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A REVIEW OF CRANIATA REPRODUCTIVE MODES

REVISÃO DE MODOS REPRODUTIVOS EM CRANIATA

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RESUMO

O clado do Craniata inclui aproximadamente 66.000 espécies, representadas por peixes, anfíbios, répteis aves e mamíferos. Com exceção dos anfíbios, há poucas informações disponíveis sobre os modos reprodutivos (MRs) de vertebrados, definidos aqui como a combinação de 10 caracteres em seus múltiplos estados. Uma classificação mais elaborada de MRs foi proposta para anfíbios, mas nunca para os outros clados de vertebrados. Além disso, mesmo as classificações de MRs disponíveis não estão baseadas nas mesmas variáveis, reduzindo assim seu valor para comparações entre grupos. Aqui, propomos uma classificação atualizada de MRs de anfíbios e estendemos essa classificação aos outros grupos de vertebrados, peixes, répteis, aves e mamíferos. Baseados em mais de 10.000 espécies com MRs descritos, nós classificamos 158 diferentes MRs possíveis para esse clado. Os anfíbios apresentaram 71, os amniotas 51 e os peixes 52 MRs. Nossa proposta é a primeira classificação abrangente de MR para o clado Craniata, que fornece insights sobre padrões mais amplos de evolução das estratégias reprodutivas e serve como uma linha de base para futuros estudos comparativos ecológicos e evolutivos. Como por exemplo, a diversidade de MRs que nunca foi explicada e que pode estar relacionada à riqueza de espécies. O Brasil abriga uma grande quantidade de espécies de anfíbios, facilitando um mapeamento da diversidade de espécies de anfíbios e diversidade de MRs. A Mata Atlântica apresentou alta diversidade de MRs quando comparada aos biomas mais quentes, como a Amazônia. Detectamos uma relação geral linear e positiva entre a diversidade de MRs e a riqueza de espécies de anfíbios. Estimamos um índice relativo de diversidade de MRs, mesclando ambos os conjuntos de dados (riqueza de espécies e diversidade de MRs), revelando que essa relação varia entre os biomas brasileiros. Ou seja, algumas regiões apresentam menos MRs do que o esperado pela relação direta. Portanto, concluímos que o principal determinante da diversidade de MRs é a riqueza de espécies locais, mas em algumas áreas, outros fatores podem estar influenciando essa relação, como condições climáticas e disponibilidade de microhabitats de reprodução.

Palavras Chave: Anfíbios, Arcossauros, Diversidade, Evolução, Peixes, Lepidossauros, História natural, Estratégias reprodutivas, Riqueza de espécies, Synapsidas, Vertebrados terrestres, Testudines.

ABSTRACT

The Craniata clade includes approximately 66,000 species, represented by amphibians, lepidosaurians, testudines, archosaurians and synapsids. Except for amphibians, there is only few information available on vertebrate reproductive modes (RMs), defined here as the combination of 10 characters in multiple states. A more elaborate classification of RMs was proposed for amphibians, but never for other vertebrate clades. In addition, even the classifications of RMs available are not based on the same variables, thereby reducing their value for comparisons across groups. Here, we propose an updated classification of amphibian RMs and extend it to other groups of the Craniata clade. Based on more than 10,000 species with described RMs, we were able to classify 156 different possible RMs to the Craniata clade. Amphibians exhibited 71, amniotans 51, and fishes 52 RMs. Our proposal is the first comprehensive RM classification for Craniata, which provides insight into broader patterns of evolution of reproductive strategies and serves as a baseline for future comparative ecological and evolutionary studies. As for example, the diversity of RMs that has never been explained and that can be related to the species richness. Brazil has a large number of amphibian species, facilitating a mapping of the diversity of amphibian species and diversity of RMs. The Atlantic Forest presented high diversity of RMs when compared to the hottest biomes, such as the Amazonia. We detected a linear and positive relationship between the diversity of RMs and the richness of amphibian species. We estimated a RMs diversity relative index, mixing both sets of data (species richness and diversity of RMs), revealing that this relationship varies among Brazilian biomes. In other words, some regions have fewer RMs than expected from the direct relationship. Therefore, we conclude that the main determinant of RM diversity is the richness of local species, but in some areas, other factors may be influencing this relationship, such as climatic conditions and availability of breeding microhabitats.

Key words: Amphibia, Archosauria, Breeding behavior, Diversity, Evolution, Fish, Lepidosauria, Natural history, Reproductive strategies, Species richness, Synapsida, Terrestrial vertebrates, Testudines.

SUMÁRIO

INTRODUÇÃO

O clado Craniata, que inclui os agnatos e vertebrados, conta com cerca de 66.000 espécies e está representado por peixes, anfíbios, répteis, aves e mamíferos (Gill, 2006; Barrowclough *et al.*, 2016; Froese & Pauly, 2017; Frost, 2018; HBW & Birdlife International, 2017; Uetz, 2018; Wilson & Reeder, 2017).

O grupo dos vertebrados aquáticos, que inclui os agnatos, peixes cartilaginosos e peixes ósseos, ocupa todos os tipos de ambientes aquáticos como, oceanos, estuários, lagos, rios, córregos e poças temporárias (Helfman *et al.*, 2009; Nelson *et al.*, 2016). Os peixes podem viver em águas oceânicas com temperaturas abaixo de zero, nos polos norte ou sul, assim como podem viver nos trópicos e desertos com temperaturas superiores a 50 ºC (Wootton & Smith, 2015; Pough *et al.*, 2016). Eles podem ser encontrados em profundidades abissais assim como, em lagos de alta altitude (Wootton & Smith, 2015; Pough *et al.*, 2016). Esse é o grupo de vertebrados mais bem distribuído globalmente, e também o mais ancestral (Pough *et al.*, 2016).

Os tetrápodes ancestrais abandonaram um estilo de vida aquático e obrigatório, e se diversificaram nos ambientes terrestres (Inger, 1957; Long & Gordon, 2004). Durante essa transição, esses vertebrados também tiveram uma diversificação na reprodução, especificamente nas estratégias de reprodução (Long & Gordon, 2004).

O interesse pelas estratégias de reprodução dos vertebrados começou no século XIX, e.g., Cuvier, 1802; Darwin, 1859; Boulenger, 1886; von Ihering, 1886; Semon, 1894; Mitsukuri, 1891; Budgett, 1899; Thilenius, 1899. Contudo, foi no grupo dos anfíbios que os modos reprodutivos (MRs) foram caracterizados, talvez devido à diversidade e complexidade das estratégias reprodutivas desse grupo (Haddad & Prado, 2005). Por exemplo, em 1886, Boulenger propôs uma classificação das estratégias reprodutivas dos anfíbios usando uma combinação das seguintes características: tamanho do ovo, local de deposição dos ovos e nascimento e desenvolvimento das larvas, que poderia ser direto ou indireto. Com base nessas características, Boulenger estabeleceu 10 tipos diferentes de estratégias de reprodução. Porém, o termo MR só apareceu em 1966, em um estudo sobre a biologia reprodutiva dos peixes, proposto por Breder Jr. & Rosen. Mais tarde, em 1973, Salthe & Duellman revisaram estudos anteriores sobre estratégias reprodutivas de anfíbios, usando como base a classificação das estratégias reprodutivas de Boulenger (1886) e a classificação e descrição de três MRs para o grupo Caudata de Salthe (1969), e criaram uma definição para MR, que passou a ser uma combinação de caracteres que incluía local da postura, características do óvulo (tamanho do óvulo e da postura), taxa e duração do desenvolvimento, tamanho da prole, caracteres com parâmetros quantitativos, e tipo de cuidado parental, se houver. Portanto, ficou caracterizado que MR não é um único fenótipo, mas sim um conjunto de caracteres e seus estados que representa todas as estratégias reprodutivas. A aplicação do conceito de MR variou entre os clados de vertebrados, isso porque os pesquisadores naturalmente focaram nas características reprodutivas presentes em seus clados de estudo (Collias, 1964; Shine, 1983; Bronson, 1989; Haddad & Prado, 2005a; b).

