & Blouin-Demers, 2017). Additionally, orange- or yellow/green-throated males with a central blue/green throat patch have been referred to as green (Hover, 1985) or blue-green (Zucker, 1994). To add further to the confusion, studies have also described a solid blue morph (e.g. Thompson & Moore, 1991*a*), a mottled blue morph (Thaker, Lima & Hews, 2009), or an additional solid green morph, distinct from the other yellow/green morph (Carpenter, 1995*a*,*b*). Consequently, a 'green' male tree lizard could, depending on the study, potentially refer to several different morphs. Even establishing the existence of discrete colour morphs can be controversial. For example, while some studies report discrete colour morphs in female European common lizards (*Zootoca vivipara*;

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Vercken & Clobert, 2008*b*; Vercken *et al.*, 2007*a*,*b*; Vercken, Sinervo & Clobert, 2008) others have argued that the ventral colour variation in this species is continuous (Cote *et al.*, 2008; discussed in detail in Olsson, Stuart-Fox & Ballen, 2013). Changing and researcher-specific definitions of coloration can therefore present challenges when attempting to compare and replicate studies, which highlights the importance of assessing which categories are recognised by the intended receivers (i.e. conspecific lizards; e.g. Pérez i de Lanuza *et al.*, 2018).

III. BIOCHEMICAL AND CELLULAR BASIS

In lizards, colour is produced by the combination of chromatophore cells and structural components of the dermis (e.g. collagen and connective tissue; Fig. 2). There are three chromatophore cell types, conserved across poikilothermic vertebrates: melanophores containing brown to black melanin pigments, iridophores containing light-scattering guanine crystals, and xanthophores containing red to yellow carotenoid and/or pteridine pigments (reviewed in Bagnara & Matsumoto, 2006; Grether, Kolluru & Nersissian, 2004; Ligon & McCartney, 2016; Olsson *et al.*, 2013). These three pigment cell types form a layered system with xanthophores in the uppermost layer, melanophores in the deepest layer and iridophores in between (Bagnara, Fernandez & Fujii, 2007). Different colour morphs can be attributed to both the relative number and arrangement of chromatophore types as well as the type and concentration of pigments within them (or density and arrangement of guanine crystals in the case of iridophores; Lewis *et al.*, 2017). For example, blue-coloured skin usually has a low density of xanthophores, a high density of iridophores containing regularly spaced guanine

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crystals producing thin-film interference, and varying density of underlying melanophores that absorb light and influence the intensity of ultra-violet and blue (Macedonia *et al.*, 2000; Morrison, Rand & Frost-Mason, 1995).

The biochemical and cellular basis of lizard colour polymorphisms has been characterised in detail for several species, including *Zootoca vivipara* (Fitze *et al.*, 2009), *Podarcis muralis* (Andrade *et al.*, 2019), *Sceloporus undulatus erythrocheilus* (Morrison *et al.*, 1995), *Uta stansburiana* (Haisten *et al.*, 2015) and *Ctenophorus modestus* (McLean *et al.*, 2017). All these species have orange and yellow morphs, but they differ in their biochemical basis. Red to yellow colours are produced by two different classes of pigment in the xanthophores; carotenoids and pteridines (Bagnara & Matsumoto, 2006; Cooper & Greenberg, 1992; Olsson *et al.*, 2013). Carotenoids must be obtained directly through the diet or metabolically converted from dietary carotenoids (in the case of red ketocarotenoids; Hill & McGraw, 2006), while pteridines are synthesised within chromatophores from purine molecules (Braasch, Schartl & Volff, 2007; Ziegler, 2003). In *Zootoca vivipara*, red to yellow colours are produced exclusively by carotenoids, with the orange morph having a higher concentration of carotenoids than the yellow morph (Fitze *et al.*, 2009). By contrast, orange and yellow in *Sceloporus undulatus erythrocheilus* appear to be produced exclusively by pteridines, with the orange morph having a higher concentration of the red pteridine, drosopterin (Morrison *et al.*, 1995). In *Uta stansburiana*, *Podarcis muralis* and *Ctenophorus modestus*, orange and yellow morphs both have a combination of pteridines and carotenoids but differ in their relative proportions (Andrade *et al.*, 2019; Haisten *et al.*, 2015; McLean *et al.*, 2017). The yellow morph has a relatively higher concentration of dietary yellow

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carotenoids while the orange morph has a relatively higher concentration of red/orange pteridines (riboflavin and/or drosopterin) in all three species.

Differences in the biochemical basis of polymorphism has implications for the cost and information content of colour signals. Specifically, costs associated with production of coloured pteridines from abundant precursors, acquisition of dietary carotenoids, potential metabolic conversion of carotenoids, and trade-offs in allocation to colour signals *versus* other physiological functions, all clearly differ for different types of pigments (McLean *et al.*, 2019). Consequently, the extent to which colour signals individual condition may differ for different morphs within species, or for similar morphs among species.

IV. GENETIC BASIS

Although the biochemical and cellular basis of colour polymorphism in lizards is relatively well understood, the genetic basis is unknown for most species. Given that colour is just one of a suite of traits which differ among morphs, the genetic basis of polymorphism is expected to involve pleiotropic regulation of, or tight physical linkage between, genes associated with both colour production and coadapted traits. Andrade *et al.* (2019) recently showed that the orange, yellow and white colour morphs of the common wall lizard (*Podarcis muralis*) are associated with two small regulatory regions near genes associated with pteridine [sepiapterin reductase (SPR)] and carotenoid [beta-carotene oxygenase 2 (BCO2)] metabolism. The presence of orange coloration is determined by a recessive allele at the SPR locus (oo), whereas the presence of yellow coloration is determined by a recessive allele at the BCO2 locus (yy), both of which are autosomal (Andrade *et al.*, 2019). Alleles at these loci were

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shared with six other *Podarcis* species exhibiting similar colour polymorphisms, with haplotype divergence among species indicating that variation at these loci likely evolved from a combination of ancestral genetic diversity and introgression by hybridisation (Andrade *et al.*, 2019). Whether this simple genetic architecture controls the multiple behavioural and physiological traits that differ among morphs, or whether these loci are also involved in similar colour polymorphisms in lizards from other families, remain open questions.

As in *Podarcis muralis*, autosomal loci underpin colour polymorphism in the three other species in which inheritance has been examined: *Uta stansburiana* (Sinervo, 2001; Sinervo *et al.*, 2001), *Ctenophorus modestus* (Rankin *et al.*, 2016) and *Ctenophorus pictus* (Olsson *et al.*, 2007*b*). Polymorphism in the side-blotched lizard (*Uta stansburiana*) appears to be controlled by a single locus with three, co-dominant alleles (o, b and y), with both alleles expressed in heterozygotes (Sinervo & Zamudio, 2001). Homozygous males have solid throat colours [orange (oo), blue (bb), or yellow (yy)], whereas heterozygotes have throats striped with two colours corresponding to the two alleles (i.e. ob, oy or by). Although alleles at the OBY locus have co-dominant effects on colour expression, they have dominant effects on male strategy. Specifically, the o allele conferring the aggressive O phenotypic strategy is dominant to the y allele conferring the sneaky Y strategy, which is dominant to the b allele conferring the cooperative mate-guarding B strategy (Sinervo, 2001; Sinervo & Clobert, 2003). Sinervo *et al.* (2007) assumed a similar genetic basis (one autosomal locus, three co-dominant alleles) for polymorphism in the European common lizard (*Zootoca vivipara*) although did not test or consider alternative models of inheritance. In the painted dragon

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(*Ctenophorus pictus*), the precise mechanism of inheritance could not be determined due to limited data; however, a single-locus three-allele model could not be rejected (Olsson *et al.*, 2007*b*). Notably, none of these studies formally considered models of inheritance with more than one locus. By contrast, in *Ctenophorus modestus*, the best supported model was one with two bi-allelic loci (an 'orange' and a 'yellow' locus) showing complete dominance (i.e. with the allele coding for orange or yellow expression respectively being dominant; Rankin *et al.*, 2016). However, these studies of inheritance are all constrained by the models considered and statistical power (i.e. the number of offspring in the pedigree).

