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Structural and environmental constraints on paired appendages reduction among vertebrates

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ABSTRACT

Burrowing habits or complex environments have been generally considered as potential drivers acting on appendicular skeleton reduction and loss among vertebrates. Herein we suggest that this may be the case for lissamphibians and squamates, but that fin loss in fishes is usually prevented due to important structural constraints, as pectoral fins are commonly used to control rolling and pitching. We provide an overview of the distribution of paired appendage reduction across vertebrates while examining the ecological affinities of finless and limbless clades. We analysed the correlation between life style and fin or limb loss using the discrete comparative analysis. The resulting Bayesian Factors indicate a strong evidence of correlation between: (i) pectoral-fin loss and coexistence of anguilliform elongation and burrowing habits or complex habitat in teleost fishes, and (ii) limb loss and burrowing or grass-swimming life style in squamate reptiles and lissamphibians. These correlations suggest that a complex environment or a fossorial habit constitute driving forces leading to appendage loss. The only locomotion style that is functional even in absence of paired appendages is the undulatory one, which is typical of all elongated reptiles and lissamphibians, but certainly less common in teleost fishes.

ADDITIONAL KEYWORDS: limb loss – eel-like fishes – elongated tetrapods – comparative phylogenetic analyses – amphibians – reptiles

INTRODUCTION

Reduction or loss of the appendicular skeleton occurred multiple times in representatives of several fish and tetrapods lineages. Among extant tetrapod classes (Moyle & Cech, 2003; Vaughan *et al.*, 2011; Pough *et al.*, 2015; Morrison *et al.*, 2018), extreme reduction or loss of limbs occurred in mammals (cetaceans and sirenians), birds (moa and kiwi), squamate reptiles (snakes, amphisbaenians and several groups of lizards) and "amphibians" (the Carboniferous-Permian aistopods and the lissamphibian caecilians plus a few groups of salamanders), whereas the loss of paired fins has been observed in several groups of teleost fishes. Even though in both mammals and birds, reduction and skeletal loss affect alternatively the forelimbs or hindlimbs only, there are several groups of squamate reptiles, amphibians and teleost fishes that exhibit a complete absence of paired limbs or fins. Despite these groups are phylogenetically distant, they all share some similarities. First of all, squamate reptiles, lissamphibians and teleosts characterized by a reduction of the appendicular skeleton usually exhibit an elongated body (Gans, 1975; Ward & Mehta, 2010 and references therein). According to Greer (1991), there are fifty-three squamate lineages that have undergone limb reduction, distributed among Agamidae, Amphisbaenia, Anguidae, Anniellidae, Chamaleonidae, Cordylidae, Dibamidae, Diploglossidae, Gekkota, Gerrhosauridae, Helodermatidae, Lanthanotidae, Ophidia, Pygopodidae, Scincidae and Teiidae. The situation is different among lissamphibians as, although different groups exhibit an elongated body, only three lineages show appendages reduction or loss. Caecilians (Gymnophiona) are the only lissamphibians characterized by a complete loss of both fore- and hindlimbs. Members of Sirenidae, on the other hand, have lost the hindlimbs, but retain reduced forelimbs. In the end, the only genus included within Amphiumidae, *Amphiuma*, has very short and motionless limbs. Among extinct basal tetrapods, the Carboniferous-Permian Aïstopoda are completely limbless, showing a remarkable convergence with the serpentiform body plan of snakes and caecilians (Carrol *et al.*, 1998; Pardo & Mann, 2018). In general, all the elongated squamates and lissamphibians exhibit a similar lateral undulation even if using different types of locomotion (Gans, 1975). Conversely, elongated fishes exhibit carangiform or anguilliform locomotion (Sfakiotakis *et al.*, 1999, Horner & Jayne, 2008; Pfaff *et al.*, 2016). If the carangiform pattern is characterized by more or less rigid movements of the caudal portion of the body and tail, the anguilliform pattern is characterized by a sinuous wave that moves through the body (e.g., eels) or only in its posterior part (e.g., catfishes). The anguilliform movement, which could be associated to the "serpent-like" movement of tetrapods, is typical of at least half of the highly elongated actinopterygians (Ward & Mehta, 2010; Reece & Mehta, 2013). In particular, anguilliform elongation (*sensu* Ward & Mehta, 2010) is typical of *Erpetoichthys calabaricus* among Polypteriformes (Suzuki *et al.*, 2010), some members of the clades Ophidiiformes, and Gobionellidae (genus *Luciogobius*; Yamada *et al.*, 2009), and most of the members of the clade Anguilliformes, Lampridiformes, Mastacembelidae, and Zoarcales (Ward & Mehta, 2010). Some elongated members of the clades Ateleopodiformes, Liparidae, and Siluriformes show a body plan with an enlarged, heavy head and their anguilliform movement is limited to the posterior part of the body (i.e., not including the pectoral area). The pelvic fins are lost in several, morphologically different groups of fishes, in more than 90 teleost lineages (Nelson, 1989; Kriwet & Pfaff, 2019), whereas the pectoral fins are primarily lost in elongated fishes with anguilliform locomotion (Mehta *et al.*, 2010). Eel-like clariid species represent a unique case among vertebrates, as their paired fins show a very high intraspecific level of morphological variability, preventing their absence to be used as a diagnostic feature at the species level (Devaere *et al.*, 2004). As in other vertebrates (O'Reilly *et al.*, 1997), the loss of fins in clariids was regarded as related to a highly specialized fossorial mode of life by Devaere *et al.* (2004), although this hypothesis has not been tested yet. More generally, the idea that the presence of appendages may represent an impediment for burrowing for both terrestrial and aquatic animals is widely accepted. Recently, Da Silva *et al.* (2018) demonstrated that fossoriality has been the evolutionary driver leading to the origin and development of the snake body plan. Extinct relatives of extant limbless forms (e.g., amphisbaenians and caecilians) indicate that fossoriality evolved before the limb loss since they have cranial adaptations for burrowing, but maintain variably developed appendages (Evans & Sigogneau-Russell, 2001; Jenkins *et al.*, 2007; Tałanda, 2016). Nevertheless, fossoriality is not the only evolutionary driver for limb loss in reptiles, and limbless squamates are traditionally divided into short-tailed burrowers or long-tailed surface dwellers, moving through loose sand or vegetation (Evans, 1998; Wiens *et al.*, 2006).

As far as fishes are concerned, it is known that a number of fishes exhibiting an eel-like body morphology are either crevice-dwellers or burrowers (tail- or head-first; De Schepper *et al.*, 2007a, b; Herrel *et al.*, 2011). Nevertheless, previous studies mainly focused on the correlation between elongation and habitat, or trophic adaptations (Ward & Mehta, 2010; Mehta *et al.*, 2010; Claverie & Wainwright, 2014), but did not find any apparent connection. Mehta *et al.* (2010), in particular, stated that, although it is generally true that terrestrial vertebrates evolved an elongated, limb-reduced body plan as an adaptation for the burrowing lifestyle, little is known about how much the elongate body form may be adapted for aquatic habits.

Herein we suggest that a distinction can be done in fishes between anguilliform and stiffer-body elongation (*sensu* Ward & Mehta, 2010) when studying correlations between habitat and body plan, as the constraints due to balance problem during swimming connected with these two body forms are different. Moreover, we attempt to address the question: once a fish has evolved an eel-like elongation, does the habitat have an influence on paired-fins loss? Is there a common trend in appendage loss in teleosts and tetrapods? Herein, we argue that the limbless body plan in vertebrates is affected by similar environmental constraints, provided by the habitat or life style, and we try to summarize how widespread this pattern (i.e. dense, complex environment acting on appendage reduction and loss) actually is.

GENETIC AND DEVELOPMENTAL CONTROL OF APPENDAGE LOSS

The development of appendages is polygenic, involving genes with pleiotropic effects (Lande, 1978; Hall, 2008). Therefore, genes involved in limbs and paired fins development also function on other developing systems, such as jaws or genitals (Rosa-Molinar & Burke, 2002). This is the reason why genes associated with limb buds are generally not lost, even in limbless forms (Bejder & Hall, 2002). The developmental mechanism of the formation of paired appendages is deeply conserved among gnathostomes (Dahn *et al.*, 2007; Letelier *et al.*, 2018) and it involves two signalling centers located in the fin/limb bud. The first of them is the apical ectodermal ridge (AER), which helps to maintain the second one, the zone of polarizing activity (ZPA), the cells of which express the Sonic hedgehog (Shh) gene, associated with the development of the fins or limbs (Cohn, 2001; Bejder & Hall, 2002; Thewissen *et al.*, 2006). At the same time Hox genes control the position of both girdles and appendages along the body. In particular, the anterior expression boundaries of HoxC-6 and HoxC-8-10 coincide with the localization of fore- and hindlimb buds respectively (Bejder & Hall, 2002). Reduction and loss of appendages can occur due to regression of different phases in the conserved genetic pathway for appendage development. Tanaka *et al.* (2005), for example, reported that pelvic-fin loss can be achieved through different mechanisms in pufferfishes and sticklebacks. In the first case, the reduction is due to an altered expression of the gene Hoxd9a in lateral mesoderm, whereas in the second case Pitx1, a gene responsible for appendage initiation, fails to be expressed (Shapiro *et al.*, 2004). In pythons, limbs development is arrested in two different ways. Forelimb buds are not developed at all, because of the widespread expression of HoxC-6 and HoxC-8 genes throughout the lateral plate mesoderm, meaning that no boundary conditions are established for forelimbs to form and therefore there is no pectoral limb initiation (Cohn & Tickle, 1999; Cohn, 2001; Bejder & Hall, 2002). On the contrary, hindlimb buds are formed, but they have a very smooth ectodermal jacket forming a small AER, which causes a precocious interruption of the growth (Cohn, 2001). Serpentiform lizards and urodeles have different levels of limb reduction that can vary considerably depending on the species (Greer, 1991). Nevertheless, in general, the formation of their limb buds starts and then regresses, or the expression of Shh can have a shortened duration, leading to loss of some digits or of a larger part of the limbs (Raynaud, 1990; Hinchliffe, 2002; Shapiro *et al.*, 2003; Tanaka *et al.*, 2005). As far as cetaceans are concerned, pelvic limb buds begin to form but fail to fully develop, in a similar way to the python hindlimbs (Bejder & Hall, 2002; Tanaka *et al.*, 2005). Nevertheless, it is likely that the mechanism is slightly different from that of snakes, as the dolphin *Stenella attenuata* shows a normal AER during development, but the absence of Hand2 – one of the upstream regulators of the Shh transcription – causes a perturbed initial establishment of the ZPA and the consequent absence of Shh expression (Thewissen *et al.*, 2006).