Essa revisão dos modos reprodutivos elaborada por Salthe e Duellman foi fundamental pois estimulou o interesse e resultou em um grande aumento de estudos relacionados à MRs de anfíbios (Salthe e Mecham, 1974; Lamotte & Lescure, 1977; McDiarmid, 1978; Wake, 1982). Duellman & Trueb (1986) incluíram uma classificação no livro "Biologia de Anfíbios" e reconheceram 29 MRs para Anura, 7 para Caudata e 2 para Gymnophiona. Haddad & Prado (2005a; b) revisitaram os MRs de anuros aumentando a lista de 29 para 39 MRs, incluindo três rearranjos de modos conhecidos e sete novos modos descritos para os anuros da Mata Atlântica. Estudos subsequentes descreveram MRs adicionais com base nos diversos critérios de classificação anteriores (Bogart *et al.*, 2007; Langone *et al.*, 2008; Gururaja, 2010; Iskandar *et al.*, 2014). Atualmente, falta um sistema atualizado e unificado que estenda uma classificação para todos os grupos de vertebrados; o que permitirá comparações entre MRs dentro de um grupo ou entre grupos, possibilitando uma melhor compreensão dessas estratégias reprodutivas dos grupos de vertebrados.

Essas classificações são úteis porque ajudam a colocar novas descobertas em um contexto evolucionário de variação já conhecido. Por exemplo, Gururaja *et al.* (2014) descreveu o comportamento reprodutivo e cuidado parental do Mud-packing Frog; esse comportamento de postura de ovos em vegetação já está classificado como MR 25, e cobrir ovos com lama é apenas um cuidado parental. Além disso, as classificações ajudam a enquadrar estudos evolutivos comparativos sobre a ordem de evolução dos MRs e os mecanismos seletivos que levam à sua diversificação (Gomez-Mestre *et al.*, 2012; Pereira *et al.*, 2015; Zamudio *et al.*, 2016). Uma classificação unificada de MRs também pode ser usada para caracterizar assembleias e investigar a diversidade da comunidade de MRs correlacionados com outras características, como tamanho-fecundidade e relações de desenvolvimento (Crump, 1974). Pode ser usada para classificar as espécies em guildas, em estudos orientados para a conservação (por exemplo, Becker *et al.*, 2007; Santoro & Brandão, 2014; Shabrani & Das, 2015). No entanto, embora a definição atual de MRs para anfíbios seja simples, quase todos os estudos anteriores que usaram os MRs de alguma forma não consideraram todos os caracteres conforme a definição de Salthe & Duellman (1973). Por exemplo, parâmetros quantitativos como tempo de desenvolvimento, tamanho do corpo da fêmea, tamanho do ovo e tamanho da postura, todos incluídos na definição original de MR (Salthe & Duellman, 1973), quase nunca foram usados (exceção Gaitonde & Giri, 2014). Além disso, existem algumas inconsistências no uso dos caracteres de MRs da atual classificação (Haddad & Prado, 2005), que é uma atualização de Duellman e Trueb (1986). Por exemplo, os modos 1 e 2 são semelhantes, com exceção de que as larvas se desenvolvem em corpos d'água lênticos ou lóticos. De acordo com esse raciocínio os MRs 4 e 5 também deveriam distinguir o desenvolvimento das larvas. Além disso, o uso de cuidados parentais para distinguir MRs é inviável, pois esta informação é inexistente para muitas espécies, não é fácil de obter e, em alguns casos é facultativa variando entre indivíduos (Martins, 1993; Wells, 2007).

Portanto, com base nas classificações anteriores de anfíbios, estamos propondo a exclusão de caracteres com parâmetros quantitativos, como tamanho da fêmea, tamanho do ovo, tamanho da ninhada e tempo de desenvolvimento larval (como previamente incluído por Salthe & Duellman, 1973), evitando o uso de cuidados parentais, e incluindo um caractere recentemente usado para anuros, a presença/ausência da construção de ninho (Zamudio *et al.*, 2016). Esse caracter se correlaciona claramente com as filogenias modernas (e.g., Faivovich *et al.*, 2010). Contudo, é difícil fazer tal argumento sem um sistema padronizado de classificação de MRs aplicado a todos os grupos. Numa tentativa de melhorar e facilitar futuros estudos de ecologia, as possíveis consequências desse novo sistema são discutidas. Além disso, essa proposta de classificação de MRs para Amphibia será estendida para todos os grupos de vertebrados, peixes, répteis, aves e mamíferos, e serve como uma linha de base para futuros estudos comparativos ecológicos e evolutivos.

Dessa forma, nós estamos propondo aqui um estudo sobre a relação da riqueza de espécies de anfíbios e a diversidade de RMs. O grupo de anfíbios, com mais de 1.100 espécies reconhecidas no Brasil (Segalla *et al.*, 2019), possui o maior número de MRs dentre todos os outros grupos de vertebrados (CAPÍTULO 2), 71 (CAPÍTULO 1). Além disso, muitas dessas espécies estão relacionadas à Mata Atlântica, que é uma região de números inesperados de RMs (Haddad & Prado, 2005).

Estudos sobre a Mata Atlântica mostraram que a diversidade de RMs de anfíbios está relacionada à topografia complexa que proporciona diferentes microhabitats e barreiras, o que permitiu uma alta diversificação de MRs (Haddad & Prado, 2005; Toledo *et al.*, 2014). Segundo Haddad & Prado (2005) e da Silveira Vasconcelos *et al.* (2010), a alta umidade também se correlaciona com a diversidade de MRs porque reduz o risco de dissecação dos ovos e girinos que se desenvolvem fora da água. Toledo et al. (2014) argumentam que a elevação e a variação latitudinal não estão correlacionadas com a riqueza de espécies raras de anfíbios. Por outro lado, da Silveira Vasconcelos *et al.* (2010) disseram que a elevação está correlacionada positivamente com a riqueza de espécies de anuros. No entanto, nenhum outro estudo realmente testou uma hipótese bastante direta, de que a riqueza de espécies de anfíbios está diretamente relacionada à diversidade de MRs.

Muitos estudos relacionaram a riqueza de espécies com a riqueza comportamental. Por exemplo, Mitra *et al.* (1996) verificaram se a riqueza de espécies estava associada ao sistema social de acasalamento em aves. Nicolakakis *et al.* (2003) argumentaram que a transmissão social de novas habilidades para outros membros de uma população de aves pode acelerar as taxas de evolução e, portanto, poderia explicar as diferenças na riqueza de espécies. A altitude e a precipitação estão positivamente correlacionadas aos MRs de anuros; por outro lado, a temperatura pode não estar correlacionada (da Silveira Vasconcelos *et al.*, 2010). A riqueza de insetos herbívoros foi correlacionada com a alimentação de uma única espécie de planta (Novotny *et al.*, 2004). Auster *et al.* (2019) analisaram grupos de peixes de espécies mistas piscívoras relacionadas a comportamentos de caça. Portanto, fica claro que a riqueza de espécies pode influenciar a diversidade de comportamentos.