For *Ctenophorus modestus* we considered an alternative model of inheritance (using data in Rankin *et al.*, 2016), where one autosomal, bi-allelic locus ('colour locus') determines whether or not individuals express orange and/or yellow (gg = grey throat; Gg, gG or GG = orange and/or yellow) and one or more loci subsequently determine the expression of orange and yellow in Gg, gG or GG individuals. Assuming that orange, orange-yellow or yellow individuals have an equal probability of possessing a Gg, gG or GG genotype at the colour locus, observed frequencies of grey offspring *versus* those with orange or yellow (12 *versus* 46 respectively) precisely match those expected (12.21, 45.70; likelihood ratio test: G_1 = 0.008; P = 0.93; model cannot be rejected). We next considered whether the expression of orange and yellow is consistent with the presence of a second locus with co-dominant alleles (i.e. orange = OO, orange-yellow = OY and yellow = YY), but this hypothesis can be confidently rejected (likelihood ratio test: G_3 = 18.38; P = 0.0004). Full details of the breeding design and analysis are given in Rankin *et al.* (2016).

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Rankin *et al.* (2016) showed that although inheritance of the discrete colour morphs is consistent with a few loci of major effect, there is continuous and highly heritable variation in the extent of orange or yellow coloration within *Ctenophorus modestus* morphs (i.e. the extent of colour expression within morphs behaves as a quantitative trait). Such continuous variation within morphs is a common, although under-appreciated feature of many polymorphic systems. The model proposed above for *Ctenophorus modestus* is consistent with the suggestion of hierarchical genetic control of colour expression, whereby at least two independently segregating loci determine the discrete morphs (i.e. presence or absence of orange, yellow or both), and multiple genes influence the extent of colour expression within morphs. For orange, yellow and orange-yellow morphs, quantitative colour expression is likely produced through a physiological cascade involving multiple genes (in combination with environmental effects). Rankin *et al.* (2016) also found evidence of potential genetic covariation between yellow and orange expression, suggesting that the loci influencing quantitative colour expression affect both yellow and orange. In a subsequent study, Lewis *et al.* (2017) found experimentally elevated stress levels impact luminance and patterning, but have little effect on the intensity or proportion of orange or yellow coloration.

Together, emerging evidence on the genetic basis of colour polymorphism in lizards confirms that discrete morphs are governed by a few loci of major effect as expected (Fig. 3), but inheritance of colour variation is unlikely to be determined by a single locus. For example, geographic variation in the polymorphism in *Uta stansburiana* indicates that the genetic basis is more complex than a single OBY locus with three co-dominant alleles. Some populations are fixed for blue throats surrounded by orange (Corl *et al.*, 2010). If the OBY locus

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determines colour expression in these populations, all individuals would be heterozygous (although OB individuals in the trimorphic populations have orange and blue striped throats rather than blue surrounded by orange). This would require exceptionally strong heterozygote advantage (i.e. very strong selection against OO and BB individuals), in addition to loss of the Y allele. Thus, additional genetic mechanisms are likely to influence genetic variation in *Uta stansburiana*. This may also be true of *Zootoca vivipara,* in which Sinervo *et al.* (2007) proposed a genetic mechanism analogous to the OBY locus, given the complex colour variation in this species (see above). Ultimately, genomic studies such as that of Andrade *et al.* (2019), are essential to resolve the genetic basis of colour polymorphism and correlated strategies.

Comparison of the genetic basis of colour morphs among species may further reveal whether polymorphism is associated with shared ancestry (homology), the repeated use of the same genes or pathways (parallelism), or multiple independent genetic solutions resulting in the same outcome. Lizard colour polymorphisms may be a good system for studying the link between phenotypic and genetic convergence for a number of reasons. Firstly, colour morphs have independently evolved multiple times in highly divergent lineages, allowing for comparisons of the underlying molecular mechanisms between both closely and distantly related species (Fig. 1). Importantly, lineages contain both polymorphic and non-polymorphic species, which is vital for confirming associations with candidate genes. Secondly, as described above, colour morphs are highly heritable in species where inheritance has been tested, confirming that the trait has a genetic basis which is likely to involve a few loci of major effect (Fig. 3). Colour morphs have also been shown to be underpinned by genes

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associated with pigment production and/or metabolism, which can be targeted in molecular studies. For these reasons, lizard colour polymorphisms provide a promising opportunity to assess the genetic basis of convergent phenotypes.

V. CORRELATED BEHAVIOURAL, PHYSIOLOGICAL AND LIFE-HISTORY TRAITS

The presence of multiple throat colour morphs is often, if not always, associated with a suite of other behavioural, physiological and life-history traits (McKinnon & Pierotti, 2010; Table 1). Morphs can be considered to display alternative strategies when they differ in multiple traits that affect fitness in combination. These strategies may represent different adaptive peaks on the fitness landscape, generated by correlational selection (McKinnon & Pierotti, 2010; Roff & Fairbairn, 2012; Sinervo & Svensson, 2002). Correlational selection is expected to generate genetic correlations between the traits under selection (Roff & Fairbairn, 2012). Genetic correlations between colour, immunity, egg mass, clutch size and laying date have been demonstrated in side-blotched lizards (*Uta stansburiana*) (Calsbeek & Sinervo, 2007; Sinervo & Svensson, 2002; Svensson *et al.*, 2001*a*, 2009*a*; Svensson, McAdam & Sinervo, 2009*b*). However, formal selection analyses and estimates of genetic correlations have been conducted in relatively few polymorphic lizard species, so in most cases, non-adaptive pleiotropy cannot be ruled out as an explanation for correlated traits. Nevertheless, correlational selection is implicated by the large number of studies showing that morphs differ in diverse traits that affect fitness (Table 1).

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(1) Male reproductive tactics

Many polymorphic agamids and iguanids have dominance hierarchies among male morphs, where one morph is more likely to win against another in male–male contests (see Table 1). Interestingly, although the most dominant morph colour varies, yellow morphs tend to be least dominant across species (e.g. Bruinjé *et al.*, 2019*a*; Healey, Uller & Olsson, 2007; Sinervo & Lively, 1996; Taylor & Lattanzio, 2016; but see Abalos *et al.*, 2016; Yewers, Pryke & Stuart-Fox, 2016). Where these hierarchies are present, less-dominant morphs can gain reproductive success through pre- or post-copulatory reproductive tactics that do not depend upon contest success.

The rock–paper–scissors system of male side-blotched lizards (*Uta stansburiana*) is a particularly well-characterised example of alternative strategies (Fig. 3; Sinervo *et al.*, 2006; Sinervo & Lively, 1996; Sinervo *et al.*, 2000*a*; Zamudio & Sinervo, 2000). Each strategy – orange/aggressive, yellow/sneaky and blue/mate-guarding – is more successful against one other strategy, but loses against the third, as in a game of 'rock–paper–scissors' (Sinervo & Lively, 1996). Each strategy entails correlated physiological traits; for example, orange males have higher levels of testosterone, which is linked with endurance and territoriality (Sinervo *et al.*, 2000*a*). Different morphs also show different tactics for escaping predators, which are more successful (as indicated by survival rates) when combined with specific dorsal patterns (Lancaster, Hipsley & Sinervo, 2009; Lancaster, McAdam & Sinervo, 2010). Accordingly, females show preferences for males that exhibit beneficial combinations of traits (Lancaster *et al.*, 2009). *Uta stansburiana* is arguably one of the best-known examples of pre-copulatory

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reproductive strategies corresponding to male colour morphs – in lizards or any other taxon; however, it is certainly not the only example.

Male tree lizard (*Urosaurus ornatus*) morphs exhibit similarly distinct pre-copulatory reproductive strategies. Blue males are dominant and aggressive, and defend large territories; orange males are non-territorial, occupy smaller home ranges, and can become nomadic when environmental conditions are stressful; and yellow males sneak copulations with females around the territories of blue males (Lattanzio & Miles, 2016; Moore, Hews & Knapp, 1998; Paterson & Blouin-Demers, 2018). The level of specialisation and flexibility required for each strategy appears to give rise to other differences between morphs. Blue males are dietary specialists, whereas yellow males show plasticity in dietary preferences and orange males are generalists (Lattanzio & Miles, 2016). Blue males prefer yellow females, which tend to have larger clutch sizes (Zucker & Boecklen, 1990), whereas yellow males show no preference and interact with more females overall (Krohmaly, Martin & Lattanzio, 2018). In captivity, blue males also compete more successfully for higher quality perches (Taylor & Lattanzio, 2016); however, in the wild, yellow males are most likely to occupy higher quality, densely populated habitat near creek beds (Paterson & Blouin-Demers, 2018). This latter finding may be because blue males defend territories more successfully in less densely populated areas, whereas the sneaking strategy of yellow males benefits from dense populations of females (Paterson & Blouin-Demers, 2018).