Therefore, fin and limb formation has indeed very conserved genetic and ontogenetic pathways among gnathostomes, but developmental causes of appendage loss can be very diverse within and among different groups (Hall, 2008).

MATERIAL AND METHODS

We compiled a database (Appendix 1 and 2) that includes 125 species of teleost fishes, 74 species of lissamphibians and 151 species of squamate reptiles. For the taxon sampling of teleost fishes, we selected all the groups characterized by pectoral fin loss: Anguilliformes, Clariidae, Gobionellidae (strong reduction of the pectoral fin in the genus *Luciogobius*), and Trichomycteridae. The groups of Zoarcales and

Mastacembelidae have some finless members, but we did not include them in our analysis, as their ecology and phylogenetic relationship are poorly known.

We combined different phylogenetic trees that contain the group included in the study (either the recent-most or the complete-most phylogenetic analyses), and in particular: Santini *et al.* (2013) for Anguilliformes, Baskin (1973), Datovo & Bockmann (2010), and DoNascimiento (2015) for Trichomycteridae, Wright (2017) for Clariidae, and Yamada *et al.* (2009) and Thacker (2013) for Gobionellidae. We sampled part of the taxa contained in these phylogenies, several of them being used as outgroups, as they do not show any pectoral fin loss. Particular attention was paid on groups with finless members included in these phylogenies, among which at least one representative species for every family has been selected, but including all the taxa with complete information about fins and ecological habits that were close to the node where pectoral fins were lost. In fact, for studies concerning causal relationships of specific traits, the most important taxa to sample are the ones near to the node where the trait we want to study (e.g., fin or limb loss) first occurred and got fixed. Any potential evolutionary innovation that originated after the first occurrence and fixation of the trait should not be considered as a potential evolutionary driver and it is therefore not essential to insert many derived taxa in the sample (Macaluso & Tschopp, 2018). The same procedure was followed to compile the database of lissamphibians (complete sample of basal Gymnophiona, Sirenidae, and Amphiumidae), starting from the phylogeny published by Pyron and Wiens (2011), and squamate reptiles (complete sample of basal limbless Agamidae, Amphisbaenia, Anguidae, Anniellidae, Dibamidae, Diploglossidae, Ophidia, Pygopodidae, and Scincidae), using the phylogenies of Reeder *et al.* (2015), Da Silva *et al.* (2018), and Pyron *et al.* (2013).

The taxon sampling was of course limited by the information available for the taxa and we chose species for which the following is known: i) phylogenetic position; ii) presence or absence of appendages; iii) behaviour or ecology. Our limited knowledge of these data is particularly relevant in the case of extinct taxa, because of the difficulty in reconstructing their life habits. Moreover, it is not so common to find a complete articulated skeleton of terrestrial animals that can tell us if appendages where present or not in a certain taxon (see for example the case of the stem-group caecilian described by Evans & Sigogneau-Russell, 2001). For these reasons, the sample of extinct taxa is limited in this study to relatives of extant taxa representing their stem, whenever information about them is available. We collected information about elongation of the body, presence or absence of the appendages, and lifestyle (see Appendix 1, 2, and 3 for the references). Elongation has only been scored for fishes, which display different kinds of elongation (anguilliform and stiffer-body; Ward & Metha, 2010; Maxwell & Wilson, 2013) and it is therefore important to consider this character in the analysis. In particular, fishes are herein considered as elongated if their length is more than five times the maximum body depth. The considered cases of fin loss in fishes are restricted to those taxa without pectoral fins because the pelvic fins are absent in a huge number of groups due to different factors (e.g., Nelson, 1989). *Luciogobius* has been scored as lacking its pectoral fins as it shows an extreme pectoral fin reduction compared to its close relatives (Hyun-Geun & Seung-Ho, 2014). Squamate reptiles and lissamphibians were scored as lacking their limbs (1) if both pairs of appendages were absent, and as intermediate (01) if only one pair of appendages has been lost. The only exceptions to this rule are snakes with underdeveloped hindlimbs (e.g., pythons, *Pachyrhachis*, *Haasiophis*), the genus *Dibamus* in which the presence of hindlimbs are a sexual dimorphic character (vestigial hindlimbs only present in males; Koppetsch *et al.*, 2019), and *Amphiuma*, which have been scored as limbless although they possess small vestigial hindlimbs useless for locomotion. Lifestyle has been divided in “fossorial” or “not fossorial”. Fishes are scored as 1 concerning “fossoriality” (i.e., column “fossoriality” in Appendix 1) when they have either burrowing habits or are crevices-dwellers, whereas squamate reptiles and lissamphibians were scored as “fossorial” (i.e., 1 in column “fossoriality” in Appendix 2) when they are either burrowers or grass-swimmers. Although burrowing and grass-swimming result in different constraints acting on the whole body, the lateral sides of the body (and consequently the appendages) of burrowing and grass-swimming animals, are constrained in a similar way, by the substrate in burrowers and crevices-dwellers and grass in grass-swimmers. Additional information and references about life style, phylogenetic position, and presence/absence of appendices are present in the supplementary material (Appendix 1, 2, and 3). After collecting these data, we compiled a composite phylogenetic tree in Mesquite (Maddison & Maddison, 2018) reporting all the included taxa, based on already existing phylogenies listed above. We performed the discrete comparative analysis available in the software BayesTraitsV3 (Meade & Pagel, 2017). Discrete comparative analysis is used to test if two binary traits are correlated and its significance is established by comparing the likelihoods (derived using Markov chain Monte Carlo – MCMC) of two models, one assuming that the traits evolved independently and the other assuming that their evolution is correlated. Two binary traits can be described by four possible states, written as "0,0", "0,1", "1,0" and "1,1". The independent model assumes that the two traits evolve independently, e.g. the transition from 0 to 1 in the first trait is independent from the state of the second trait, whereas the dependent model assumes that the traits are correlated and the rate of change in one trait is dependent from the state of the other. The test was performed structuring an input database as an Excel file of a table at two entrances (see Appendix 1, 2): species in the rows and characters in the columns. Concerning fishes, the two binary characters are pectoral fin loss and a character that is scored as 1 only if the taxon is both elongated (as defined above) with anguilliform locomotion and either fossorial or crevices-dweller. As all the fossorial (or grass-swimmers) lissamphibians and squamates have an extremely elongated body, elongation has not been considered as an essential character in their case and the two binary characters are therefore limb loss and fossoriality or grass-swimming. Given that arbitrary branch lengths are commonly used and well-supported in the literature using Comparative Methods (Grizante *et al.*, 2012, and references therein), we performed the statistical analyses using an arbitrary branch length of 1.0 and all branches were scaled to 0.1, as suggested for the software BayesTraitsV3 (Meade & Pagel, 2017). As is usual in this kind of analysis, we set all the priors to an exponential with a mean of 10 and use the stepping stone sampler with 100 stones and 1000 iterations per stone to estimate the marginal likelihood (see the manual for users of BayesTraitsV3). We performed two different analyses, one for teleost fishes and a separate one for lissamphibians and squamate reptiles, to make it easier to manipulate the large trees in Mesquite. The phylogenetic trees we built are reported in Figures 1 and 2. It is worth noting that in the discrete analysis of BayesTraitsV3 it is not necessary to infer the ancestral state of the characters and thus the coloured branches in the figures are just graphical representations. Here, we evidence the character states with different colours, referring to appendices 1 and 2. In particular, names depicted in red indicate species scored with 1 for appendage loss, whereas light blue species are the ones scored as 01. Colour of the branches refers to the second character, intended as the co-occurrence of eel-like elongation and burrowing behaviour (or crevices or sea-grass inhabitants) for teleost fishes and burrowing or grass-swimming habits for squamate reptiles and lissamphibians.

RESULTS

The analysis resulted in two values of the marginal likelihood, one for the dependent model and one for the independent model (Table 1). Both are described in a logarithmic scale. To test whether the traits are correlated or not, we calculate a log Bayes Factor between the dependent and independent models. The calculations for Log Bayes factors are given below.

Log BF = 2 (log marginal likelihood dependent model – log marginal likelihood independent model)

The Log BF of 41.467358 in one case and of 44.253558 in the other suggest that there is strong evidence for correlated evolution, as a "strong evidence" of correlation is considered when Log BF has values higher than 5 (Gilks *et al.*, 1996).

DISCUSSION

The environmental conditions may represent relevant evolutionary drivers leading to the emergence of new body morphologies within clades. Nevertheless, very different environmental conditions may provide similar constraints on organisms living – and moving – in them, thereby leading to the development of convergent morphologies. Burrowing (or interstitial) animals, grass-swimmers, and marine crevices-dwellers represent an example of this, because the presence of appendages is not favoured in the environment where they live.

SQUAMATES AND LISSAMPHIBIANS

Previous hypotheses about squamate reptiles and lissamphibians developing a limbless body plan as an adaptative response to burrowing or grass-swimming (Evans, 1998; Wiens *et al.*, 2006; Da Silva *et al.*, 2018) are confirmed by our results. Basal scolecophidian snakes and more derived fossil taxa (e.g., *Dinilysia*, *Wonambi*) are fossorial (or semifossorial as in the case of *Yurlunggur*; Palci *et al.*, 2018) and several lines of evidence support the hypothesis that the fossoriality of basal snakes is plesiomorphic (Miralles *et al.*, 2018). Moreover, comparative geometric morphometric studies on skulls demonstrated that lizards could not have transitioned to snakes by any other evolutionary path than through fossoriality (Da Silva *et al.*, 2018).