Assim, testamos a hipótese de que a riqueza de espécies de anfíbios está diretamente relacionada à diversidade de MRs. Para tanto, foi realizada uma análise espacial comparando a diversidade de MRs com a riqueza de espécies de anfíbios no Brasil. Além disso, como o habitat pode influenciar, também comparamos diferentes biomas, esperando que biomas com maior estrutura e umidade da vegetação (Mata Atlântica e Amazônia) teriam mais diversidade de MRs do que biomas menos estruturados e secos (Caatinga, Cerrado, Pantanal e Pampa).

Essa tese está dividida em três capítulos. O primeiro capítulo é sobre a definição e a classificação de modos reprodutivos de vertebrados terrestres, o segundo é sobre a classificação de modos reprodutivos de vertebrados aquáticos e o terceiro é sobre a relação espacial entre a riqueza de espécies e diversidade de modos reprodutivos de anfíbios.

Capítulo 1. A UNIFIED CLASSIFICATION FOR TETRAPOD REPRODUCTIVE MODES

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ABSTRACT

Tetrapods include approximately 32,000 species of Amphibia, Lepidosauria, Testudines, Archosauria and Synapsida. With the exception of Amphibians, there is little information available on tetrapod reproductive modes (RMs), defined here as the combination of 10 characters in multiple states. A more elaborate classification of RMs was proposed for amphibians, but never for other vertebrate clades. In addition, even the classifications available for amphibians are not based on the same variables, thereby reducing their value for comparisons across groups. Here, we propose an updated classification of amphibian RMs and extend it to all tetrapods. Based on 6,200 tetrapod species, we built a dichotomous tree with 116 different possible RMs. Amphibians alone exhibited 71 of these RMs, and Amniota exhibited 51 RMs. Our proposal is the first comprehensive RM classification for tetrapods, which provides insight into broader patterns of evolution of reproductive strategies and serves as a baseline for future comparative ecological and evolutionary studies across tetrapod clades.

INTRODUCTION

Terrestrial vertebrates or tetrapods include over 32,000 living species of Amphibians, Testudines, Lepidosauria, Archosauria and Synapsida (Gill, 2006; Barrowclough *et al.*, 2016; Frost, 2018; HBW & Birdlife International, 2017; Uetz, 2018; Wilson & Reeder, 2017). The ancestral tetrapod abandoned an obligate aquatic lifestyle and diversified in terrestrial environments (Inger, 1957; Long & Gordon, 2004). During this transition, tetrapods also diversified in reproduction, specifically in reproductive modes (RMs) (Long & Gordon, 2004). The study of vertebrate breeding biology substantially expanded in the 19th century (e.g., Cuvier, 1802; Darwin, 1859; Boulenger, 1886; von Ihering, 1886; Semon, 1894; Mitsukuri, 1891; Budgett, 1899; Thilenius, 1899), but the term reproductive mode only appeared in a study of the reproductive biology of fishes in mid 20th century (Breder Jr. & Rosen, 1966). Salthe & Duellman (1973) defined the RM as a combination of traits that include oviposition site, ovum and clutch characteristics, rate and duration of development, stage and size of hatchling, and type of parental care, if any. Hence, it is not a single phenotype, but rather a set of characters. One outcome of this set of characters is that the application of the concept of RM varies among the vertebrate clades, because researchers naturally focus on the reproductive traits present within their clades of study (Collias, 1964; Shine, 1983; Bronson, 1989; Haddad & Prado, 2005). Currently, there is no updated and unified system that extends the classification to all groups of tetrapods, which would allow comparisons among RMs and a better understanding of reproductive strategies.

RMs have been well characterized in amphibians, perhaps because of their diversity and complexity. Boulenger (1886) proposed a classification of RMs (without using the term RM) using the following traits: size of the ovum, site of egg deposition and larval hatching, and development, which could be direct or indirect. Based on these traits he established 10 amphibian RMs. Subsequently, with the discovery of more diverse reproductive traits, the resolution of RM categories increased to include additional traits. Salthe (1969) classified and described three RMs for salamanders (Caudata). Later, Salthe & Duellman (1973) revisited the RMs of amphibians. Besides the traits selected by Boulenger (1886) and Salthe (1969), their newer categorization included ovum and clutch characteristics, rate and duration of larval development, stage of hatching, and presence of parental care (Salthe & Duellman, 1973).

This review was pivotal because it promptly stimulated interest and resulted in a large increase in studies of amphibian RMs and their specific components (Salthe & Mecham, 1974; Lamotte & Lescure, 1977; McDiarmid, 1978; Wake, 1982). Duellman & Trueb (1986) included this classification in their book "*Biology of Amphibians*" and recognized 29 RMs for anurans, 7 for salamanders, and 2 for caecilians. Haddad & Prado (2005 a;b) reviewed anuran RMs and increased the list to include 39 RMs, including three rearrangements from known modes and seven new modes described for the Atlantic forest amphibians. Subsequent studies have described additional RMs based on these earlier classification criteria (Bogart *et al.*, 2007; Langone *et al.*, 2008; Gururaja, 2010; Iskandar *et al.*, 2014).

These classifications are useful because they help place new discoveries in an evolutionary context of already known variation. For example, Gururaja *et al.* (2014) used the system to classify the reproductive mode of mud-packing frogs as RM 25, which consists of arboreal egg laying behavior, coupled with the parental care of covering eggs with mud. In addition, the classifications help frame comparative evolutionary studies on the order of evolution of RMs and the selective mechanisms that lead to their diversification (Gomez-Mestre *et al.*, 2012; Pereira *et al.*, 2015; Zamudio *et al.*, 2016). A single classification system that covers all tetrapods could also be used to characterize assemblages and investigate community diversity of RMs correlated with other traits such as size-fecundity and developmental relationships (Crump, 1974). Finally, it can also be used to classify species into groups in conservation-oriented studies (e.g., Becker *et al.*, 2007; Santoro & Brandão, 2014; Shabrani & Das, 2015). However, although the current definition of RMs for amphibians is straightforward, nearly all of the past studies that applied RMs did not consider all characters to define specific RMs. For example, quantitative parameters like time of development of larvae, female body size, egg size and clutch size, all included in the original definition of RM (Salthe & Duellman, 1973), have almost never been used (see exception in Gaitonde & Giri, 2014). In addition, there are some inconsistencies in the use of RM characters. For example, in the RMs listed by Haddad & Prado (2005a;b), which was an update of Duellman & Trueb (1986), RMs 1 and 2 are similar, except that larvae develop in lentic water bodies in one and lotic water bodies in the other. According to this rationale, RMs 4 and 5, neither of which specify a lentic or lotic environment for larval development, should also be divided into two RMs each. Furthermore, the use of parental care to distinguish between modes is impracticable, as this information is lacking for many species, difficult to obtain, and in some cases, facultative, and variable among individuals (Martins, 1993; Wells, 2007). Therefore, based on previous amphibian classification, we are proposing the exclusion of female size, egg size, clutch size, and time of larval development (as previously included by Salthe & Duellman, 1973), avoiding the use of parental care, and including a trait recently applied to anurans, the presence/absence of nest construction (Zamudio *et al.*, 2016), which is easy to obtain and clearly correlates with modern phylogenies (e.g., Faivovich *et al.*, 2010). In an attempt to improve and facilitate future ecological studies, the possible consequences of such a new system will be discussed. In addition, this proposed classification of RMs can be extended to other groups of terrestrial vertebrates, enabling broader, especially ecological, comparisons.