Less-dominant male morphs may also succeed through alternative post-copulatory tactics. Yellow-headed painted dragon (*Ctenophorus pictus*) males tend to be less aggressive, lose contests, and reside on lower quality territories, compared with red-headed males (Healey *et*

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al., 2007; Olsson *et al.*, 2007*b*). On the other hand, yellow-headed males have larger testes (relative to their body size and condition), copulate for less time, and sire three times as many offspring per copulation (Olsson *et al.*, 2009*b*). These two distinct strategies appear to be equally successful, as there is no evidence for a difference in reproductive success between morphs (Olsson *et al.*, 2007*b*) or female preferences for different head colour morphs (Healey, Uller & Olsson, 2008). However, females prefer males with a yellow bib (McDiarmid *et al.*, 2017) and the cost of having a bib, which is condition dependent (Olsson *et al.*, 2009*a*), appears to differ depending on head colour, linking these two polymorphic traits (Healey & Olsson, 2009).

(2) Non-reproductive correlated traits

Other trade-offs and selective pressures, unrelated to dominance, might also favour alternative fitness optima among male morphs. In common wall lizards (*Podarcis muralis*), orange morphs (both male and female) are more conspicuous to both conspecifics and predators than yellow or white morphs, respectively (Pérez i de Lanuza & Font, 2015; Fig. 3). Greater risk of predation might therefore explain why orange morphs, after successive predatory threats, take progressively longer to emerge from a refuge compared with other morphs (Pellitteri-Rosa *et al.*, 2017). Likewise, orange morphs tend to be more restricted to vegetated habitat close to water (Pérez i de Lanuza & Carretero, 2018). Yellow males also differ from other morphs in a number of traits, the adaptive value of which are perhaps less clear. For example, yellow males have a lower immune response than white and orange males (Sacchi *et al.*, 2017*a*, 2007*a*), different seasonal patterns of testosterone (Sacchi *et al.*,

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2017*b*), better homing abilities (Scali *et al.*, 2013), different diets (particularly when compared with the orange males (Scali *et al.*, 2016); and show more rapid desensitisation to predatory threats (Pellitteri-Rosa *et al.*, 2017). Otherwise, these morphs are similar in body size (Sacchi *et al.*, 2007*a*,*b*; but see Calsbeek, Hasselquist & Clobert, 2010), body condition (Abalos *et al.*, 2016), and aggression (Sacchi *et al.*, 2009). Even though differences among morphs have been reported (Table 1), for many polymorphic lizard species, including *P. muralis*, it is unclear whether or how these traits relate to alternative fitness optima or strategies.

(3) Correlated traits in females

In species with polymorphic females, different female morphs can exhibit alternative life-history strategies. Specifically, one female morph may produce many, small offspring (*r*-strategy) while another produces fewer, large offspring (*K*-strategy). For example, in *Uta stansburiana*, orange females are *r*-strategists and yellow females are *K*-strategists (Sinervo, Svensson & Comendant, 2000*b*). In *Podarcis muralis*, yellow and white females may be *r*- and *K*-strategists respectively, whereas orange females may change their strategy depending on their size and age (Galeotti *et al.*, 2013). *Urosaurus ornatus* shows more continuous variation in clutch size, with females with yellower throats having larger clutches (Zucker & Boecklen, 1990). *Zootoca vivipara* shows the opposite trend, with yellow females tending to lay smaller clutches than orange or mixed females, which have higher hatching success (Vercken *et al.*, 2007*b*).

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As in males, female morphs have correlated behavioural and physiological traits that likely relate to their life-history strategies. For example, in *Uta stansburiana*, orange and yellow morphs differ in the relationship between clutch size, local social environment (number of orange or yellow neighbours), immunocompetence, condition and survival (Svensson, Sinervo & Comendant, 2002). However, not all findings are consistent across studies (Comendant *et al.*, 2003; Svensson *et al.*, 2002) and there is also evidence in some species that females may modulate their strategy depending on mate morph (Galeotti *et al.*, 2013).

(4) Environmental effects on correlated traits

In both male and female lizards, environment, including social environment, can have an important influence on the strategies of different morphs. For example, having a bib is more costly for male *Ctenophorus pictus*, particularly yellow-headed males, when exposed to more red-headed, aggressive neighbours (as measured by body condition; Healey & Olsson, 2009). Consequently, although bibbed males are preferred by females, their relative success likely varies depending on their social context. Dominance hierarchies are also not necessarily fixed across space and time. In a study of long-tailed brush lizards (*Urosaurus graciosus*), orange males were dominant over yellow males in an initial experiment, but yellow males became increasingly aggressive over successive experiments until this hierarchy was no longer apparent (Brown & Lattanzio, 2018). In female lizards, the success of alternative reproductive strategies is likely highly dependent on environment, with *K*-strategies favoured when populations exceeded carrying capacity and *r*-strategies favoured at lower densities (Sinervo *et al.*, 2000*b*). However, if clutch size is unrelated to the rate of hatching success or

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offspring development, the opposite trend may be true. In *Zootoca vivipara*, orange females produce fewer offspring when female density is high, and also when yellow females are more frequent in the population (Vercken *et al.*, 2007*b*). This adjustment in reproductive output may represent strategic allocation of resources, as orange females appear to be weaker competitors (Vercken & Clobert, 2008*b*); therefore, it may be more beneficial for orange females to allocate more resources to reproduction when their offspring have greater likelihood of survival. Such variation in morph-specific responses to environmental conditions, as well as the fitness consequences, may play a critical role in the maintenance of the colour polymorphism.

VI. MAINTENANCE OF POLYMORPHISM WITHIN POPULATIONS

Like all heritable polymorphisms, the maintenance of colour polymorphism over time requires balancing selection, that is, selection to maintain the different alleles that underlie the polymorphism. The most common mechanism generating balancing selection in polymorphic systems is negative frequency-dependent selection, whereby the fitness of each morph is higher at relatively lower frequencies. One of the best-known examples is the 'rock–paper–scissors' system of male reproductive strategies in the side-blotched lizard (*Uta stansburiana*) (see Section V.1). The fitness of each strategy depends on its relative frequency within the population; for example, the yellow sneaker strategy has higher fitness when it is rare relative to the frequency of the aggressive orange strategy from which it sneaks mating opportunities. Similarly, the blue mate-guarding strategy has higher fitness

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when it is rare relative to the yellow sneaker strategy. Consequently, the frequency of each strategy varies cyclically and the polymorphism is maintained (Sinervo & Lively, 1996). Frequency-dependent selection is not the only mechanism generating balancing selection. Balancing selection may be generated by heterozygote advantage (Gray & McKinnon, 2007), although we are not aware of any examples of heterozygote advantage maintaining colour polymorphism in lizards. Balancing selection can also be generated by spatiotemporal variation in environmental conditions affecting morph fitness (Svensson, 2017). Environmental characteristics could affect relative morph fitness directly (e.g. through costs of acquiring dietary carotenoids) or indirectly by altering inter- and intra-specific interactions (e.g. the competitive advantage of morphs could differ depending on resources and population density). Evidence for environmental effects on relative morph fitness can be found in *Ctenophorus modestus*, where populations in more arid environments have a higher proportion of orange males, and fewer yellow males (McLean, Stuart-Fox & Moussalli, 2015). Similarly, in *Uta stansburiana*, the fitness of female morphs depends on population density, which is a function of environmental conditions. Low population densities favour *r*-strategist orange females that lay large clutches of small progeny and high densities favour *K*-strategist yellow females that lay small clutches of large progeny (Sinervo *et al.*, 2001). Because environmental variation is generally cyclical over short timescales (even though it may be directional over long timescales), temporal variation in selection likely contributes to the maintenance of polymorphism in many species.