The phylogenetic relationships of the stem lineage of Ophidia are still highly controversial and it is therefore difficult to understand the ecology of the basal-most fossil snakes. For example, the life style of the Cretaceous snake *Coniophis* has been reconstructed as fossorial (Longrich *et al.*, 2012), but its phylogenetic position is not resolved. In fact, Longrich *et al.* (2012) consider it as the basalmost stem ophidian, but Caldwell *et al.* (2015) place this taxon in a more derived position. The situation is similar as far as most of the stem taxa are concerned. In general, caution is warranted when using single fossil snakes to make broad extrapolations about early snake biology (Palci *et al.*, 2018). It is also still unresolved which one between the body- or head-first hypotheses is the most likely, with different evidence sustaining either the former or the latter (Longrich *et al.*, 2012; Caldwell *et al.*, 2015; Da Silva *et al.*, 2018). It is important, nevertheless, to remark that our results suggest a general evolutionary trend connecting fossoriality (and, more broadly, complex habitats) with limb-loss, but this does not mean that this same evolutionary force acted in every single group that evolved a reduction or loss of the limbs, as different constraints can act in different groups (Macaluso & Tschopp, 2018). There are, in fact, few groups of squamates that evolved a limbless body, which are generalist surface-dwellers. Two remarkable exceptions are, for example, the skinks and the pygopodids. Skinks evolved limblessness independently in several lineages, even within a single genus (e.g., *Lerista*; Skinner *et al.*, 2008; Fig. 3G), many of which are burrowers, whereas some others are also more generalist surface-dwellers (Weins *et al.*, 2006; Camaiti *et al.*, 2019). Pygopodidae is the only family of gekkotans that has members devoid of limbs. They are generally surface-dwellers, even if the basal-most forms live in the litter (Dorrough & Ash, 1999; Wall & Shine, 2013), a lifestyle that can regarded as fossorial. The fact that limb loss is so common within squamates is not surprising, since elongated reptiles are characterized by an undulatory locomotion and appendages that primarily help to carry forward the body (Sfakiotakis *et al.*, 1999; Grillner, 2011) and limbs can therefore be lost without a relevant impact on their fitness.

Within Amphisbaenia (Fig. 3I), the stem taxon *Slavoia darevskii* apparently proves that fossoriality evolved before the limb loss, as it has clear cranial adaptations for burrowing, but also limbs (Tałanda, 2016). A different phylogenetic analysis placed *Cryptolacerta hassiaca* on the stem of this group (Müller *et al.*, 2011), but the situation is substantially unchanged, as it shows partially reduced limbs and cranial adaptations for burrowing. The same situation is found in the clade Gymnophiona, in which the fossil taxon *Eocaecilia micropodia* possesses fossorial adaptations and small limbs (Jenkins *et al.*, 2007). Salamanders of the family Sirenidae (Fig. 3E) lack hind limbs and show some digital reduction of the forelimbs and Amphiumidae have very small and motionless limbs, but there is no information on the appendicular skeleton of stem forms referred to these groups (Lande, 1978).

Studies of developmental genetics clearly evidence that there are multiple ways to produce a limbless body plan (Kohlsdorf *et al.*, 2008). In a similar way, it is likely that fin or limb loss in different, unrelated groups may be originated through different evolutionary drivers. In any case, our analysis suggests that there is a general correlation between burrowing or grass-swimming habits and limb loss.

TELEOSTS

As far as fishes are concerned, the situation is more complex, because of their locomotion style. Fishes generally use the caudal fin as a propulsor, whereas the paired fins are used to control lateral movement and to prevent rolling and pitching, although there are also fishes that use oscillatory or undulatory movements of the paired fins as thrust generation (see Sfakiotakis *et al.*, 1999 for an extensive review on fish swimming mode). Short-bodied fishes with ostraciiform swimming mode as well as elongated fishes with carangiform locomotion use their pectoral (and pelvic) fins to control their body and therefore they simply cannot lose their fins, even if this change would be advantageous in their environment. On the contrary, the anguilliform swimming mode may permit the loss of paired fins without a remarkable effect on locomotion capability. In this case, in fact, the paired fins are not useful to prevent rolling or pitching, even if they can help locomotion (Sfakiotakis *et al.*, 1999). This is also clearly demonstrated by the cetaceans and sirenians, the only mammal clades with representatives characterized by elongated bodies, which lose a pair of appendages. During the course of their evolutionary history, cetaceans and sirenians have lost pelvic fins, in a similar way to numerous fish clades (e.g., Nelson, 1989, Bejder & Hall, 2002). Their locomotion is undulatory, but differently from that of eel-like fishes, since waves are produced in a vertical plane, which do not prevent from the rolling and pitching problems. This is surely coupled with the fact that they did not lose their pectoral fins, which have acquired a stabilizing and steering function, not generating any propulsive movements (Bejder & Hall, 2002). Our results show that fin loss in fishes is restricted to taxa characterized by an eel-like morphology of the body and most likely related to the burrowing lifestyle or to cryptic life in reef ecosystems. This is clearly evidenced by the consistently eel-like morphology of finless taxa that are characterized by burrowing or crevice-dwelling habits (e.g., Muraenidae; Fig. 3A). The most diverse clade of eel-like fishes is the elopomorph order Anguilliformes, in which pelvic fins are generally absent, but pectoral fins are present in some groups. Although the interpretation of the ecological preference of extinct fishes is not always easy, it is reasonable to hypothesize that basal anguilliforms (e.g., *Anguillavus* or *Luenchelys*; Belouze, 2002; Belouze *et al.*, 2003 a,b) were in some ways reef-associated, because the Cretaceous plattenkalk deposits in which they have been found originated on the outer part of the Lebanese carbonate platform, which was mostly occupied by oyster and rudist mounds and patch reefs (Hemleben & Swimburne, 1991). Members of the extant families Protanguillidae and Synaphobranchidae, regarded as the most basal lineages of crown Anguilliformes (Santini *et al.*, 2013), have small pectoral fins, and are characterized by a variety of ecological adaptations. For example, protoanguillids live in submarine caves (Johnson *et al.*, 2011) and the most basal synaphobranchid, *Simenchelys parasitica*, developed a peculiar parasitic lifestyle (e.g., Jaquet, 1920). The main anguilliform group of real burrowers is the Moringuidae, whose members are in general burrowers (head or tail-first) or crevice-dwellers with a marked reduction of paired fins (Castle, 1986; Allen & Steene, 1988; De Schepper *et al.*, 2005). The extant species of the genus *Anguilla* are demersal and do not show a clear reduction of the paired fins, a pattern also shared with three extinct species, *A. ignota*, *A. multiradiata* and *A. elegans* (Winckler, 1861; Micklich, 1985; Riede, 2004; Gaudant *et al.*, 2018). Some lineages within the family Congridae (i.e. the clade composed by *Ariosoma*, *Heteroconger* and *Paraconger*, see Santini *et al.*, 2013) includes burrowing fishes devoid of paired fins (Smith, 1981; Riede, 2004; Bacchet *et al.*, 2006). Pectoral fins are lost also in certain crevices-dwelling species belonging to the family Muraenidae (Robins *et al.*, 1991; Chen *et al.*, 1994; Lieske & Myers, 1994; McCosker, 2010; Reece *et al.*, 2010).

A unique case is the benthic gobionellid genus *Luciogobius*, because it is probably the only fish taxon adapted to an interstitial life in gravel beaches (Yamada *et al.*, 2009). The main adaptation consists in an anguilliform elongation of the body that confer it enough agility to move in a three-dimensional complex habitat, similar to that characteristic of terrestrial and aquatic burrowers (Gans, 1975; Yamada *et al.*, 2009). Interestingly, in parallel with the elongation of the body, interstitial species of *Luciogobius* (Fig. 3C) underwent fin reduction, whereas elongated species of Gobionellidae, which are not interstitial but have a benthic or nektonic lifestyle (e.g., genera *Inu* or *Clariger*), exhibit completely developed paired fins. A similar condition is also characteristic of those species of the Gobionellidae that live in reefs or on muddy substrates but are not eel-shaped (e.g., *Periophtalmus barbarous*, *Scartelaos histiophorus*).

Within the Neotropical catfish family Trichomycteridae, the Glanapteryginae are interstitial fishes living in complex habitats and they are mostly eel-shaped with a clear reduction of paired fins, which are usually very thin becoming filiform and without any equilibrium function (De Pinna, 1988; Schaefer *et al.*, 2005; Villa-Verde & Costa, 2006). Catfishes belonging to Clariidae are generally elongated, with an anguilliform swimming mode that is often limited to the posterior part of the body, also extending to its anterior part in some species. All the species devoid of paired fins live in complex or highly vegetated habitats, thereby confirming the hypothesis of fin reduction driven by environmental complexity (Fig. 3B; see Appendix 1 for references).

Finally, the Mastacembelidae represent another very peculiar case, as they are eel-shaped fishes, also called spiny eels because of the long series of dorsal-fin spines (Vreven, 2005). It is worth mentioning them because of the particular case of the only two species of this group (*Mastacembelus apectoralis* (Fig. 3D) and its sister taxon, *M. micropectus*) that exhibit a considerable reduction in pectoral-fin size, which is considered to be related to the highly structured environments they live in (Brown *et al.*, 2011). Their phylogenetic relationships are poorly known, and thus they have not been sampled in our comparative analysis.

Our study reveals the existence of a correlation between the reduction and/or loss of pectoral fins and the coexistence of an eel-like body morphology, which makes unnecessary the use of pectoral fins to prevent rolling and pitching, and of an environmental constraint due to burrowing and crevice- or seagrass-dwelling. In fact, whereas being different habitat, the latter all have a similar effect on the appendages of fishes, because paired fins may hamper a free movement in these constrained environments. A similar correlation between burrowing or grass-swimming habits and limb loss is found also in squamate reptiles and lissamphibians, but the structural constraints are much less important in these groups as the locomotion is less constrained by appendages than in fishes due to the absence of balance problems.

FUTURE PERSPECTIVES

A relation between long-tailed patterns and surface dwelling, and conversely pre-caudally elongated morphotypes and burrowers has been proposed for squamates reptiles (Bellairs & Underwood, 1951; Evans, 1998), even if this hypothesis has never been proved with rigorous analyses. An interesting future perspective is to expand this hypothesis to anguilliform fishes. In fact, crevice- and seagrass-dwellers could be somehow associated with terrestrial surface-dwellers. Mehta *et al.* (2010) reported that the elongation in muraenids (i.e., crevices-dwellers) results from the addition of caudal rather than precaudal vertebrae to their axial skeleton, whereas elongation of the body in ophichthids and congrids (i.e. burrowers) is achieved by adding a similar number of vertebrae to their precaudal and caudal regions; however, additional studies on this subject including a larger taxon sampling and much more comparative information would be desirable.