Based on the proposed classification system, future studies will be able to test for phylogenetic signals in RM. For example, most species of the genus *Scinax* (Anura) lay eggs in ponds, as well as species of the sister genus *Ololygon* belonging to the *S. perspusillus* group (Faivovich *et al.*, 2010) lay eggs in bromeliads, while individuals belonging to species in the *O. catharinae* group may lay eggs in both bromeliads and ponds (Toledo *et al.*, 2012). In addition, in the family Megapodidae (Non-Passeriform birds), all species of the the "Brush turkey" clade lay eggs only in depressions covered by sand (Harris *et al.*, 2014), while the "Scrubfowl" clade, lay eggs in burrows, depressions, or both (Birks & Edwards, 2002).

Besides testing for phylogenetic signal in RM, it is also possible to perform RM ancestral state reconstruction. For example, among the species of the family Hirundinidae (Passeriformes), some species construct mud nests in cliff walls, others dig burrows, while still others adopt excavated burrows (ancestral modes), tree holes, termite mounds, or nest in tree branches (Winkler & Sheldon, 1993). Ancestral state reconstruction has been previously proposed but has only considered oviparity and viviparity among several genera of squamates (see Watson *et al.*, 2014). Deeper analyses of groups with a large diversity of RMs would be interesting cases for future evolutionary studies.

The aim of this study is to develop a simpler and more cohesive definition for RMs of tetrapods and to classify these RMs.

METHODS

Set of Characters of reproductive modes

After reviewing the literature on terrestrial vertebrates reproductive biology, we selected the most common set of characters traditionally used for the classification of amphibian RMs, and defined their categories and subcategories hierarchically from eggs to offspring. We thereby redefined the concept of the RM as a combination of 10 reproductive traits: reproduction type, egg laying macro-habitat, nest type, egg laying substrate, medium surrounding eggs, nest construction, egg laying microhabitat, offspring development, offspring nutrition, and place of offspring development. These traits are mostly physical and we did not consider purely behavioral aspects such as courtship, amplexus/copulation, and parental care. The different traits and their states are presented below, and we illustrate them with some representative examples.

(1) Reproduction type

a. Oviparity – Embryos in the oviduct provided with yolk. After egg laying, the embryonic development continues outside the female body, within complex extraembryonic membranes (egg) that may include gelatinous capsules or hard shells (e.g., amphibians, lepidosaurians, archosaurians, and monotremes: Shine, 1983; Blackburn & Evans, 1986; Thorbjarnarson, 1996; Beard & Grigg, 2000; Lodé, 2012).
b. Viviparity – This occurs when egg laying (as in oviparity) is absent. The parent may give birth to larvae, as in the anuran *Limnonectes larvaepartus* (Iskandar *et al.*, 2014) or to developed offspring (several vertebrate groups). In this last case, after exhaustion of vitellogenic yolk, either embryos feed on oviductal material, such as secretions (e.g., snakes, placental mammals, and marsupials: Shine, 1983; Blackburn, 1999; Pough *et al.*, 2016) or an ovum in the ovary to complete their development (e.g., some amphibians: McDiarmid & Altig, 1999), or the offspring are born after the yolk is exhausted and there is no other form of nourishment from the mother (e.g., *Nectophrynoides* spp., *Sceloporus jarrovi*: Goldberg, 1971; Wake 2015). The term ovoviviparity is here included in the viviparity category, as suggested by Blackburn (1992; 1999; 2000),

because the terms lecithotrophy and matrotrophy, used in conjunction with the reproduction mode viviparity, hampers the use of the term ovoviviparity.

(2) Egg laying macro-habitat

a. Environment – Eggs are laid in the environment, in or outside nests, as in amphibians (e.g., *Micrixalus saxicola*: Gururaja, 2010), lepidosaurians (e.g., *Amphisbaena mertensii*, *Oplurus cuvieri*: Pianka & Vitt, 2003; Andrade *et al.*, 2006), archosaurians (e.g., *Caiman yacare*, *Picumnus albosquamatus* and *Veniliornis passerinus*: Thorbjarnarson, 1996; Gussoni *et al.*, 2013) and monotremes (e.g., *Echidna* spp., *Ornithorhynchus anatinus*: Beard & Grigg, 2000; Temple-Smith & Grant, 2002).

b. Animal – Eggs in or on the body of one of the parents, as in amphibians (e.g., *Gastrotheca* spp. and *Rheobatrachus silus*: Duellman, 2015; Tyler & Carter, 1981), reptiles (e.g., *Zootoca vivipara* and *Vipera aspis*: Cornetti *et al.*, 2015; Dupoué *et al.*, 2015), birds (e.g., *Aptenodytes forsteri*: Le Maho, 1977; Stonehouse, 1953), and all mammal infraclasses (Rismiller & Seymour, 1991; Pough, *et al.*, 2016; Figures 5A, B).

(3) Nest type

a. Froth – Eggs are laid in two types of froth nest: foam and bubble nests:
   a. Foam nests are produced by amphibians and birds. In amphibians it is produced by limbs motion (beating) of parents on the mucus secreted by the female's oviduct, which is mixed with air (e.g., in the families Leptodactylidae and Racophoridae). In birds, it is produced by the saliva of some species of the genus *Aerodromus* (Kang *et al.*, 1991; Nakagawa *et al.*, 2006; Figure 6F).
   b. Bubble nests are produced by jumps of female frogs in the middle of the spawn, allowing air bubbles to be trapped in the mucus secreted by the female's oviduct (e.g., *Ololygon rizibilis*: Haddad *et al.*, 1990). Alternatively, both anuran parents expel bubbles from the nares under the spawn and the air bubbles become trapped in the mucus (e.g.,

Chiasmocleis leucosticta: Haddad & Hödl, 1997).

Some of the froth nests are on the water surface or on the ground surface or in burrows, others on leaves or branches (Crump, 2009) (Figure 6A to E). Froth nest is not considered a constructed nest (see below).

b. Non-froth – Eggs are laid in non-frothy nests, without the production of foam, bubbles, or saliva.

(4) Egg laying substrate

a. Aquatic – Eggs are laid in the water, as observed in most of the amphibians (e.g., *Ambystoma gracile*, *Itapotihyla langsdorffii*, *Ololygon angrensis*, *Rhinella icterica*, *Proceratophrys appendiculata*, *Taricha tososa*) (Petranka, 1998; Hartmann *et al.*, 2010) (Figure 7).

b. Non-aquatic – Eggs are laid on the ground, rocks, trees, scrubs, or grass as seen in the amphibians *Allobates alagoanus, Eurycea quadridigitata, Limnonectes palavanensis* (Petranka, 1998; Haddad *et al.*, 2013; Shabrani & Das, 2015).

c. In/on animal – Eggs stay in different parts of the body of the parents, e.g., the oviduct and uterus. In amphibians, the eggs may be incubated in the oviduct as in *Nectophrynoides* spp. and *Mertensiella* spp., or in the dorsum, as in *Pipa* spp. and *Gastrotheca* spp. (Lutz, 1947; Wells, 2007; Duellman, 2015). In squamates, the eggs may be incubated in the oviduct, as in *Carinascincus coventryi* and *Boa constrictor* (Shine, 1983; Marques *et al.*, 2005). In birds, the only example is observed in penguin, *Aptenodytes forsteri*, where the egg is incubated on the feet (Le Maho, 1977). Finally, in mammals, as marsupials and placentals, the ovum is incubated in the uterus (Pough *et al.*, 2016).