Sexual selection is also an important mechanism influencing the maintenance of polymorphism because it affects the evolution of alternative reproductive strategies and

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assortative mating. For example, in the common wall lizard (*Podarcis muralis*), there are more male colour morphs in populations with male-biased sex ratios, suggesting a relationship between the intensity of male intrasexual selection and male morph diversity (Pérez i de Lanuza, Carretero & Font, 2017). Additionally, unless counteracted by some form of balancing selection, the tendency to mate assortatively might drive further divergence between morphs, and if heteromorphic pairs are sufficiently rare, could even eventually lead to speciation. Assortative mating may be favoured by correlational selection to maintain optimal trait combinations and prevent their breakdown by recombination (Jamie & Meier, 2020; Lancaster *et al.*, 2014). By contrast, disassortative mating can prevent the loss of rare morphs and maintain polymorphism (Gray & McKinnon, 2007; Lancaster *et al.*, 2014; Wellenreuther, Svensson & Hansson, 2014). Disassortative mating can be promoted by negative frequency-dependent selection because females should mate with rare male morphs to produce the fittest offspring (Lancaster *et al.*, 2014). Conversely, negative frequency-dependent selection can promote disassortative mating because rarer morphs have more mating opportunities and thus higher fitness (Jamie & Meier, 2020). A combination of assortative and disassortative mating strategies could contribute to maintenance of colour polymorphism in *Podarcis muralis* (Sacchi *et al.*, 2018). Females of different morphs appear to show both assortative and disassortative association preferences in captivity (Sacchi *et al.*, 2018, 2015), although it is unclear the extent to which these preferences determine pairings in the wild. Same-morph (homomorphic) pairs are more commonly found than heteromorphic pairs in wild populations (Pérez i de Lanuza *et al.*, 2013, 2016), and yellow homomorphic pairs achieve higher breeding success than any other morph-pair combination (Galeotti *et al.*,

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2013) although it is not known whether this pattern varies over time. Ultimately, the maintenance of polymorphism will depend on the complex interaction between correlational selection, balancing selection and mating patterns, all of which may vary depending on environmental conditions that affect population density and relative morph fitness. Processes maintaining polymorphism are best determined using direct measures of selection on colour morphs in the wild. This has been attempted in several lizard species that reach sexual maturity within a year: side-blotched lizards (*Uta stansburiana*), common lizards (*Lacerta vivipara*) and painted dragons (*Ctenophorus pictus*). Measurement of selection in the wild is challenging for lizard species with longer lifespans, overlapping generations, and that take longer than a year to reach sexual maturity. Therefore, in many polymorphic lizards, processes that might maintain the polymorphism are inferred indirectly from hypothesised fitness advantages of the life-history, reproductive or behavioural strategies corresponding to the morphs.

VII. GEOGRAPHIC VARIATION IN POLYMORPHISM

Geographic variation in the number, type and/or frequency of colour morphs is common in polymorphic species. Given that McLean & Stuart-Fox (2014) have extensively reviewed this topic previously, we discuss it only briefly here. Most widespread polymorphic lizard species exhibit geographic variation in morphs. For example, some populations and subspecies of *Uta stansburiana* are trimorphic, while others are dimorphic or monomorphic, and phylogenetic reconstruction suggests that the polymorphism has been independently lost eight times (Corl *et al.*, 2010). Similarly, polymorphism is likely to have been lost from

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Ctenophorus decresii (sister species to *C. modestus*, previously recognised as divergent lineages of the same species), resulting in the evolution of a unique blue-throated morph (McLean, Stuart-Fox & Moussalli, 2014). Morph frequencies also vary substantially among polymorphic populations in both of these species (Corl *et al.*, 2010; McLean *et al.*, 2015), as well as *Podarcis muralis* (Pérez i de Lanuza & Carretero, 2018; Sacchi *et al.*, 2007*b*), *Podarcis gaigeae* (Runemark *et al.*, 2010), *Anolis distichus favillarum* (Ng *et al.*, 2017), *Urosaurus ornatus* (Hews *et al.*, 1997; Thompson & Moore, 1991*a*), and *Sceloporus grammicus* (Bastiaans *et al.*, 2014). Such geographic variation reflects the balance between local selective pressures, gene flow and stochastic processes (Svensson, 2017), and may play an important role in speciation if populations with different morph compositions become reproductively isolated (McLean & Stuart-Fox, 2014).

VIII. CONCLUSIONS AND FUTURE DIRECTIONS

(1) Lizards show remarkable convergence in polymorphism of throat/head/ventral colour signals, with red/orange, yellow, white/blue/grey and mixed-colour morphs. Despite similarities in the polymorphisms, the number of recognised morphs, particularly mixed-morph categories, differ among species. This may be partially attributed to the way in which colour variation has been measured and categorised by researchers, or may reflect biological differences in the mechanisms generating and maintaining the polymorphism.

(2) We suggest that colour variation should be quantified using objective measures, ideally based on receiver (i.e. lizard) colour vision (e.g. Pérez i de Lanuza *et al.*, 2019; Pérez i de Lanuza & Carretero, 2018; Teasdale *et al.*, 2013). Such measures can now be obtained

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relatively easily from both spectral data and digital images using free software (Maia *et al.*, 2019; van den Berg *et al.*, 2020). Morph categories should ideally be determined based on clear statistical clustering (i.e. discontinuities in the variation). Even when categories can be statistically defined, however, it does not mean that they are biologically relevant. This is particularly the case for mixed morphs, which may be objectively categorised but exhibit behavioural or life-history strategies similar to the pure morph of one of the constituent colours.

(3) An outstanding question is whether seemingly convergent colour morphs in distantly related species arise from similar or different genetic mechanisms. Recent studies in lizards suggest that the genetic basis of colour polymorphism is likely to be more complex than a single locus, with at least two loci generating the polymorphism. Sequencing skin transcriptomes across developmental stages may help to pinpoint genes associated with colour production and polymorphism. Studies of the genetic basis of lizard polymorphisms have sampled adult lizards, but it would be informative to investigate gene expression at the onset of ventral coloration, or in developing scale buds. Genomic studies of lizard colour polymorphisms, especially in relation to the genetic basis of convergent phenotypes, are an exciting area of future research.

(4) Despite apparent convergence in lizard colour polymorphisms, there is substantial divergence in correlated traits or strategies. While in some species, morphs differ in life-history or reproductive strategies (and associated behavioural and physiological traits), in others the differences appear to be more subtle.

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(5) Most discussion of the maintenance of polymorphism has focussed on the role of frequency-dependent selection. We suggest that temporal variation in environmental conditions may play an equally important role and warrants further research. Environmental variation may affect morph fitness both directly and indirectly (e.g. by affecting population density) and may interact with frequency-dependent selection *via* its effects on morph frequencies.

(6) There is a growing appreciation of geographic variation in polymorphism within species or closely related groups of species. Polymorphism may predispose populations to diverge in colour traits, ultimately leading to speciation (McLean & Stuart-Fox, 2014). Geographic variation in colour polymorphism and its role in speciation has been reviewed in detail elsewhere (McLean & Stuart-Fox, 2014) but lizards are a promising group in which to examine these processes.

(7) The study of colour polymorphism in lizards has contributed substantially to our understanding of the evolutionary processes generating and maintaining discrete phenotypic variation in natural populations. Research in this very active field promises to continue to provide novel insights with broad significance to evolutionary biologists.