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Figure and tables captions

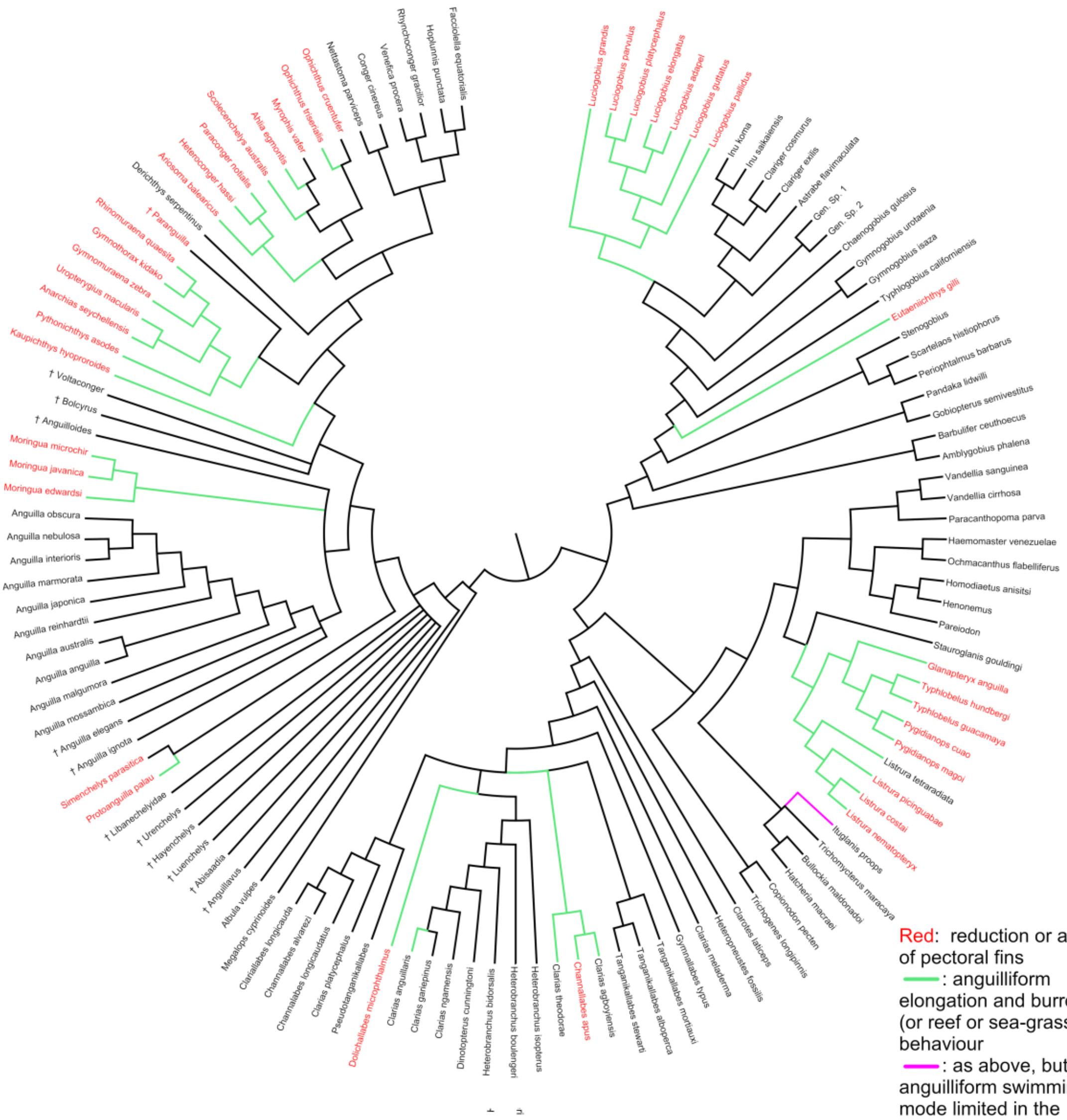
Figure 1. Composite phylogenetic tree of teleost fishes used for the analysis. See material and methods for the references concerning phylogenetic position and character state reconstruction. The coloured branches in the figure are just graphical representations and they do not represent any ancestral state reconstruction, as it is not a necessary step for the discrete comparative analysis using BayesTraitsV3.

Figure 2. Composite phylogenetic tree of lissamphibians and squamates used for the analysis. See material and methods for the references concerning phylogenetic position and character state reconstruction. The coloured branches in the figure are just graphical representations and they do not represent any ancestral state reconstruction, as it is not a necessary step for the discrete comparative analysis using BayesTraitsV3.

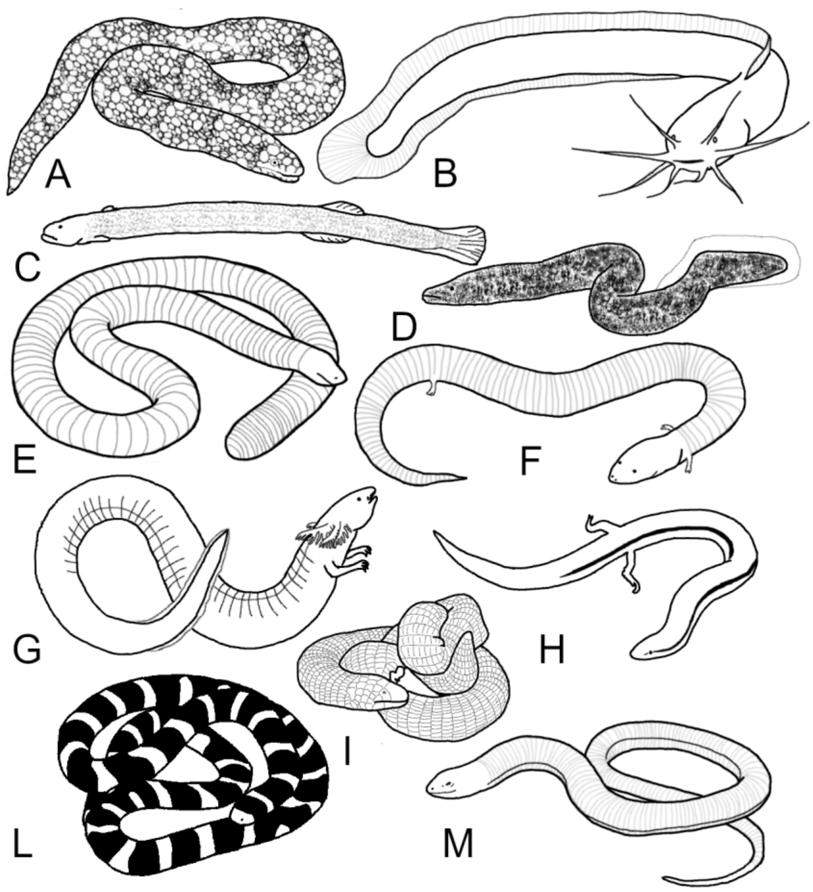
Figure 3. Examples of elongated vertebrate with fin or limb reduction or loss. A, *Anarchias seychellensis*, crevice-dweller (fish); B, *Channalabes apus*, living among tree roots (fish); C, *Luciogobius elongatus*, interstitial (fish); D, *Mastacembelus apectoralis*, living among sea vegetation (fish); E, *Caecilia volcani*, burrower (amphibian); F, *Amphiuma means*, burrower (amphibian); G, *Siren lacertina*, burrower (amphibian); H, *Lerista bipes*, surface-dweller (reptile); I, *Blanus cinereus*, burrower (reptile); L, *Anilius scytale*, burrower (reptile); M, *Pseudopus apodus*, grass-swimmer (reptile).

Table 1. Values of Log of marginal likelihood of the dependent and independent models, and Bayes Factor (BF) obtained using BayesTraitsV3. In both teleost fishes and lissamphibians and reptiles the logarithmic values of the Bayes Factor indicate a strong evidence of correlation.


Red: absence of at lesta one pair of limbs
: fossorial (or semifossorial) behaviour or grass-swimmer



Red: reduction or absence of pectoral fins
: anguilliform elongation and burrowing (or reef or sea-grass) behaviour
: as above, but anguilliform swimming mode limited in the posterior part of the body



Appendix 1. Teleost fishes database. Grey columns are the two columns used for the discrete analysis.

Taxon	**Group**	**Elongation**	**Anguilliform locomotion**	**Pectoral fins absent**	**Fossorial/complex habitat**	**Notes**	**Anguilliform + fossoriality**	**Data's reference**	**Phylogeny's reference**
Megalops cyprinoides	Elopomorpha	0	0	0	0	reef-associated	0	Riede, 2004	Santini *et al.,* 2013
Albula vulpes	Elopomorpha	0	0	0	0	reef-associated	0	Riede, 2004	Santini *et al.,* 2013
† Anguillavus	Elopomorpha	1	1	0	0	reef	0	Belouze, 2002	Pfaff *et al.*, 2016
† Abisaadia	Elopomorpha	1	1	0	0	reef	0	Belouze *et al.*, 2003 a	Pfaff *et al.*, 2016
† Luenchelys	Elopomorpha	1	1	0	0	reef	0	Belouze *et al.*, 2003 b	Pfaff *et al.*, 2016
† Hayenchelys	Elopomorpha	1	1	0	0	reef	0	Belouze *et al.*, 2003 a	Pfaff *et al.*, 2016
†Urenchelys	Elopomorpha	1	1	0	0	reef	0	Belouze, 2002	Pfaff *et al.*, 2016
† Libanechelyidae	Elopomorpha	1	1	0	0	reef	0	Taverne, 2004	Pfaff *et al.*, 2016