(5) Eggs surrounding medium

a. Lentic – Eggs are laid in still water, such as lakes, ponds, or swamps, as seen in *Chelodina rugosa* (Testudines), where the eggs are laid in underwater depressions and hatched after the wetland is dry (Kennett *et al.*, 1998), and most amphibians (Haddad & Prado, 2005).

b. Lotic – Eggs are laid in flowing waters, such as rivulets, creeks, streams or rivers, as seen in many amphibians (as in *Rhinella* spp., *Hylodes* spp.: McDiarmid & Altig, 1999; Haddad & Prado, 2005).

c. Terrestrial – Eggs are laid on terrestrial environment, as seen in several amphibians, birds, lepidosaurians, and monotremes (Collias, 1964; Bustard, 1965; Lima *et al.*, 2013; Grant *et al.*, 2004).

d. Not oviduct – Eggs are embedded in dorsum or dorsal pouches of amphibians (e.g., anurans of the family Hemiphractidae: Shine, 1983; McDiarmid & Altig, 1999; Duellman, 2015). They can also be laid on the feet of the parents, as observed in birds, *Aptenodytes forsteri* (Stonehouse, 1953).

e. Oviduct/uterus – Eggs are developed in a specialized portion of the oviduct, being nourished by yolk, by tissue of the oviduct, or other substances secreted by the parent, as seen in amphibian (*Dermophis mexicanus* and *Nimbaphrynoides occidentalis*: Wake & Dickie, 1998; Wells, 2007; Lodé, 2012; Wake, 2015), squamates (*Oligosoma zelandicum* and *Coralus caninus*: Tinkle *et al.*, 1970; Fraga *et al.*, 2013), and mammals, as marsupials and placentals (Novoa, 1970; Hanák & Mazák, 1979; Morton *et al.*, 1982; Hes, 1997; Pough, *et al.*, 2016).

(6) Nest construction

As defined by Simon and Pacheco (2005), a nest is any place selected by a bird for laying its eggs, regardless of how much digging, cleaning, lining, or building it performs. We extend this definition to all groups of vertebrates.

a. Constructed – We define construction as all sorts of environmental modification.

b. Not constructed – Nest used by a vertebrate, which did not build it (e.g., nest made by *Myiopsitta monachus*, occupied by other birds, such as *Passer domesticus*: Wagner, 2012).

c. Absent (Nest absent) – Although many placentals such as gorillas, coatis, squirrels, and even rats that keep altricial pups construct nests, these are for care of offspring, a developmental phase that we are not considering in this classification. We consider only the nests in the egg/embryo phase (Figure 5C to F).

(7) Egg laying microhabitat

a. Floating – Eggs are laid on the surface of lentic water, froth or non-froth. As observed in several amphibians (*Boana crepitans*, *Dendropsophus nanus*, *Leptodactylus labyrinthicus*: Haddad *et al.*, 2013; Nascimento *et al.*, 2015) (Figure 7A, B).

b. Ground – Eggs are laid on the soil, as reported for several amphibians (e.g., *Platymantis* spp. and *Rhombophryne roseifemoralis*: Wells, 2007), lizards (e.g., *Neusticurus bicarinatus* and *Anadia bogotensis*: Magnusson, 1996; Medina-Rangel, 2013), and birds (e.g., *Nyctidromus albicollis* and several species of the Caprimulgidae family: C. H. L Nunes-de-Almeida, personal observation; Harrison, 1998) (Figure 5C, D).

c. Subaquatic ground (SGD) – Eggs are laid on the bottom of lentic or lotic water bodies. As in amphibians (e.g., *Rhinella diptycha* and *Scinax fuscomarginatus*: Haddad *et al.*, 2013) (Figure 7C, D).

d. Depression – Eggs are laid in a ground depression, dug or not, covered or not. This is referred as a “basin” in previous literature. This state is observed in amphibians (e.g., *Amphiuma means* and *Boana faber*: Petranka, 1998; Haddad & Prado, 2005), lizards (e.g., *Plestiodon fasciatus* and *Plestiodon laticeps*: Hecnar, 1994; Conant & Collins, 1998), archosaurians (e.g., *Crocodylus porosus*, *Eremophila alpestris* and *Alaudala raytal*; Roberts, 1992; Thorbjarnarson, 1996; Harrison, 1998).

e. Burrow – Eggs are laid in a subterranean burrow dug or not by parents, as observed in amphibians (e.g., *Xenorhina* spp. and *Microcaecilia dermatophaga*: Wells, 2007; Wilkinson *et al.*, 2013), lizards (e.g., *Gambelia wislizenii* and *Eumeces laticeps*: Montanucci, 1967; Hecnar, 1994), birds (e.g., *Megaceryle torquata* and *Chloroceryle americana*: C. H. L Nunes-de-Almeida, personal observation; Harrison, 1998), and monotremes (e.g., *Ornithorhynchus anatinus*: Temple-Smith & Grant, 2002; Grant *et al.*, 2004; Munks *et al.*, 2004).

f. Subaquatic chamber (SCH) – Eggs are laid in a chamber within a body of water, as observed in some amphibians (*Dicamptodon ensatus*, *Hylodes* spp.: Petranka, 1998; Haddad & Prado, 2005).

g. Insect mound (IMO) – Terrestrial or arboreal, made by wasps, termites or ants. Eggs are usually laid in holes dug by birds, (e.g., *Colaptes campestris*: C. H. L. Nunes-de-Almeida, personal observation), Amphisbaenids (e.g., *Amphisbaena mertensii* and *A. kingii*: Boulenger, 1885; Andrade *et al.*, 2006) or anurans (e.g., *Lithodytes lineatus*: Schlüter & Regös, 1981; Schlüter *et al.*, 2009).

h. Rock – Eggs are laid on or underneath rocks as seen in amphibians (e.g., *Desmognathus* spp. and *Cycloramphus* spp., and *Thoropa* spp.: Petranka, 1998; Haddad & Prado, 2005).

i. Wall – Eggs are laid on rocky cliffs, ravines, cave walls, and rock stacks in the sea. This state is observed in snakes (e.g., *Coluber constrictor* and *Contiatenuis*: Greene, 1997), birds (e.g., *Tyto alba*, *Gygis alba*: C. H. L. Nunes-de-Almeida, personal observation; Harrison, 1975; Burton, 1985), and anurans (e.g., *Thoropa* spp.: Haddad & Prado, 2005).

j. Tree hole – Eggs are laid in natural or constructed cavities in trees or logs by birds and other animals (Harrison, 1998). This state is observed in amphibians (e.g., *Eleutherodactylus hedricki*: Wells, 2007), snakes (e.g., *Boiga angulata* and *Lamprophis abyssinicus*: Greene, 1997), and birds (e.g., *Colaptes melanochloros*, *Dryocopus lineatus*, and *Aratinga auricapilla*: Buzzetti & Silva, 2005; C. H. L. Nunes-de-Almeida, personal observation).

k. Bamboo – Eggs are laid inside the internodes of bamboo without water, as seen in the anuran *Raorchestes chalazodes* (Seshadri *et al.*, 2015).

l. Plant leaf – Eggs are laid on or underneath leaves of trees, shrubs, and grass, either rolled (constructed nest) or not. This state is observed in amphibians (e.g., *Phyllomedusa* spp. and *Rhacophorus* spp.: Haddad & Prado, 2005; Meegaskumbura *et al.*, 2015), lizards (*Gonatodes humeralis*: Pianka & Vitt, 2003; Maciel *et al.*, 2005), and birds (e.g., *Phaethornis pretrei* and *Tachornis squamata*: C. H. L. Nunes-de-Almeida, personal observation; Buzzetti & Silva, 2005) (Figure 8).