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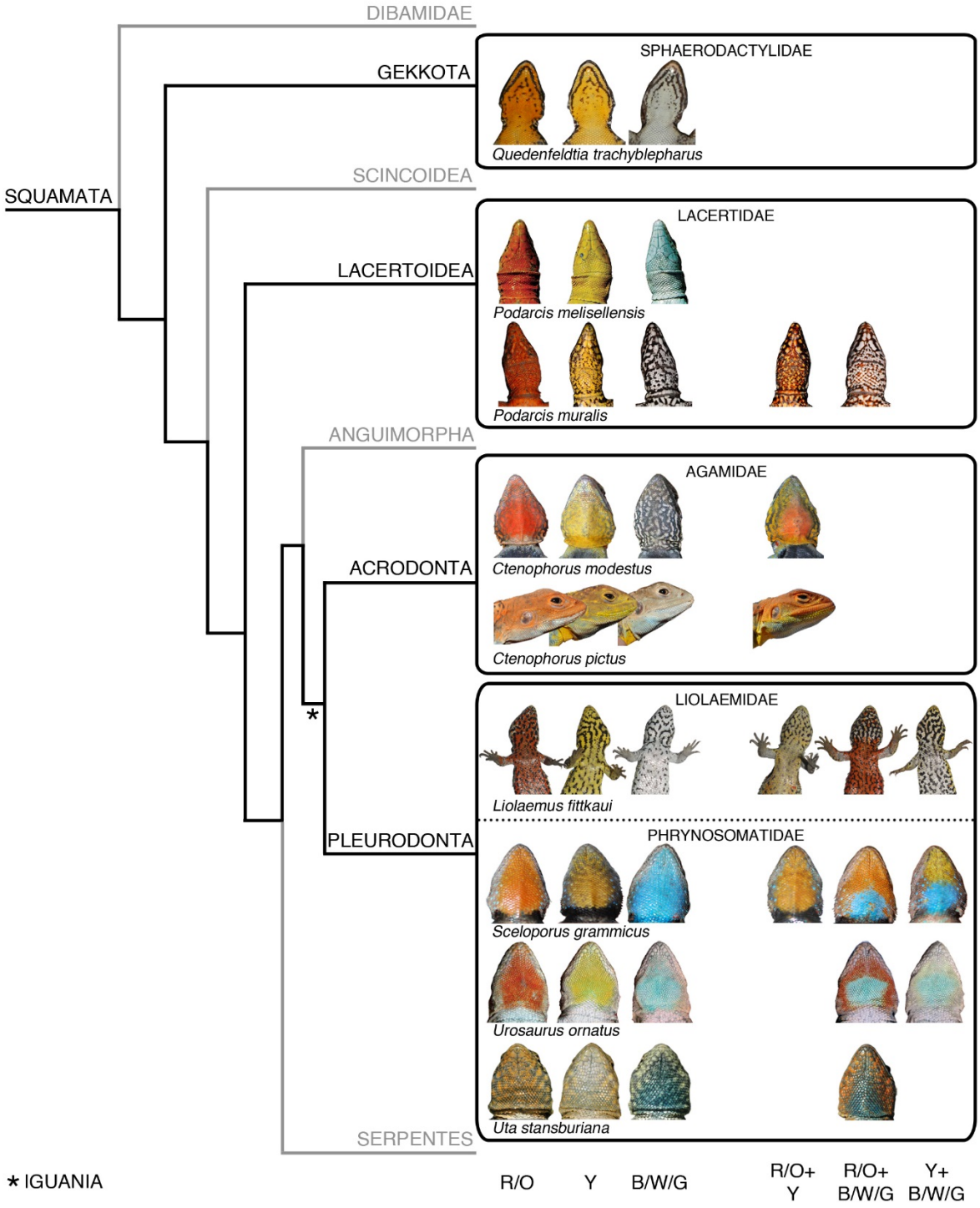

Fig. 1. Pure and mixed male colour morphs in well-studied polymorphic species across the order Squamata (lizards and snakes). Black branches contain species with known

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throat/head/ventral colour polymorphism while grey branches do not. Phylogenetic tree adapted from Pyron *et al.* (2013). Images used with permission: *Q. trachyblepharus* (from Blouin-Demers *et al.*, 2013); *P. melisellensis* (from Huyghe *et al.*, 2007); *P. muralis* (from Andrade *et al.*, 2019); *C. modestus* (from McLean *et al.*, 2013); *C. pictus* (from Friesen *et al.*, 2017*b*); *L. fittkaui* (from Jiménez-Robles *et al.*, 2016); *S. grammicus* (from Bastiaans *et al.*, 2014); *U. ornatus* (from Meyers *et al.*, 2006); *U. stansburiana* (from Corl *et al.*, 2010). B/W/G, blue/white/grey; R/O, red/orange; Y, yellow.

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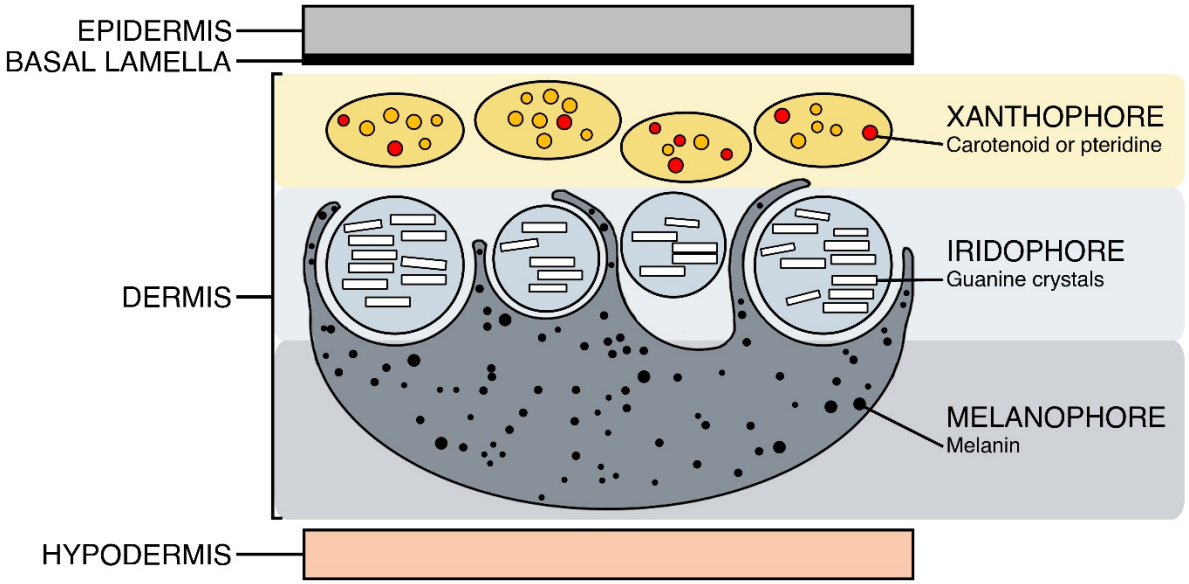

Fig. 2. Schematic representation of the cellular structure of lizard skin including the three chromatophore types: brown-black melanophores containing melanin pigments, colourless iridophores containing light-reflecting guanine crystals, and yellow-red xanthophores containing carotenoid and/or pteridine pigments. Note that the melanophore dendritic processes can extend around and above the overlying iridophores.

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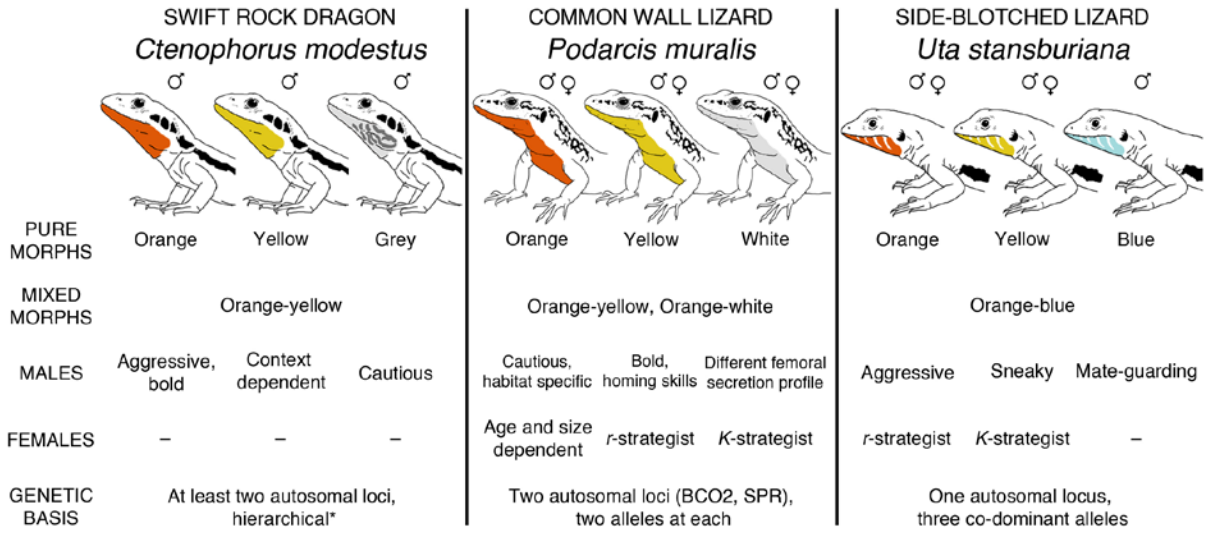

Fig. 3. Colour polymorphism in three well-studied lizard species: the Australian swift rock dragon, *Ctenophorus modestus* (formerly northern lineage *C. decresii*), the European common wall lizard, *Podarcis muralis*, and the North American side-blotched lizard, *Uta stansburiana*. Each species has three pure morphs, which are present in males or both sexes, and at least one mixed morph. Male and/or female morphs differ in behavioural, physiological and/or life-history traits (details in Table 1). In all three species, the polymorphisms appear to be underpinned by a few autosomal loci of major effect. *In *C. modestus*, the most likely model of inheritance is one where a bi-allelic locus determines whether or not orange and/or yellow is expressed, and one or more loci subsequently determine the expression of orange or yellow. BCO2, beta-carotene oxygenase 2; SPR, sepiapterin reductase.