Protoanguilla palau	Anguilliformes	1	1	01	1	cave, reef associated	1	Belouze *et al.*, 2003 a	Santini *et al.,* 2013
Simenchelys parasitica	Synaphobranchidae	1	1	1	0	parasitic	0	Sulak & Shcherbachev, 1997	Santini *et al.,* 2013
† Anguilloides	Anguilliformes	1	1	0	0	reef	0	Blot, 1984	Pfaff *et al.*, 2016
Moringua edwardsi	Moringuidae	1	1	1	1	burrower, head-first; small, vestigial pectoral fins	1	Smith, 1997	Santini *et al.,* 2013
Moringua microchir	Moringuidae	1	1	1	1	burrower in sand; small, vestigial pectoral fins	1	Castle, 1986	Santini *et al.,* 2013
Moringua javanica	Moringuidae	1	1	1	1	reef	1	Allen & Steene, 1988	Santini *et al.,* 2013
†Anguilla ignota	Anguillidae	1	1	0	0	freshwater	0	Micklich, 1985	Pfaff *et al.*, 2016
†Anguilla multiradiata	Anguillidae	1	1	0	0	freshwater	0	Micklich, 1985	Pfaff *et al.*, 2016
†Anguilla elegans	Anguillidae	1	1	0	0	freshwater	0	Winckler, 1861	Pfaff *et al.*, 2016
Anguilla mossambica	Anguillidae	1	1	0	0	demersal	0	Riede, 2004	Santini *et al.,* 2013
Anguilla malgumora	Anguillidae	1	1	0	0	under rocks in flowstreams	0	Martin-Smith & Tan, 1998	Santini *et al.,* 2013
Anguilla anguilla	Anguillidae	1	1	0	0	demersal	0	Riede, 2004	Santini *et al.,* 2013
Anguilla australis	Anguillidae	1	1	0	0	demersal	0	McDowall & Beumer, 1980	Santini *et al.,* 2013
Anguilla reinhardtii	Anguillidae	1	1	0	0	demersal	0	Riede, 2004	Santini *et al.,* 2013
Anguilla japonica	Anguillidae	1	1	0	0	demersal	0	Yamada *et al.*, 1995	Santini *et al.,* 2013
Anguilla marmorata	Anguillidae	1	1	0	0	demersal	0	Rainboth, 1996	Santini *et al.,* 2013
Anguilla	Anguillidae	1	1	0	0	demers	0	Allen *et*	Santini *et*

obscura						al		*al.*, 2002	*al.,* 2013
Anguilla interioris	Anguillidae	1	1	0	0	demersal	0	Riede, 2004	Santini *et al.,* 2013
Anguilla nebulosa	Anguillidae	1	1	0	0	demersal	0	Riede, 2004	Santini *et al.,* 2013
† Voltaconger	Congroidea	1	1	0	0	?	0	Blot, 1984	Pfaff *et al.*, 2016
† Bolcyrus	Congroidea	1	1	0	0	?	0	Blot, 1984	Pfaff *et al.*, 2016
Derichthys serpentinus	Derichthydae	1	1	0	0	mesopelagic	0	Mundy, 2005	Santini *et al.,* 2013
Nettastoma parviceps	Congridae	1	1	0	0	abissale	0	Smith *et al.*, 1981	Santini *et al.,* 2013
Conger cinereus	Congridae	1	1	0	0	reef	0	Myers, 1991	Santini *et al.,* 2013
Venefica procera	Congridae	1	1	0	0	abissale	0	McEachran & Fechhelm, 1998	Santini *et al.,* 2013
Rhynchoconger gracilior	Congridae	1	1	0	0	abissale	0	Robins & Ray, 1986	Santini *et al.,* 2013
Facciolella equatorialis	Congridae	1	1	0	0	abissale	0	Love *et al.*, 2005	Santini *et al.,* 2013
Hoplunnis punctata	Congridae	1	1	0	0	abissale	0	Smith, 1990	Santini *et al.,* 2013
Ariosoma balearicus	Congridae	1	1	01	1	burrower, reef	1	Riede, 2004	Santini *et al.,* 2013
Heteroconger hassi	Congridae	1	1	1	1	burrower, reef	1	Bacchet *et al.*, 2006	Santini *et al.,* 2013
Paraconger notialis	Congridae	1	1	01	1	burrower, tail-first	1	Smith, 1981	Santini *et al.,* 2013
Scolecenchelys australis	Ophichthidae	1	1	1	1	seagrass	1	Hibino & Kimura, 2015	Santini *et al.,* 2013
Ahlia egmontis	Ophichthidae	1	1	1	1	seagrass and crevices	1	Robins & Ray, 1986	Santini *et al.,* 2013
Myrophis vafer	Ophichthidae	1	1	01	0	benthic but not burrower	0	Charter & Moser, 1996	Santini *et al.,* 2013
Ophichthus triserialis	Ophichthidae	1	1	01	1	burrower	1	McCosker & Rosenblatt, 1998	Santini *et al.,* 2013
Ophichthus cruentufer	Ophichthidae	1	1	01	0	offshore water	0	Robins & Ray, 1986	Santini *et al.,* 2013
Kaupichthys hyoproroides	Anguilliformes	1	1	01	0	reef	01	Claro, 1994	Santini *et al.,* 2013
† Paranguilla	Anguilliformes	1	1	01	0	reef	0	Blot, 1984	Pfaff *et al.*, 2016
Pythonichthys asodes	Heterenchelidae	1	1	1	1	burrower in	1	Rosenblatt &	Santini *et al.,* 2013

						mud		Rubinoff, 1972	
Anarchias seychellensis	Muraenidae	1	1	1	1	crevices	1	Reece *et al.*, 2010	Santini *et al.,* 2013
Uropterygius macularis	Muraenidae	1	1	1	1	crevices	1	Robins *et al.*, 1991	Santini *et al.,* 2013
Gymnomuraena zebra	Muraenidae	1	1	1	1	crevices	1	Lieske & Myers, 1994	Santini *et al.,* 2013
Gymnothorax kidako	Muraenidae	1	1	1	1	crevices	1	Chen *et al.*, 1994	Santini *et al.,* 2013
Rhinomuraena quaesita	Muraenidae	1	1	1	1	crevices	1	McCosker, 2010	Santini *et al.,* 2013
Luciogobius elongatus	Gobionellidae	1	1	01	1	burrower, interstitial, small pectoral fins	1	Hyun-Geun & Seung-Ho, 2014; Yamada *et al.*, 2009	Yamada *et al.*, 2009
Luciogobius adapel	Gobionellidae	1	1	01	1	burrower, interstitial, small pectoral fins	1	Yamada *et al.*, 2009	Yamada *et al.*, 2009
Luciogobius parvulus	Gobionellidae	1	1	01	1	burrower, interstitial, small pectoral fins	1	Yamada *et al.*, 2009	Yamada *et al.*, 2009
Luciogobius platycephalus	Gobionellidae	1	1	01	1	burrower, interstitial, small pectoral fins	1	Hyun-Geun & Seung-Ho, 2014; Yamada *et al.*, 2009	Yamada *et al.*, 2009
Luciogobius guttatus	Gobionellidae	1	1	01	1	burrower, small pectoral fins	1	Yamada *et al.*, 2009	Yamada *et al.*, 2009
Luciogobius pallidus	Gobionellidae	1	1	01	1	burrower, small pectoral fins	1	Yamada *et al.*, 2009	Yamada *et al.*, 2009
Luciogobius grandis	Gobionellidae	1	1	01	1	burrower, small	1	Yamada *et al.*, 2009	Yamada *et al.*, 2009

						pectoral fins			
Inu koma	Gobionellidae	1	1	0	0	intertidal rocky shore	0	Yamada *et al.*, 2009	Yamada *et al.*, 2009
Inu saikaiensis	Gobionellidae	1	1	0	0	intertidal rocky shore	0	Yamada *et al.*, 2009	Yamada *et al.*, 2009
Gen. Sp. 1	Gobionellidae	1	1	0	0	intertidal rocky shore,	0	Yamada *et al.*, 2009	Yamada *et al.*, 2009
Gen. Sp. 2	Gobionellidae	1	1	0	0	intertidal rocky shore,	0	Yamada *et al.*, 2009	Yamada *et al.*, 2009
Clariger cosmurus	Gobionellidae	1	1	0	0	subtidal rocky shore	0	Yamada *et al.*, 2009	Yamada *et al.*, 2009
Clariger exilis	Gobionellidae	1	1	0	0	subtidal rocky shore	0	Yamada *et al.*, 2009	Yamada *et al.*, 2009
Astrabe flavimaculata	Gobionellidae	0	0	0	0	subtidal rocky shore	0	Yamada *et al.*, 2009	Yamada *et al.*, 2009
Chaenogobius gulosus	Gobionellidae	0	0	0	0	subtidal rocky shore	0	Yamada *et al.*, 2009	Yamada *et al.*, 2009
Gymnogobius isaza	Gobionellidae	0	0	0	0	freshwater lake	0	Yamada *et al.*, 2009	Yamada *et al.*, 2009
Gymnogobius urotaenia	Gobionellidae	0	0	0	0	freshwater lake	0	Yamada *et al.*, 2009	Yamada *et al.*, 2009
Typhlogobius californiensis	Gobionellidae	0	0	0	1	mudshrimp burrow	0	Yamada *et al.*, 2009	Yamada *et al.*, 2009
Eutaeniichthys gilli	Gobionellidae	1	1	1	1	mudshrimp burrower	1	Henmi & Itani, 2014	Henmi & Itani, 2014
Stenogobius	Gobionellidae	0	0	0	0		0	Watson, 1991	Thacker, 2013
Periophtalmus barbarus	Gobionellidae	1	0	0	1	reef, amphibious	0	Miller, 1981	Thacker, 2013
Scartelaos histiophorus	Gobionellidae	1	0	0	1	mud, amphibious	0	Riede, 2004	Thacker, 2013
Gobiopterus semivestitus	Gobionellidae	0	0	0	0		0	Thacker, 2013	Thacker, 2013
Pandaka lidwilli	Gobionellidae	0	0	0	0	pelagic	0	Masuda *et al.*, 1984	Thacker, 2013
Barbulifer ceuthoecus	Gobiidae	0	0	0	1	reef	0	Cervigón, 1994	Thacker, 2013
Amblygobius phalena	Gobiidae	0	0	0	1	reef	0	Randall, 1995	Thacker, 2013
Copionodon	Copionodont	1	0	0	0		0	Zanata &	Datovo &