m. Plant branch – Eggs are laid on branches, sticks, or trunks of trees and shrubs, as observed in some anurans, lizards and birds (Harrison, 1998; Figure 5E, F).

n. Plant root – Eggs are laid on or between tree roots, as observed in some amphibians (e.g., some species of *Cycloramphus*: Wells, 2007) and birds (e.g., *Crypturellus variegatus*: Sick, 1997).

o. Subaquatic plant branch or root (SPBR) – Eggs are laid on or around subaquatic plant branches or roots, as observed in *Melanophryniscus montevidensis* C. Bardier, unpublished data; and *Sphaenorhynchus caramaschii*: C. F. B. Haddad, unpublished data; Figure 7E, F.

p. Floating vegetation (FLV) – Eggs are laid on floating vegetation platforms in constructed nests, as observed in the birds *Oxyura leucocephala* and *Podilymbus podiceps* (Flint *et al.*, 1984; Harrison, 1998; C. H. L. Nunes-de-Almeida, personal observation).

q. Water-filled container (WFC) – Amphibians lay eggs in plants (Phytotelmata) that accumulate water, such as *Bromeliads axils* or tanks used by the anurans, as *Melanophryniscus alipioi* (Langone *et al.*, 2008), *Crinum* sp. used by *Anodonthyla* spp., *Cophyla* spp., *Platypelis* spp., and *Plethodontohyla* spp. (Glaw & Vences, 2007; Andreone *et al.*, 2010), *Musa* sp. used by *Leptopelis uluguruensis* (Barbour & Loveridge, 1928), *Pandanus* sp. used by *Pelophryne brevipes* (Malkmus & Dehling, 2008), pitcher plants like *Nepenthes ampularia* and *N. bicalcarata* used by *Microhyla* sp. and *Philautus kerangae* (Malkmus & Dehling, 2008), and fruit capsules of *Bertholletia excelsa* on the ground used by *Adelphobates castaneoticus* and *Rhinella castaneotica* (Caldwell, 1993). WFC also includes holes in branches or trunks that are used by anurans, as *Metaphrynella sundana* (Malkmus & Dehling, 2008), holes in logs used by *Chaperina fusca* (Malkmus & Dehling, 2008), including bamboo internodes used by *Fritziana ohausi* (Haddad *et al.*, 2013). Finally, snail shells (Gastropoda) containing water are used by *Phrynobatrachus guineensis* and *Stumpffia achillei* (Wells, 2007; Rakotoarison *et al.*, 2017; Figure 9).

(8) Offspring development

In this category, two sets of nomenclature are currently used. For amphibians, the terms direct and indirect development are recognizable discrete categories, referring to the absence or presence of the larval stage, respectively. For amniotes, the terms precocial and altricial are extremes of a continuum (Nice, 1962), referring to offspring with different levels of parental dependency. Therefore, we define the boundary between these two categories (precocial and altricial) as the ability of the young to survive without parental (or other adult) providing locomotion and feeding. In mammals as marsupials, placentals and monotremes, all species were considered altricial, due to at least maternal milk dependency. However, there are various levels of altriciality, just as there are precocity levels and we are not considering this in this study. We maintained both sets of nomenclature, but they represent the same two category states of classification: direct/precocial *vs.* indirect/altricial.

a. Indirect – This describes development with a larval stage, and is observed in most amphibians with eggs that hatch into larvae (tadpoles in anurans).

b. Direct – This describes development without a larval stage and is observed in all amphibians where eggs hatch into post-metamorphic juveniles, such as anurans of the *Brachycephaloidea* clade (Padial *et al.*, 2014).

c. Altricial – This is used to describe birds, except Paleognatha, and all mammals (monotremes, marsupials and placentals), where the young may be borne or hatched with their eyes closed, without the ability to swim, walk, or fly, and rely on their parents, siblings, or related individuals for feeding (Pough *et al.*, 2016). The altricial stage lasts until the offspring is independent from their caregivers. In the case of mammals, this boundary is known as weaning.

d. Precocial – This is applied to lepidosaurians and birds. In this case, the young is not dependent on their parents. For example, megapodid birds present a high level of precocity, where the chicks are hatched with feathers on their bodies and with the ability to fly (Pough *et al.*, 2016).

(9) Offspring nutrition

a. Endotrophic – This is the condition where larvae obtain their entire developmental energy from vitellogenic yolk (McDiarmid & Altig, 1999). This category is applied only to indirect developing amphibians, such as *Eupsophus emiliopugini* and *Allobates sumtuosus* (Nuñez & Úbeda, 2009; Simões & Lima, 2012).

b. Exotrophic – The condition where the larvae obtain energy by oral consumption of food, when the vitellogenic yolk runs out (McDiarmid & Altig, 1999). We applied this category only to indirect developing amphibians, as *Rhinella proboscidea* and *Nymphargus lasgralarias* (Menin *et al.*, 2006; Guayasamin *et al.*, 2014).

c. Lecithotrophic – Embryos obtain energy from the vitellogenic yolk (Pough, Janis & Heiser, 2016). We applied this category to direct developing amphibians, such as *Brachycephalus ephippium* (Pombal Jr, 1999); turtles, such as *Chelonia mydas* (Pritchard, 1979); tuataras, such as *Sphenodon punctatus* (Cree *et al.*, 1991); lizards, such as *Calotes ceylonensis* (Pradeep & Amarasinghe, 2009); snakes, such as *Alopoglossus angulatus* (Vitt *et al.*, 2008); all birds and few monotremes, such as *Tachyglossus aculeatus* (Temple-Smith & Grant, 2002).

d. Matrotrophic – Embryos or nestlings that obtain energy not only by vitellogenic yolk, but supplemented by nourishment derived from the mother (Pough *et al.*, 2016). We applied this category to direct developing amphibians, like *Pipa pipa* (Wells, 2007), all mammals (marsupials, placentals and monotremes) (Pough *et al.*, 2016), and several birds that feed their offspring with crop milk (Horseman & Buntin, 1995). Crop milk, here defined as milk, is a lipid rich material produced by secretion of epithelial cells of the esophagus or crop, used by birds to feed their offspring. It can be observed in birds of the families Columbidae and Phoenicopteridae (Horseman & Buntin, 1995).

e. Patrotrophic – Embryos or nestlings that obtain energy not only by vitellogenic yolk, but also through paternal provision of nutrients (Blackburn, 2015). We applied this category to amphibians and birds that produce milk (e.g., *Rhinoderma darwini* and *Aptenodytes forsteri* (Prévost & Vilter, 1963; Goicoechea *et al.*, 1986; Horseman & Buntin, 1995; Crump, 2009).