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Table 1. Evidence for associations between colour morph and behavioural, physiological and life-history traits in lizards. For species with more than two morphs, not all studies compared traits among all morphs, which can explain some (but not all) discrepancies in results. 'Mixed' evidence for correlation refers to where a study found evidence for an association in some contexts, but not in others. * indicates that there was only evidence for differences among morphs in interaction with the environment (including social environment), other traits, or in specific contexts.

Family	Species	Sex	Morph colours	Trait	Evidence for correlation	References
Agamidae	Swift rock dragon (*Ctenophorus modestus)*	Male	Orange, yellow, grey, orange-yellow	Aggression	Yes	Yewers *et al.* (2016)
				Bite force	No	Yewers *et al.* (2017)
				Body temperature	Yes	Yewers *et al.* (2017)
				Boldness	Yes	Yewers *et al.* (2016)
				Immunity (ectoparasite load)	Yes	Hacking *et al.* (2018)
				Stress response (corticosterone)	No	Yewers *et al.* (2017)
				Testosterone/other androgens	Yes*	Yewers *et al.* (2017)
	Painted dragon (*Ctenophorus pictus*)	Female	Yellow bib, no bib	Body mass	No	Tobler *et al.* (2011)
				Body size	No	Tobler *et al.* (2011)
				Morphology (digit ratio)	Yes	Tobler *et al.* (2011)

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Male	Yellow bib, no bib	Antipredator behaviour	Yes	Tobler *et al*. (2012)
		Body condition	Yes*	Healey & Olsson (2009)
			No	McDiarmid *et al*. (2017)
		Body mass	No	Tobler *et al*. (2011)
		Body size	No	Tobler *et al*. (2011)
		Copulation duration	Yes	Friesen *et al*. (2020)
		Dominance	Yes (bib quality)	McDiarmid *et al*. (2017)
		Endurance/stamina	Yes	Tobler *et al*. (2012)
		Mate choice (by female)	Yes	McDiarmid *et al*. (2017)
		Resting metabolic rate	Yes	Friesen *et al*. (2017*a*)
		Morphology (digit ratio)	Yes	Tobler *et al*. (2011)
		Sperm number	Yes	Friesen *et al*. (2020)
		Sperm performance	Yes	Friesen *et al*. (2020)
			No	McDiarmid *et al*. (2017)
		Sperm telomere length	Yes	Friesen *et al*. (2020)
		Superoxide levels	Yes	Olsson *et al*. (2012)
			No	Friesen *et al*. (2020)
	Orange, red, yellow, blue (head colour)	Body condition	Yes*	Olsson *et al*. (2007*b*); Friesen *et al*. (2017*b*)
		Body mass	No	Olsson *et al*. (2007*b*); Tobler *et al*. (2011)
		Body size	No	Olsson *et al*. (2007*b*), Tobler *et al*. (2011)
		Copulation duration	No	Friesen *et al*. (2020)
		Dominance	Yes	Healey *et al*. (2007)
		Endurance/stamina	No	Tobler *et al*. (2012)
		Mate choice (by female)	No	Healey *et al*. (2008)

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				Reproductive strategy	Yes	Olsson *et al.* (2009*b*)
				Sperm number	No	Friesen *et al.* (2020)
				Sperm performance	No	Friesen *et al.* (2020)
				Sperm telomere length	Yes	Friesen *et al.* (2020)
				Stress response (corticosterone)	Non-significant trend	Olsson *et al.* (2007*a*)
				Superoxide levels	Yes	Olsson *et al.* (2012)
					No	Friesen *et al.* (2020)
				Territory acquisition	No	Healey & Olsson (2008)
				Territory quality	Yes	Olsson *et al.* (2007*b*)
				Territory size	No	Olsson *et al.* (2007*b*, 2008)
				Testosterone	Yes	Olsson *et al.* (2007*a*)
Dactyloidae	*Anolis apletophallus*	Male	Orange, orange-white	–	–	Stapley *et al.* (2011)
	Bark anole (*Anolis distichus favillarum*)	Male	Orange, yellow	–	–	MacGuigan *et al.* (2017); Ng *et al.* (2016)
Lacertidae	European common or viviparous lizard (*Zootoca vivipara*; previously *Lacerta vivipara*)	Female	Orange, yellow, orange-yellow	Body mass	No	Vercken *et al.* (2007*b*)
				Dominance	Yes	Vercken & Clobert (2008*b*)
				Offspring behaviour	Yes	Vercken *et al.* (2012)
				Reproductive strategy	Yes*	Vercken *et al.* (2010, 2007*b*)
				Social behaviour	Yes*	Vercken & Clobert (2008*a*)
				Stress response (behaviour)	Yes	Vercken & Clobert (2008*b*)
		Male	Orange, yellow, white, orange-yellow, orange-white, yellow-white	Body mass	Yes	Sinervo *et al.* (2007)
				Endurance/stamina	Yes	Sinervo *et al.* (2007)
				Survival	Yes	Sinervo *et al.* (2007)
	Podarcis bocagei	Unknown	Orange, yellow, white	–	–	Andrade *et al.* (2019)

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Skyros wall lizard (*Podarcis gaigeae*)	Female	Orange, yellow, white, orange-yellow, orange-white, yellow-white	Mate choice (by male)	No	Runemark & Svensson (2012)
	Male	Orange, yellow, white, orange-yellow, orange-white, yellow-white	Mate choice (by female)	Yes	Runemark & Svensson (2012)
Podarcis liolepis	Unknown	Orange, yellow, white	–	–	Andrade *et al.* (2019)
Dalmation wall lizard (*Podarcis melisellensis*)	Male	Orange, yellow, white	Activity patterns	No	Huyghe *et al.* (2007)
			Bite force	Yes	Huyghe *et al.* (2009, 2007)
			Body size	Yes	Huyghe *et al.* (2007)
			Body temperature	No	Huyghe *et al.* (2007)
			Endurance/stamina	No	Huyghe *et al.* (2007)
			Immunity (ectoparasite prevalence and load)	No	Huyghe *et al.* (2010)
			Immunity (endoparasite load)	Yes	Huyghe *et al.* (2010)
			Immunity (endoparasite prevalence)	Yes*	Huyghe *et al.* (2010)
			Immunity (phytohaemagluttinin response)	No Yes*	Huyghe *et al.* (2009) Huyghe *et al.* (2010)
			Morphology (head size)	Yes	Huyghe *et al.* (2007)
			Morphology (limb length)	No	Huyghe *et al.* (2007)
			Sprint speed	No	Huyghe *et al.* (2007)
			Stress response (corticosterone)	Yes	Huyghe *et al.* (2009)
			Testosterone	No	Huyghe *et al.* (2009)