pecten	inae							Primitivo, 2014	Lindam, 2005
Trichogenes longipinnis	Trichogeninae	1	0	0	0		0	Britski & Ortega, 1982; Sazima, 2004	Datovo & Lindam, 2005
Bullockia maldonadoi	Trichomycterinae	1	0	0	0		0	Bockmann & Sazima, 2004	Datovo & Lindam, 2005
Hatcheria macraei	Trichomycterinae	1	0	0	0		0	Bockmann & Sazima, 2004	Datovo & Lindam, 2005
Ituglanis proops	Trichomycterinae	1	1	0	0		01	Bockmann & Sazima, 2004	Datovo & Lindam, 2005
Trichomycterus maracaya	Trichomycterinae	1	0	0	0		0	Bockmann & Sazima, 2004	Datovo & Lindam, 2005
Listrura tetraradiata	Glanapteryginae	1	1	0	1	interstitial	1	Villa-Verde & Costa, 2006	Baskin, 1973; Datovo & Lindam, 2005; Villa-Verde *et al.*, 2012
Listrura picinguabae	Glanapteryginae	1	1	1	1	interstitial, filiform fins	1	Villa-Verde & Costa, 2006	Baskin, 1973; Datovo & Lindam, 2005; Villa-Verde *et al.*, 2012
Listrura nematopteryx	Glanapteryginae	1	1	1	1	interstitial, filiform fins	1	De Pinna, 1988; Villa-Verde & Costa, 2006	Baskin, 1973; Datovo & Lindam, 2005; Villa-Verde *et al.*, 2012
Listrura costai	Glanapteryginae	1	1	1	1	interstitial, filiform fins	1	Villa-Verde & Costa, 2006; Villa-Verde *et al.*, 2012	Baskin, 1973; Datovo & Lindam, 2005; Villa-Verde *et*

									al., 2012
Glanapteryx anguilla	Glanapterygi nae	1	1	1	1	leaf litter	1	De Pinna, 1988; Schaefer *et al.*, 2005	Baskin, 1973; Datovo & Lindam, 2005
Pygidianops cuao	Glanapterygi nae	1	1	1	1	small, filiform pectoral fins	1	Schaefer *et al.*, 2005	Baskin, 1973; Datovo & Lindam, 2005
Pygidianops magoi	Glanapterygi nae	1	1	1	1	sand-bottom	1	Schaefer *et al.*, 2005	Baskin, 1973; Datovo & Lindam, 2005
Typhlobelus hundbergi	Glanapterygi nae	1	1	1	1	sand-bottom	1	Schaefer *et al.*, 2005	Baskin, 1973; Datovo & Lindam, 2005
Typhlobelus guacamaya	Glanapterygi nae	1	1	1	1	sand-bottom	1	Schaefer *et al.*, 2005	Baskin, 1973; Datovo & Lindam, 2005
Stauroglanis gouldingi	Sarcoglanidi nae	0	0	0	0	rheophi lic	0	Zuanon & Sazima, 2004	Baskin, 1973; Datovo & Lindam, 2005
Paracanthopo ma parva	Vandelliinae	1	1	0	0	parasiti c	0	Schmidt, 1993; Zuanon & Sazima, 2005	Baskin, 1973; DoNascim iento, 2015
Vandellia sanguinea	Vandelliinae	1	1	0	0	blood parasit	0	Baskin *et al.*, 1980	Baskin, 1973; DoNascim iento, 2015
Vandellia cirrhosa	Vandelliinae	1	1	0	0	blood parasit	0	Baskin *et al.*, 1980	Baskin, 1973; DoNascim iento, 2015
Haemomaster venezuelae	Stegophilina e	1	1	0	0	parasiti c	0	DoNascim iento, 2015	DoNascim iento, 2015
Ochmacanthus flabelliferus	Stegophilina e	1	1	0	0	parasiti c	0	DoNascim iento, 2015	DoNascim iento, 2015

Homodiaetus anisitsi	Stegophilinae	1	1	0	0	parasitic	0	DoNascimiento, 2015	DoNascimiento, 2015
Henonemus	Stegophilinae	1	1	0	0	parasitic	0	DoNascimiento, 2015	DoNascimiento, 2015
Pareiodon	Stegophilinae	1	1	0	0	parasitic	0	DoNascimiento, 2015	DoNascimiento, 2015
Clarotes laticeps	Siluroidea	0	0	0	0		0	Risch, 2003	Wright, 2017
Heteropneustes fossilis	Siluroidea	1	0	0	0		0	Ali *et al.*, 2015	Wright, 2017
Clarias meladerma	Clariidae	1	01	0	0		0	Vidthayanon, 2002	Wright, 2017
Gymnallabes typus	Clariidae	1	1	0	0		0	Teugels, 2003; Ward *et al.*, 2015	Wright, 2017
Tanganikallabes mortiauxi	Clariidae	1	1	0	0		0	Seegers, 2008	Wright, 2017
Tanganikallabes alboperca	Clariidae	1	1	0	0		0	Seegers, 2008	Wright, 2017
Tanganikallabes stewarti	Clariidae	1	1	0	0		0	Seegers, 2008	Wright, 2017
Channallabes apus	Clariidae	1	1	1	1	among trees roots, testa piccola rispetto agli altri	1	Teugels, 1986; Devaere *et al.*, 2007; Seegers, 2008	Wright, 2017
Clarias agboyiensis	Clariidae	1	1	0	1	grasslands	1	Ezenwaji & Inyang, 1998	Wright, 2017
Clarias theodorae	Clariidae	1	1	0	1	shallows in vegetated areas	1	Teugels, 1986	Wright, 2017
Dolichallabes microphthalmus	Clariidae	1	1	1	1	high variability in fins, but often very small	1	Devaere *et al.*, 2004; Seegers, 2008	Wright, 2017
Heterobranchus isopterus	Clariidae	1	01	0	0		0	Teugels *et al.*, 1990	Wright, 2017
Heterobranchus boulengeri	Clariidae	1	01	0	0		0	Teugels *et al.*, 1990	Wright, 2017
Heterobranchus bidorsalis	Clariidae	1	01	0	0		0	Teugels *et al.*, 1990	Wright, 2017
Dinotopterus	Clariidae	1	01	0	0	on	0	Poll, 1953	Wright,

cunningtoni						rocky substrates			2017
Clarias ngamensis	Clariidae	1	1	0	0	permanent swamps	0	Teugels, 1986	Wright, 2017
Clarias anguillaris	Clariidae	1	1	0	1	burrower	1	Teugels, 1986	Wright, 2017
Clarias gariepinus	Clariidae	1	1	0	0	rivers	0	Teugels, 1986	Wright, 2017
Pseudotangani kallabes	Clariidae	1	01	0	0		0	Wright, 2017	Wright, 2017
Clarias platycephalus	Clariidae	1	1	0	0		0	Teugels, 1986	Wright, 2017
Channallabes longicaudatus	Clariidae	1	1	0	0		0	Devaere *et al.*, 2007	Wright, 2017
Channallabes alvarezi	Clariidae	1	1	0	0		0	Devaere *et al.*, 2007	Wright, 2017
Clariallabes longicauda	Clariidae	1	1	0	0		0	Teugels, 1986	Wright, 2017

Appendix 2. Database of squamate reptiles and lissamphibians. Grey columns are the two columns used for the discrete analysis.

Taxon	**Group**	**Absence forelimb**	**Absence hindlimb**	**Absence limb**	**Burrowing or grass-swimmer**	**Notes**	**Data's reference**	**Phylogeny's reference**
Anelytropsis papillosus	Squamata, Dibamidae	1	1	1	1	burrower	IUCN Red List; Vitt & Caldwell, 2009; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Dibamus novaeguineae	Squamata, Dibamidae	1	1	1	1	burrower	IUCN Red List; Vitt & Caldwell, 2009; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Nephrurus vertebralis	Gekkota, Carphodactylidae	0	0	0	0	wood	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Underwoodisaurus seorsus	Gekkota, Carphodactylidae	0	0	0	0	rocky areas	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Lialis burtonis	Gekkota, Pygopodidae	1	1	1	0	litter	IUCN Red List; Vitt & Caldwell, 2009; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Delma labialis	Gekkota, Pygopodidae	1	1	1	0	litter	IUCN Red List; Vitt & Caldwell,	Reeder *et al.*, 2015

							2009; Uetz *et al.*, 2019	
Pygopus nigriceps	Gekkota, Pygopodidae	1	1	1	0	generalist	IUCN Red List; Vitt & Caldwell, 2009; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Aprasia aurita	Gekkota, Pygopodidae	1	1	1	0	generalist (burrowing, according to IUCN Red List)	IUCN Red List; Vitt & Caldwell, 2009; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Rhacodactylus leachianus	Gekkota, Diplodactylidae	0	0	0	0	arboreal	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Coleonyx variegatus	Gekkota, Eublepharidae	0	0	0	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Eublepharis hardwickii	Gekkota, Eublepharidae	0	0	0	0	wood	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Hemitheconyx caudicinctus	Gekkota, Eublepharidae	0	0	0	0	savannah	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Hemidactylus turcicus	Gekkota, Gekkonidae	0	0	0	0	generalist	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Mediodactylus kotschyi	Gekkota, Gekkonidae	0	0	0	0	rocky areas	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Phelsuma lineata	Gekkota, Gekkonidae	0	0	0	0	arboreal	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Gonatodes albogularis	Gekkota, Sphaerodactylidae	0	0	0	0	arboreal, generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Euleptes europaea	Gekkota, Sphaerodactylidae	0	0	0	0	rocky areas	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Pristurus rupestris	Gekkota, Sphaerodactylidae	0	0	0	0	rocky areas	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Sphaerodactylus schwartzi	Gekkota, Sphaerodactyli	0	0	0	0	litter	IUCN Red List; Uetz	Reeder *et al.*, 2015

	dae						*et al.*, 2019	
Asaccus platyrhynchus	Gekkota, Phyllodactylidae	0	0	0	0	rocky areas	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Tarentola mauritanica	Gekkota, Phyllodactylidae	0	0	0	0	rocky areas	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Phyllodactylus reissii	Gekkota, Phyllodactylidae	0	0	0	0	arid areas	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
† *Ardeosaurus brevipes*	Scincoidea	0	0	0	0	generalist	Talanda, 2018	Talanda, 2018
† *Yabeinosaurus robustus*	Scincoidea	0	0	0	0	generalist	Talanda, 2018	Talanda, 2018
Acontias meleagris	Squamata, Scincidae, Acontinae	1	1	1	1	burrowing	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Acontias gariepensis	Squamata, Scincidae, Acontinae	1	1	1	-	?	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Acontias lineatus	Squamata, Scincidae, Acontinae	1	1	1	-	?	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Typhlosaurus braini	Squamata, Scincidae, Acontinae	1	1	1	1	burrowing	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Typhlosaurus caecus	Squamata, Scincidae, Acontinae	1	1	1	1	burrowing	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Typhlosaurus lomiae	Squamata, Scincidae, Acontinae	1	1	1	1	burrowing	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Egernia kingii	Squamata, Scincidae, Egerniinae	0	0	0	0	rocky areas	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Tiliqua scincoides	Squamata, Scincidae, Egerniinae	0	0	0	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Cyclodomorphus michaeli	Squamata, Scincidae, Egerniinae	0	0	0	0	coastal environment	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Liopholis whitii	Squamata, Scincidae, Egerniinae	0	0	0	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Ablepharus kitaibelii	Squamata, Scincidae, Eugongylinae	0	0	0	0	arid areas	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Ablepharus budaki	Squamata, Scincidae, Eugongylinae	0	0	0	0	litter	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015