(10) Place of offspring development

a. Lentic – Larvae are developed in still water, such as lakes, ponds, or swamps, as seen in the anurans *Heterixalus madagascariensis* and *Vandijkophrynus amatolicus* (Glaw & Vences, 2007; Wells, 2007), including fossorial larvae that develop under the sand bed, gravel bed, or mud as in *Scaphiophryne gottlebei* and *Staurois parvus* (Mercurio & Andreone, 2006; Preininger *et al.*, 2012).

b. Lotic – Larvae are developed in flowing waters, such as rivulets, streams or rivers, as seen in amphibians *Ansonia torrentis* and *Cycloramphus rhyakonastes* (Wells, 2007; Nunes-de-Almeida *et al.*, 2016), including larvae that are developed under the sand bed, gravel bed, or mud such as *Vitreorana eurygnatha*, *Micrixalus herrei* and *Staurois guttatus* (Heyer, 1985; Haas & Das, 2012; Senevirathne *et al.*, 2016). Some aquatic placentals also fall in this category (e.g., *Inia geoffrensis*: Best & da Silva, 1984).

c. Marine – Offspring develop in marine water, such as in the cetaceans (e.g., *Balaenoptera musculus*: Lockyer, 1984).

d. Terrestrial – Offspring develop in a terrestrial environment, as in amphibians *Allobates tapajos* and *Zachaenus parvulus* (Lutz, 1943; Simões *et al.*, 2013), birds *Crypturellus variegatus* and *Aratinga auricapilla* (Sick 1997; C. H. L. Nunes-de-Almeida, personal observation), and mammals (marsupials, placentals and monotremes.

e. Internal – This is only applied to indirect or altricial viviparous animals. In anurans, eggs hatch inside the parents into tadpoles and complete development into froglets inside the male's hip pouch, as in *Assa darlingtoni* (Wells, 2007). Eggs are swallowed and hatch into tadpoles and complete the development as froglets inside the mother's stomach, as in *Rheobatrachus silus* (McDiarmid & Altig, 1999). Eggs are hatched as tadpoles that develop inside the male's vocal sacs, as in *Rhinoderma* spp. (McDiarmid & Altig, 1999). In marsupials, eggs develop in the uterus and, after hatching, the larval development is completed inside a marsupium, as in *Macropus parma* and *Dromiciops gliroides* (Maynes, 1973; Muñoz Pedreros *et al.*, 2014). A marsupium is a body pouch where their offspring develop (Pough *et al.*, 2016). It is found in most marsupials (not all of them: marsupia are not present in species of short-tailed opossums, genus *Monodelphis*, and species of the tribe Marmosinae; Johnson-Delaney & Lenox, 2017) and amphibians (known as marsupial frogs) of the family Hemiphractidae. In these frogs, females have a body pouch on their back where eggs, tadpoles, or froglets are kept (e.g., *Gastrotheca* spp., *Fritziana* spp., *Hemiphractus* spp.: Duellman, 2015).

f. Animal – This is only applied to indirect or altricial oviparous animals. This state is observed for amphibians that give birth to tadpoles/juveniles, as in *Limnonectes larvaepartus* and *Nectophrynoides* spp. (Lee *et al.*, 2006; Iskandar *et al.*, 2014), and lizards of the Scincidae family that give birth to juveniles, as in *Pseudemoia spenceri* (Thompson *et al.*, 1999).

PROPOSED ANALYSIS SYSTEM

After all tetrapods with adequate data, based on literature review and additional unpublished data (6,200 species; Table S1), were classified into the proposed RM system, a heat map was built with the number and proportion of shared RMs for Amphibia and other groups of Tetrapoda: Lepidosauria, Archosauria, Testudines, and Synapsida.

RESULTS

The study covers 6,200 species and recognizes 116 RMs (Figures 1,2,3, S3; Table S1). Amphibians, which is the class represented by the largest number of species (2,159 species; 35% of the species; 80% of the species represented), exhibit the largest number of RMs (71). Anurans (2,001 species sampled) exhibit 69 RMs, of which 54 were exclusive to this group, especially from RMs 79 to 98, which include froth nests, and RMs 100 to 103 and 106 to 110, which include eggs or tadpoles carried by parents. Salamanders (109 species sampled) exhibit 16 RMs, with two exclusives (RM 7 and RM 41) and caecilians (49 species sampled) exhibited six RMs, of which none was exclusive to this group (Table 1).

The anuran *Rhacophorus viridis* exhibits four different RMs, representing the maximum number of modes known from one species. In the Caudata, four plethodontid species, *Desmognathus carolinensis*, *D. ocoee, D. orestes*, and *Hemidactylium scutatum* exhibit three different RMs. Among the Gymnophiona, the maximum number of RM was one (Tables 1; S1). In the exclusive reproductive character key for the Amphibia (Figure S1), it is possible to compare the current 71 RMs with previous classifications (Boulenger, 1886, Duellman & Trueb, 1986; Haddad & Prado, 2005).

Based on 4,041 species (65% of the total sample), Amniota exhibit 51 different RMs, of which 36 were exclusive to this group (Figure S2). Among these, 496 were exhibited in members of the Lepidosauria (2 rhynchocephalids, 344 snakes, 150 lizards and amphisbaenids), which represent 84% of the families that were analyzed. A single lizard species, *Gonatodes humeralis*, exhibited five different RMs, which represents the largest number of RMs observed in a single tetrapod species (Table 1).

Among the Testudines, 167 species have previously classified RMs (130 Cryptodira and 37 Pleurodira). For this group we collected data from all families. Testudines have three RMs and RM 11 were unique among Amniota. This is represented by *Chelodina rugosa*, which lays eggs underwater, although the development only occurs when the nest is dry, and the offspring development is precocial (Table 1).

Among Archosauria we obtained data on 2,519 species (23 Crocodilia, 40 Aves Paleognatha, 1,126 Aves Neognatha non-Passeriformes, and 1,330 Aves Neognatha Passeriformes), which represent 99% of archosaurian families. Archosauria exbhibit 37 RMs and the maximum number of RM for one species was four (observed in *Strix varia*, *Bubo virginianus*, *Aegotheles cristatus*, *Falco columbarius*, and *Passer domesticus*). Aves Neognathae non-Passeriformes exbhibit 21 exclusive RMs (Table 1).

Among the Synapsida (living mammals), 859 species (5 Monotremata, 330 Marsupialia, and 524 Placentaria, 97 % of Synapsida families) have previously described RMs. Only six RMs were listed, two were exclusive (RMs 113 and 114; Table 1), and two was the maximum number of RMs observed in one species (*Ornithorhynchus anatinus*).

We found that Amphibia and Amniota shared only five RMs: Amphibia and Lepidosauria shared RMs 21, 115 and 116; Amphibia, Lepidosauria, and Archosauria shared RM 32; Amphibia, Lepidosauria, Testudines and Archosauria shared RM 69. Among Amniota, only seven modes were shared between groups: RMs 20, 44, and 74 were present in Lepidosauria and Archosauria, RMs 68, 70, and 104 in Archosauria and Synapsida, and RM 76 in Lepidosauria, Testudines, and Archosauria. Therefore, we found that less than 8% (varying from 1.3 to 7.5%) of RMs were shared between the major tetrapod groups (Figure 4).

DISCUSSION

Reproductive modes aspects

This review is the first comprehensive RM classification proposal for tetrapods. For the Amniota this classification is novel and, although RMs had been previously classified in amphibians (e.g., Haddad & Prado, 2005 – 39 RMs), we added 32 RMs to the current set of amphibians RMs. With the addition of these new RMs, it is now possible to compare RMs among tetrapods. For example, Amphibia is the vertebrate Class with the largest number of RMs. This is probably due to the generalized use of aquatic environments by this group, including all gradients between water and land, which increases the possibilities for egg laying and larval development sites. Therefore, it would be interesting to compare amphibians with fishes, which has been indicated as a group with a large number of RMs (Balon, 1975; 1981) that may be equivalent to the amphibians (Gomez-Mestre *et al.*, 2012), but has never been properly compared. Bony fishes (piscine Osteichthyes) comprise a very diverse group of species and, consequently, might possess a high diversity of RMs. It is worth noting that the previous amphibian RM 1 was divided (eggs laid in lentic water) into three different RMs, depending on whether the eggs are floating (RM 1), subaquatic on the ground (RM 2), or subaquatic attached to plant branches or roots (RM 3). This division is reasonable and tentatively balanced comparisons with terrestrial habitats and with aquatic animals, as fishes or invertebrates, allowing future comparisons. On the other hand, this subdivision also revealed that this information is lacking for many amphibian species, probably because of simpler classifications used in the past. Therefore, we expect higher resolution in the description of RMs in future studies, based on our proposed method.