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Common wall lizard (*Podarcis muralis*)	Female	Orange/red, yellow, white, orange-yellow, orange-white	Body size	Yes	Sacchi *et al.* (2007*b*) Calsbeek *et al.* (2010)
			Diet	Yes	Scali *et al.* (2016)
			Habitat use	Yes	Pérez i de Lanuza & Carretero (2018)
			Homing ability	Yes	Scali *et al.* (2013)
			Immunity (endoparasite prevalence and load)	Yes	Calsbeek *et al.* (2010)
			Immunity (humoral immune response)	No	Calsbeek *et al.* (2010)
			Immunity (phytohaemagluttinin response)	Yes	Sacchi *et al.* (2017*a*)
			Mate choice (assortative mating)	Yes	Pérez i de Lanuza *et al.* (2013); Sacchi *et al.* (2018)
				No	Sacchi *et al.* (2015)
			Morphology (head height)	Yes	Sacchi *et al.* (2007*b*)
			Reproductive strategy	Yes	Galeotti *et al.* (2013)
			Sprint speed	No	Zajitschek *et al.* (2012)
			Stress response (endoparasite load)	No	Galeotti *et al.* (2010)
			Stress response (white blood cell ratio)	Yes*	Galeotti *et al.* (2010)
	Male	Orange/red, yellow, white, orange-yellow, orange-white	Aggression	No	Sacchi *et al.* (2009); Abalos *et al.* (2016)
			Antipredator behaviour	Yes	Pellitteri-Rosa *et al.* (2017)
			Body condition	No	Abalos *et al.* (2016)

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Body size	Yes (marginal)	Calsbeek *et al*. (2010)
	No	Sacchi *et al*. (2007*a*,*b*); Abalos *et al*. (2016)
Diet	Yes	Scali *et al*. (2016)
Dominance	No	Sacchi *et al*. (2009)
	Yes	Abalos *et al*. (2016)
Femoral gland secretions (chemical profile)	Yes	Pellitteri-Rosa *et al*. (2014)
Habitat use	Yes	Pérez i de Lanuza & Carretero (2018)
Homing ability	Yes	Scali *et al*. (2013)
Immunity (endoparasite prevalence and load)	Yes	Calsbeek *et al*. (2010)
Immunity (humoral immune response)	No	Calsbeek *et al*. (2010)
Immunity (phytohaemagluttinin response)	Yes	Sacchi *et al*. (2007*a*) Sacchi *et al*. (2017*a*)
Mate choice (assortative mating)	Yes	Pérez i de Lanuza *et al*. (2013, 2016)
Morphology (head height)	No	Sacchi *et al*. (2007*b*)
Sprint speed	No	Zajitschek *et al*. (2012)
Stress response (endoparasite load)	No	Galeotti *et al*. (2010)
Stress response (white blood cell ratio)	Yes*	Galeotti *et al*. (2010)
Testosterone	Yes*	Sacchi *et al*. (2017*b*)

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	P. sicula	Unknown	Orange, white, orange-white	–	–	Andrade *et al.* (2019)
	P. vaucheri	Unknown	Orange, yellow, white	–	–	Andrade *et al.* (2019)
	P. wagleriana	Unknown	Orange-white, orange-yellow	–	–	Andrade *et al.* (2019)
Liolaemidae	*Liolaemus fittkaui*	Male	Red, yellow, white, red-yellow, yellow-white, red-white	–	–	Jiménez-Robles *et al.* (2016)
	Liolaemus sarmientoi	Male	Red, yellow, red-yellow	Aggression	Yes	Fernandez *et al.* (2018)
				Body size	No	Fernandez *et al.* (2018)
				Body temperature	Yes	Fernandez *et al.* (2018)
				Endurance/stamina	No	Fernandez *et al.* (2018)
				Morphology (head height)	Yes	Fernandez *et al.* (2018)
				Morphology (head length)	No	Fernandez *et al.* (2018)
				Morphology (head width)	No	Fernandez *et al.* (2018)
Phrynosomatidae	Mesquite lizard (*Sceloporus grammicus*)	Male	Orange, yellow, blue or white, orange-yellow, orange-blue, yellow-blue	Mate choice (by female)	Yes	Bastiaans *et al.* (2014)
	Eastern fence lizard (*Sceloporus undulates erythrocheilus*)	Female	Orange, yellow, white	–	–	Rand (1992)
		Male	Orange, yellow, white	–	–	Rand (1992)
	Long-tailed brush lizard (*Urosaurus graciosus*)	Male	Orange, yellow	Dominance	Yes*	Brown & Lattanzio (2018)
	Tree lizard (*Urosaurus ornatus*)	Female	Orange, yellow	Mate choice (by female)	Yes	Lattanzio *et al.* (2014)
				Mate choice (by male)	Yes	Krohmaly *et al.* (2018)
		Male	Orange, yellow/green, blue, green, yellow/green with	Aggression	Yes	Thompson & Moore (1991*b*, 1992)

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blue/green patch, orange with blue/green patch	Antipredator behaviour	Yes	Thaker *et al*. (2009)
	Bite force	No	Meyers *et al*. (2006)
	Body condition	No	Taylor & Lattanzio (2016)
	Body mass after food limitation	No	Jaworski & Lattanzio (2017)
	Body size	Yes	Hover (1985)
		No	Thompson & Moore (1992); Meyers *et al*. (2006); Taylor & Lattanzio (2016)
	Body temperature	No	Paterson & Blouin-Demers (2018)
	Boldness	Yes	Taylor & Lattanzio (2016)
	Diet	Yes*	Lattanzio & Miles (2016)
	Display behaviour	Yes	McElroy *et al*. (2007); Hover (1985); Thompson & Moore (1992)
	Display duration	No	McElroy *et al*. (2007)
	Dominance	Yes (but results not entirely consistent)	Hover (1985); Carpenter (1995*a*); Thompson & Moore (1991*b*); Taylor & Lattanzio (2016)
	Endurance/stamina	Yes	Jaworski & Lattanzio (2017)
	Endurance/stamina after food limitation	No	Jaworski & Lattanzio (2017)
	Growth rate	Yes	Thompson *et al*. (1993); Thompson & Moore (1991*b*)
	Mate choice (by female)	Yes	Lattanzio *et al*. (2014)

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			Mate choice (by male)	Yes	Krohmaly *et al*. (2018)
			Morphology (body height, head length)	No	Meyers *et al*. (2006)
			Morphology (head shape, jaw length)	Yes*	Lattanzio & Miles (2016)
			Mating behaviour	Yes	Krohmaly *et al*. (2018); Thompson & Moore (1991*b*)
			Sprint speed	No	Meyers *et al*. (2006)
			Stress response (corticosterone)	No	Thompson & Moore (1992); Knapp *et al*. (2003)
			Survival	No	Paterson & Blouin-Demers (2018)
			Territory quality	Yes	Paterson & Blouin-Demers (2018)
			Territory size	Yes	Paterson & Blouin-Demers (2018)
			Testosterone	Yes*	Knapp *et al*. (2003)
				No	Thompson & Moore (1992)
Side-blotched lizard (*Uta stansburiana*)	Female	Orange, yellow	Immunity (humoral immune response)	Yes*	Svensson *et al*. (2001*a*); Svensson *et al*. (2001*b*)
			Mate choice (by female)	Yes	Bleay & Sinervo (2007)
			Offspring fitness	Yes*	Sinervo *et al*. (2001)
			Reproductive costs	Yes	Svensson *et al*. (2001*a*); Svensson *et al*. (2002); Bleay & Sinervo (2007)
			Reproductive strategy	Yes*	Lancaster *et al*. (2010); Sinervo *et al*. (2000*b*)

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				Social behaviour	Yes	Svensson *et al*. (2002); Comendant *et al*. (2003)
				Stress response (corticosterone)	Yes*	Comendant *et al*. (2003)
		Male	Orange, yellow, blue, orange-blue	Anti-predator behaviour	Yes	Thaker *et al*. (2009)
				Endurance/stamina	Yes	Mills *et al*. (2008)
				Immunity (humoral immune response)	No	Mills *et al*. (2008)
				Mate choice (by female)	Yes	Bleay & Sinervo (2007)
				Reproductive strategy	Yes	Sinervo & Lively (1996)
				Social behaviour	Yes	Bleay *et al*. (2007)
				Sprint speed	No	Mills *et al*. (2008)
				Stress response (corticosterone)	No	Mills *et al*. (2008)
				Testosterone	Yes	Sinervo *et al*. (2000*a*); Mills *et al*. (2008)
Sphaerodactylidae	Atlas day gecko (*Quedenfeldtia trachyblepharus*)	Female	Orange, yellow, white	Body condition	No	Blouin-Demers *et al*. (2013)
				Body size	No	Blouin-Demers *et al*. (2013)
				Immunity (ectoparasite prevalence)	No	Blouin-Demers *et al*. (2013)
				Morphology (relative jaw size)	No	Blouin-Demers *et al*. (2013)
		Male	Orange, yellow, white	Body condition	No	Blouin-Demers *et al*. (2013)
				Body size	No	Blouin-Demers *et al*. (2013)
				Immunity (ectoparasite prevalence)	No	Blouin-Demers *et al*. (2013)
				Morphology (relative jaw	Yes	Blouin-Demers *et al*. (2013)