Feylinia currori	Squamata, Scincidae, Scincinae	1	1	1	01	semi fossorial	IUCN Red List; Wagner & Schmitz, 2006; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Chalcides ocellatus	Squamata, Scincidae, Scincinae	0	0	0	0	generalist	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Chalcides chalcides	Squamata, Scincidae, Scincinae	0	0	0	0	grassy areas	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Melanoseps ater	Squamata, Scincidae, Scincinae	1	1	1	0	in litter	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Mesoscincus schwartzei	Squamata, Scincidae, Scincinae	0	0	0	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Mesoscincus managuae	Squamata, Scincidae, Scincinae	0	0	0	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Ophiomorus latastii	Squamata, Scincidae, Scincinae	1	1	1	1	burrowing	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Ophiomorus punctatissimus	Squamata, Scincidae, Scincinae	1	1	1	1	burrowing	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Brachymeles apus	Squamata, Scincidae, Scincinae	1	1	1	1	burrowing	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Brachymeles miriamae	Squamata, Scincidae, Scincinae	1	1	1	1	burrowing	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Brachymeles talinis	Squamata, Scincidae, Scincinae	0	0	0	-	?	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Plestiodon multilineatus	Squamata, Scincidae, Scincinae	0	0	0	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Scincus mitranus	Squamata, Scincidae, Scincinae	0	0	0	0	sandy dunes	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Hakaria simonyi	Squamata, Scincidae, Scincinae	0	0	0	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015

Scelotes caffer	Squamata, Scincidae, Scincinae	1	1	1	1	burrowing	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Scelotes bipes	Squamata, Scincidae, Scincinae	1	0	01	1	burrowing	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Ameiva bifrontata	Squamata, Teiidae	0	0	0	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Teius teyou	Squamata, Teiidae	0	0	0	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Pholidobolus montium	Squamata, Gymnophthalmidae	0	0	0	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Rhineura floridana	Amphisbaenia, Rhineuridae	1	1	1	1	burrowing	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Blanus cinereus	Amphisbaenia, Blanidae	1	1	1	1	burrowing	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Cadea blanoides	Amphisbaenia, Cadeidae	1	1	1	1	burrowing	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Bipes biporus	Amphisbaenia, Bipedidae	0	1	01	1	burrowing	IUCN Red List; Vitt & Caldwell, 2009; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Trogonophis wiegmanni	Amphisbaenia, Trogonophidae	1	1	1	1	burrowing	IUCN Red List; Vitt & Caldwell, 2009; Uetz *et al.*, 2019	Reeder *et al.*, 2015
† Slavoia darevskii	Amphisbaenia	0	0	0	1	burrowing	Talanda, 2016	Talanda, 2016
Amphisbaena alba	Amphisbaenia, Amphisbaenidae	1	1	1	1	burrowing	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Chirindia langi	Amphisbaenia, Amphisbaenidae	1	1	1	1	burrowing	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Anomalepis mexicanus	Serpentes, Anomalepididae	1	1	1	01	under trunk	IUCN Red List; Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Leptotyphlops	Serpentes, Leptotyphlopidae	1	1	1	1	burrowing	IUCN Red List	Da Silva *et al.*, 2018
Indotyphlops braminus	Serpentes, Typhlopidae	1	1	1	1	burrowing	Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Xerotyphlops	Serpentes,	1	1	1	1	burrowin	IUCN Red	Da Silva *et*

vermicularis	Typhlopidae					g	List; Uetz *et al.*, 2019	*al.*, 2018
† Dinlysia	Serpentes	1	1	1	1	burrowing	Da Silva *et al.*, 2018	Da Silva *et al.*, 2018
† Wonambi	Serpentes	1	1	1	-	generalist?	Da Silva *et al.*, 2018; Palci *et al.*, 2018	Da Silva *et al.*, 2018
† Yurlunggur	Serpentes	1	1	1	1	semifossorial	Da Silva *et al.*, 2018; Palci *et al.*, 2018	Da Silva *et al.*, 2018
Anilius scytale	Serpentes, Aniliidae	1	1	1	1	burrowing	Maschio *et al.*, 2010; Uetz *et al.*, 2019	Da Silva *et al.*, 2018
† Haasiophis	Serpentes	1	1	1	1	burrowing	Da Silva *et al.*, 2018	Da Silva *et al.*, 2018
† Pachyrhachis	Serpentes	1	1	1	1	burrowing	Da Silva *et al.*, 2018	Da Silva *et al.*, 2018
Tropidophis melanurus	Serpentes, Tropidophiidae	1	1	1	1	burrowing	Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Casarea dussumieri	Serpentes, Bolyeriidae	1	1	1	0	arboreal	IUCN Red List	Da Silva *et al.*, 2018
Eryx jaculus	Serpentes, Boidae	1	1	1	1	burrowing	Insacco *et al.*, 2015; Uetz *et al.*, 2019	Reynolds *et al.*, 2014; Da Silva *et al.*, 2018
Boa constrictor	Serpentes, Boidae	1	1	1	0	generalist	Uetz *et al.*, 2019	Reynolds *et al.*, 2014; Da Silva *et al.*, 2018
Corallus hortulanus	Serpentes, Boidae	1	1	1	0	arborical	IUCN Red List; Uetz *et al.*, 2019	Reynolds *et al.*, 2014; Da Silva *et al.*, 2018
Eunectes murinus	Serpentes, Boidae	1	1	1	0	shallow water	Uetz *et al.*, 2019	Reynolds *et al.*, 2014; Da Silva *et al.*, 2018
Uropeltis ceylanica	Serpentes, Uropeltidae	1	1	1	1	burrowing	Gower *et al.*, 2008; Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Python sebae	Serpentes, Pythonidae	1	1	1	0	generalist	Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Crotalus horridus	Serpentes, Viperidae	1	1	1	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Wüster *et al.*, 2008; Da Silva *et al.*, 2018
Bitis arietans	Serpentes, Viperidae	1	1	1	0	generalist	Uetz *et al.*, 2019	Wüster *et al.*, 2008; Da Silva *et al.*,

								2018
Macrovipera schweizeri	Serpentes, Viperidae	1	1	1	0	rocky areas	IUCN Red List; Uetz *et al.*, 2019	Wüster *et al.*, 2008; Da Silva *et al.*, 2018
Daboia siamensis	Serpentes, Viperidae	1	1	1	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Wüster *et al.*, 2008; Da Silva *et al.*, 2018
Vipera ammodytes	Serpentes, Viperidae	1	1	1	0	rocky areas	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Wüster *et al.*, 2008; Da Silva *et al.*, 2018
Vipera aspis	Serpentes, Viperidae	1	1	1	0	generalist	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Wüster *et al.*, 2008; Da Silva *et al.*, 2018
Vipera berus	Serpentes, Viperidae	1	1	1	0	generalist	Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Wüster *et al.*, 2008; Da Silva *et al.*, 2018
Micrurus nigrocinctus	Serpentes, Elapidae	1	1	1	1	burrowing	IUCN Red List; Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Hydrophis fasciatus	Serpentes, Elapidae	1	1	1	0	coastal water	IUCN Red List; Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Hydrophis cyanocinctus	Serpentes, Elapidae	1	1	1	0	coastal water	IUCN Red List; Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Naja atra	Serpentes, Elapidae	1	1	1	-	generalist	IUCN Red List; Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Naja senegalensis	Serpentes, Elapidae	1	1	1	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Ophiophagus hannah	Serpentes, Elapidae	1	1	1	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Macroprotodon cucullatus	Serpentes, Colubridae	1	1	1	0	open habitats	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Calamaria albiventer	Serpentes, Colubridae	1	1	1	1	burrowing, in litter	IUCN Red List; Uetz *et al.*, 2019	Da Silva *et al.*, 2018

Coronella girondica	Serpentes, Colubridae	1	1	1	0	generalist	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Elaphe dione	Serpentes, Colubridae	1	1	1	0	generalist	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Eirenis modestus	Serpentes, Colubridae	1	1	1	0	rocky areas	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Hierophis viridiflavus	Serpentes, Colubridae	1	1	1	0	open habitats	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Natrix natrix	Serpentes, Colubridae	1	1	1	0	humid, open habitats	Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Virginia valeriae	Serpentes, Colubridae	1	1	1	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Da Silva *et al.*, 2018
Cordylus cordylus	Squamata, Cordylidae	0	0	0	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Ouroborus cataphractus	Squamata, Cordylidae	0	0	0	0	rocky areas	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Smaug giganteus	Squamata, Cordylidae	0	0	0	1	burrowing and grass-swimming	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Cricosaura typica	Squamata, Xantusiidae	0	0	0	0	wood	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Xantusia vigilis	Squamata, Xantusiidae	0	0	0	0	arid areas	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Lacerta viridis	Squamata, Lacertidae	0	0	0	0	generalist	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Reeder *et al.*, 2015

Podarcis muralis	Squamata, Lacertidae	0	0	0	0	generalist	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Takydromus sexlineatus	Squamata, Lacertidae	0	0	0	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Shinisaurus crocodilurus	Squamata, Shinisauridae	0	0	0	0	semiaquatic	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Heloderma horridum	Squamata, Helodermatidae	0	0	0	0	wood	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Varanus exanthematicus	Squamata, Varanidae	0	0	0	0	agricultural areas	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Xenosaurus grandis	Squamata, Xenosauridae	0	0	0	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
†Ophisauriscus quadrupes	Anguidae (Anniellidae secondo Conrad et al. 2011)	0	0	0	1	burrowing	Sullivan *et al.*, 1999	Conrad *et al.*, 2011
† Apodosauriscus minutus	Squamata, Anniellidae	1	1	1	1	burrowing	Gauthier, 1982; Bell *et al.*, 1995	Conrad *et al.*, 2011
Anniella pulchra	Squamata, Anniellidae	1	1	1	1	burrowing	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Celestus enneagrammus	Squamata, Diploglossidae	0	0	0	0	wood	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Diploglossus bilobatus	Squamata, Diploglossidae	0	0	0	01	semi-fossorial	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Diploglossus pleii	Squamata, Diploglossidae	0	0	0	1	burrowing, in litter	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Ophiodes intermedius	Squamata, Diploglossidae	1	1*	1	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Ophiodes striatus	Squamata, Diploglossidae	1	1	1	-	?	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Celestus agasepsoides	Squamata, Diploglossidae	01	01	01	1	burrowing	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Celestus haetianus	Squamata, Diploglossidae	0	0	0	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Ophisaurus	Squamata,	1	1	1	01	semi-	IUCN Red	Reeder *et al.*,

ventralis	Anguidae					fossorial	List; Uetz *et al.*, 2019	2015
Anguis fragilis	Squamata, Anguidae	1	1	1	1	burrowing and grass-swimmer	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Pseudopus apodus	Squamata, Anguidae	1	1	1	1	grass-swimmer	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Elgaria multicarinata	Squamata, Anguidae	0	0	0	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Abronia oaxacae	Squamata, Anguidae	0	0	0	0	arboreal	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Barisia levicollis	Squamata, Anguidae	0	0	0	0	wood	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Gerrhonotus parvus	Squamata, Anguidae	0	0	0	0	wood	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Chamaeleo chamaeleon	Squamata, Chamaeleonidae	0	0	0	0	arboreal	IUCN Red List; Speybroeck *et al.*, 2016; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Uromastyx aegyptia	Squamata, Agamidae	0	0	0	0	open habitats	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Agama spinosa	Squamata, Agamidae	0	0	0	0	rocky areas	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Draco cornutus	Squamata, Agamidae	0	0	0	0	arboreal	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Hydrosaurus amboinensis	Squamata, Agamidae	0	0	0	0	semiaquatic	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Basiliscus basiliscus	Squamata, Iguanidae (s.l.), Corytophanidae	0	0	0	0	semiaquatic	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Anolis proboscis	Squamata, Iguanidae (s.l.), Dactyloidae	0	0	0	0	arboreal	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015

Iguana delicatissima	Squamata, Iguanidae (s.l.), Iguanidae (s.s.)	0	0	0	0	arboreal	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Phrynosoma asio	Squamata, Iguanidae (s.l.), Phrynosomatidae	0	0	0	0	generalist	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Leiocephalus carinatus	Squamata, Iguanidae (s.l.), Leiocephalidae	0	0	0	0	rocky areas	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Polychrus gutturosus	Squamata, Iguanidae (s.l.), Polychrotidae	0	0	0	0	arboreal	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Enyalioides heterolepis	Squamata, Iguanidae (s.l.), Hoplocercidae	0	0	0	0	wood	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Leiosaurus catamarcensis	Squamata, Iguanidae (s.l.), Leiosauridae	0	0	0	0	wood	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Oplurus saxicola	Squamata, Iguanidae (s.l.), Opluridae	0	0	0	0	rocky areas	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Liolaemus anomalus	Squamata, Iguanidae (s.l.), Liolaemidae	0	0	0	0	arid, salty areas	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
Tropidurus torquatus	Squamata, Iguanidae (s.l.), Tropiduridae	0	0	0	0	wood	IUCN Red List; Uetz *et al.*, 2019	Reeder *et al.*, 2015
† Eocaecilia micropodia	Gymnophiona	0	0	0	1	burrowing	Jenkins *et al.*, 2007	Evans & Sigogneau-Russell, 2011
Epicrionops marmoratus	Gymnophiona	1	1	1	1	burrowing	Amphibia Web, 2019	Pyron & Wiens, 2011
Epicrionops niger	Gymnophiona	1	1	1	1	burrowing	Amphibia Web, 2019	Pyron & Wiens, 2011
Rhinatrema bivittatum	Gymnophiona	1	1	1	1	burrowing	Amphibia Web, 2019	Pyron & Wiens, 2011
Uraeotyphlus natayani	Gymnophiona	1	1	1	1	burrowing	Amphibia Web, 2019	Pyron & Wiens, 2011
Ichthyophis bombayensis	Gymnophiona	1	1	1	1	burrowing	Amphibia Web, 2019	Pyron & Wiens, 2011
Ichthyophis tricolor	Gymnophiona	1	1	1	1	burrowing	Amphibia Web, 2019	Pyron & Wiens, 2011

Ichthyophis orthoplicatus	Gymnophiona	1	1	1	1	burrowing	Amphibia Web, 2019	Pyron & Wiens, 2011
Ichthyophis glutinosus	Gymnophiona	1	1	1	1	burrowing	Amphibia Web, 2019	Pyron & Wiens, 2011
Ichthyophis bannanicus	Gymnophiona	1	1	1	1	burrowing	Amphibia Web, 2019	Pyron & Wiens, 2011
Caecilia tentaculata	Gymnophiona	1	1	1	1	burrowing	Amphibia Web, 2019	Pyron & Wiens, 2011
Cryptobranchus alleganiensis	Cryptobranchidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Onychodactylus fischeri	Hynobiidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Pseudobranchus striatus	Sirenidae	0	1	01	1	burrowing	Amphibia Web, 2019	Pyron & Wiens, 2011
Pseudobranchus axanthus	Sirenidae	0	1	01	1	burrowing	Amphibia Web, 2019	Pyron & Wiens, 2011
Siren intermedia	Sirenidae	0	1	01	1	burrowing	Amphibia Web, 2019	Pyron & Wiens, 2011
Siren lacertina	Sirenidae	0	1	01	1	burrowing	Amphibia Web, 2019	Pyron & Wiens, 2011
Dicamptodon tenebrosus	Dicamptodontidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Ambystoma cingulatum	Ambystomidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Salamandrina terdigitata	Salamandridae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Chioglossa lusitanica	Salamandridae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Salamandra lanzai	Salamandridae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Proteus anguinus	Proteidae	0	0	0	1	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Necturus lewisi	Proteidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Necturus punctatus	Proteidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Necturus beyeri	Proteidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Necturus alabamensis	Proteidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Necturus maculosus	Proteidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Rhyacotriton kezeri	Rhyacotritonidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Rhyacotriton variegatus	Rhyacotritonidae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Amphiuma tridactylum	Amphiumidae	1	1	1	1	burrowing	Amphibia Web, 2019	Pyron & Wiens, 2011
Amphiuma pholeter	Amphiumidae	1	1	1	1	burrowing	Amphibia Web, 2019	Pyron & Wiens, 2011
Amphiuma means	Amphiumidae	1	1	1	1	burrowing	Amphibia Web, 2019	Pyron & Wiens, 2011
Hydromantes	Plethodontinae	0	0	0	0	generalist	Amphibia	Pyron &

shastae							Web, 2019	Wiens, 2011
Ensatina eschscholtzii	Plethodontinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Desmognathus carolinensis	Plethodontinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Plethodon larselli	Plethodontinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Hemidactylium scutatum	Hemidactylinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Gyrinophilus porphyriticus	Spelerpinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Eurycea multiplicata	Spelerpinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Haideotriton wallacei	Spelerpinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Euricea quadridigitata	Spelerpinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Batrachoseps wrignti	Bolitoglossinae	0	0	0	1	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Batrachoseps diabolicus	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Batrachoseps gabrieli	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Batrachoseps pacificus	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Batrachoseps attenuatus	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Batrachoseps nigriventris	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Thorius minutissimus	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Thorius troglodytes	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Thorius dubitus	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Chiropterotriton dimidiatus	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Dendrotriton rabbi	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Cryptotriton alvarezdeltoroi	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Nototriton brodiei	Bolitoglossinae	0	0	0	0	litter	Amphibia Web, 2019	Pyron & Wiens, 2011
Bradytriton silus	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Oedipina quadra	Bolitoglossinae	0	0	0	0	litter	Amphibia Web, 2019	Pyron & Wiens, 2011
Oedipina carablanca	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Oedipina elongata	Bolitoglossinae	0	0	0	0	litter	Amphibia Web, 2019	Pyron & Wiens, 2011
Oedipina maritima	Bolitoglossinae	0	0	0	0	litter	Amphibia Web, 2019	Pyron & Wiens, 2011

Oedipina alleni	Bolitoglossinae	0	0	0	0	litter	Amphibia Web, 2019	Pyron & Wiens, 2011
Oedipina stenopodia	Bolitoglossinae	0	0	0	0	litter	Amphibia Web, 2019	Pyron & Wiens, 2011
Oedipina gracilis	Bolitoglossinae	0	0	0	0	litter	Amphibia Web, 2019	Pyron & Wiens, 2011
Parvimolge townsendi	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Pseudoeurycea cephalica	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Pseudoeurycea boneti	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Pseudoeurycea gigantea	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Lineatriton lineolus	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Pseudoeurycea firscheini	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Pseudoeurycea obesa	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Pseudoerycea melanomolga	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Bolitoglossa hartwegi	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Bolitoglossa platydactyla	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Bolitoglossa subpalmata	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011
Bolitoglossa alvaradoi	Bolitoglossinae	0	0	0	0	generalist	Amphibia Web, 2019	Pyron & Wiens, 2011

Appendix 3. References cited in Appendix 1 and 2.

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