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				length)		
	Roze's gecko (*Gonatodes rozei*)	Male	Orange/yellow, dull yellow, grey-brown with pale yellow markings, grey-brown with black suffusions between yellow markings	–	–	Rivero-Blanco & Schargel (2012)
Tropiduridae	Striped lava lizard (*Tropidurus semitaeniatus*)	Male	Yellow, black	Aggression Body size Dominance Sprint speed	Yes Yes Yes No	Bruinjé *et al*. (2019*a*) Bruinjé *et al*. (2019*b*) Bruinjé *et al*. (2019*a*) Bruinjé *et al*. (2019*a*)

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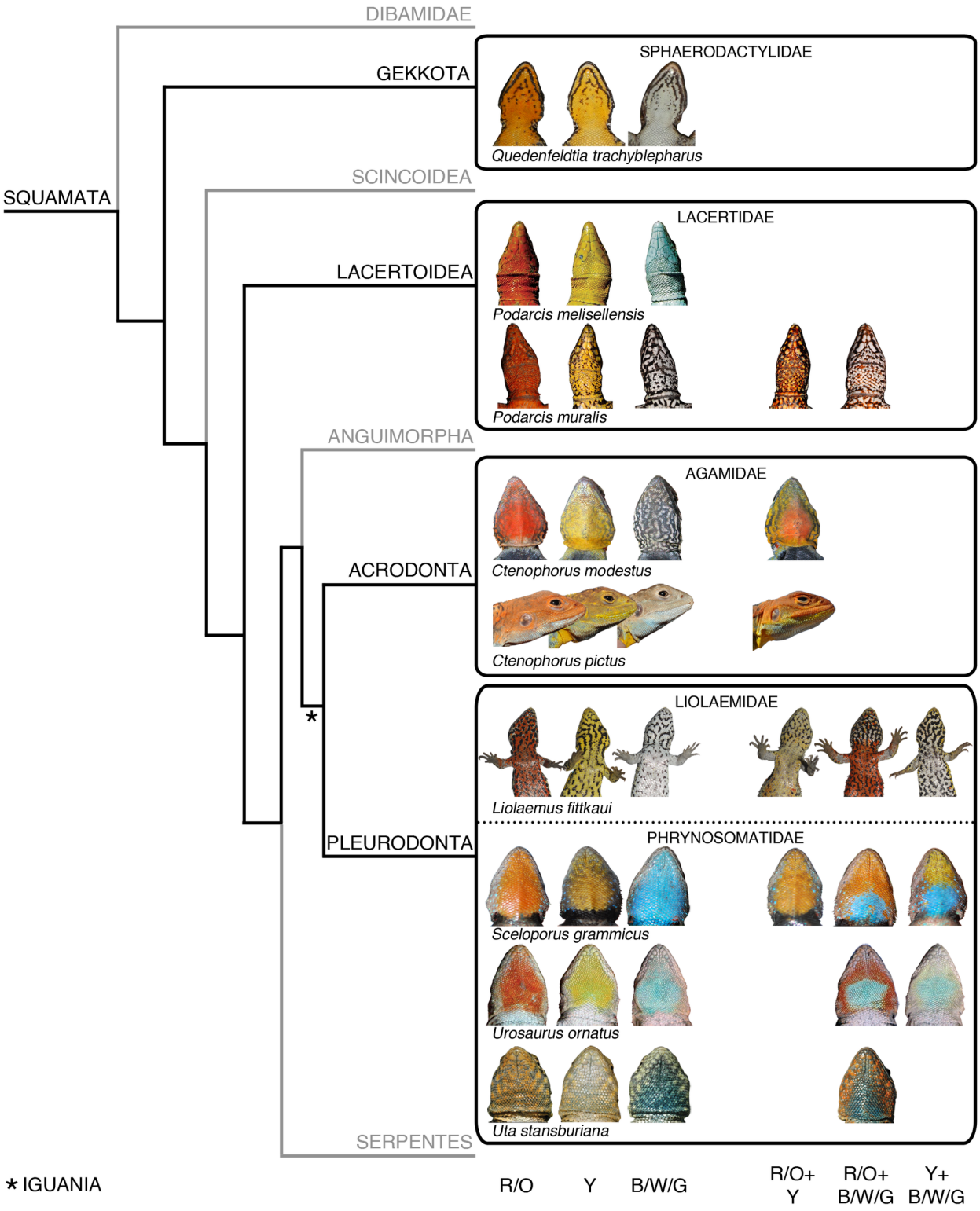

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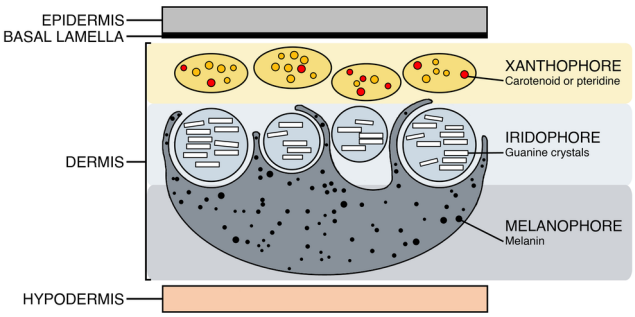

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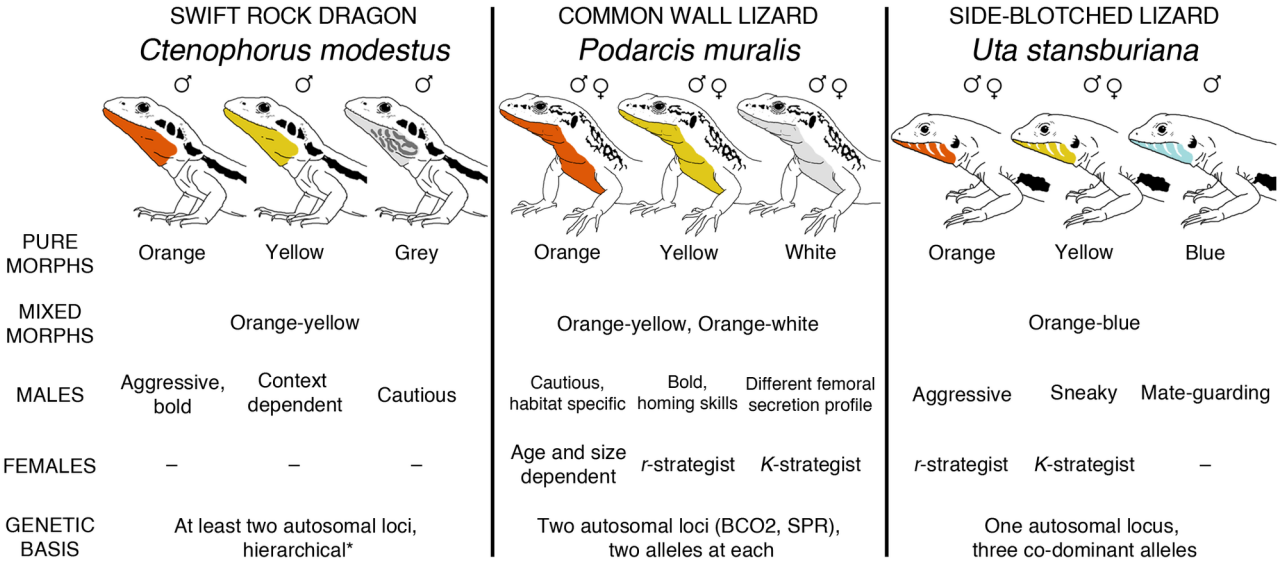

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