Surprisingly, there are few modes shared among major groups of tetrapods (with less than 8% of overlaps). One explanation may be historical disruptive selection, that is, species present different RMs thus avoiding niche overlap (e.g., for egg laying; Thoday & Boam, 1959). In addition, ecophysiology is variable among vertebrate classes and is directly related to breeding biology. For example, most amphibians are restricted to aquatic environments for egg laying sites, while most amniotes must avoid aquatic sites and their breeding biology.

RM plasticity

Anurans, especially those that produce froth nests, exhibit plasticity in their RMs; specifically these species vary in oviposition site, probably as an evolutionary response to aquatic predation (Hödl, 1990; Drewes & Altig, 1996; Menin & Giaretta, 2003; Altig & McDiarmid, 2007), competition (Heyer, 1969; Altig & McDiarmid, 2007), and abiotic factors (Gorzula, 1977; Heyer, 1969; Hödl, 1986; Altig & McDiarmid, 2007). For example, *Physalaemus signifer*, which lays eggs in froth nests, uses shallow pools, water accumulated in the axils of bromeliads, or directly uses humid soil (Haddad & Pombal, 1998; Haddad & Prado, 2005). Amphibians may exhibit facultative exotrophy, like *Fritziana goeldii* (Weygoldt & Carvalho e Silva, 1991). Other species of the same family (Leptodactylidae) also make froth nests on the ground or in terrestrial bromeliads, showing similar behavioral plasticity (Toledo *et al.*, 2012). Furthermore, the lizard *Gonatodes humeralis*, which present the richest variation in RM (five different modes), can lay its eggs on rock walls, termite mounds, tree bark, leaves, or among tree roots (Pianka & Vitt, 2003; Maciel *et al.*, 2005). Such plasticity may be adaptive, providing advantages in cases of rapid environmental changes. For example, if one species is able to lay eggs both in bromeliads and directly in ponds (e.g., Toledo *et al.*, 2012), and bromeliads are locally extinct but ponds are present, the population will still thrive in that site.

Froth nests (RMs 79 to 98) can be aquatic or terrestrial, placed in trees, attached to rocks, or laid on the water surface (Wells, 2007). Froth nests play an important role in protecting the eggs and embryos, keeping the eggs hydrated and oxygenated, providing thermal insulation, and limiting predation (Heyer, 1969; Villa *et al.*, 1982; Downie, 1988; Seymour, 1999; Prado *et al.*, 2005; Méndez-Narváez *et al.*, 2015). Froth nests increase thermo-hydric conditions and provide protection from predators when wrapped in plant leaves, such as in *Afrixalus* spp., *Opisthothylax immaculatus*, *Rhacophorus kio*, and *R. lateralis* (Wells, 2007; Grosjean *et al.*, 2008; Biju, 2009; Meegaskumbura *et al.*, 2015; Seshadri *et al.*, 2015). Other variations include producing froth nests inside tree holes or tree root buttresses, as in *Theloderma horridum* (Malkmus & Dehling, 2008; Figueroa & Selveindran, 2011), in burrows, such as some species of *Adenomera* spp., *Leptodactylus* spp., *Rhombophryne* spp., and *Limnodynastes dorsalis* (Heyer, 1969; Glaw & Vences, 2007; Wells, 2007; Pereira *et al.*, 2015), or underneath rocks in rivers, such as in *Rhacophorus viridis* (Seshadri *et al.*, 2015).

Evolution of modes

While several cases of variation are observed within the same clade and strong ecological constrains act in the evolution of RMs, other groups appear to be quite conservative. For example, almost all species within the *Brachycephaloidea* clade (over 1,000 anuran species) have the same RM (RM 32: eggs on ground, offspring with lecithotrophic development). The few exceptions to this mode include eggs laid on vegetation (e.g. *Ischnocnema nasuta* and *I. venancioi*; Lynn & Lutz, 1947; Izecksohn & Albuquerque, 1972), eggs possibly laid in burrows (*Eleutherodactylus aporostegus*; Schwartz, 1965; Hedges *et al.*, 2008), and viviparity (*Eleutherodactylus jasperi*; Wake, 1978).

The observed reduced overlap in RM among groups indicates that there is no relationship between phylogenetic groups and RMs, but rather, there may be ecological influence. Many of the characters listed in this study did not have the same origin, i.e., they are not homologous. For example, eggs are not all the same, as we are not considering anamniotic and amniotic eggs as distinct modes. Likewise, froth nests and viviparity evolved independently and several times within tetrapods, even among anurans or within some families. Therefore, those interested in testing homology and convergence within tetrapods must delimit the characters or states differently (e.g., Gomez-Mestre *et al.*, 2012). In spite of that, our study may serve as a baseline from which deeper evolutionary approaches can be developed.

Based on the listed RMs for amphibians, we note that some possible alternatives are not described for this group. For example, froth nests have not been observed on lotic water bodies. This could be explained by the likelihood of nests being destroyed in such conditions. In addition, the fact that there is no direct development of eggs laid in aquatic environments indicates that it is an adaption to terrestrial environment; it probably indicates an apomorphic condition in relation to indirect development. On the other hand, other not yet described RMs seem plausible; for example, a nest constructed on a rocky wall, or eggs laid without a nest in an insect mound with direct or indirect development, and the offspring relatively mature and mobile from the moment of birth or hatching, being able to feed alone (precocious development). Therefore, we expect that future natural history observations will increase the number of known modes not only for amphibians, but also for other tetrapods.

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TABLE

Taxon / group	Number of known species	Percentage of represented species	Percentage of represented families	Number of species with RM data	Number of RMs	Maximum number of RMs for one species	Number of exclusive RMs
Amphibia	**7,913**	**27%**	**80%**	**2,159**	**71**	**4**	**56**
Anura	6,982	29%	80%	2,001	69	4	54
Caudata	722	15%	100%	109	16	3	2
Gymnophiona	209	23%	60%	49	6	2	-
Lepidosauria	**10,513**	**5%**	**84%**	**496**	**16**	**5**	**2**
Rhynchocephalia	2	100%	100%	2	1	1	-
Amphisbaenia	196	5%	6%	10	4	2	-
Lizards	6,409	2%	75%	140	16	5	2
Serpentes	3,906	9%	100%	344	7	2	-
Testudines	**355**	**47%**	**100%**	**167**	**3**	**1**	**1**
Cryptodira	262	50%	100%	130	2	1	-
Pleurodira	93	40%	100%	37	2	1	1
Archosauria	**11,149**	**23%**	**99%**	**2,519**	**37**	**4**	**21**
Crocodylia	24	96%	100%	23	2	1	-
Aves Paleognathae	64	64%	100%	40	8	3	1
Aves Neognatha Non-Passeriformes	4,413	26%	100%	1,126	35	4	20
Aves Neognatha Passeriformes	6,648	20%	99%	1,330	11	4	-
Synapsida	**5,416**	**16%**	**97%**	**859**	**6**	**2**	**2**
Monotremata	5	100%	100%	5	3	2	-
Marsupialia	331	99%	100%	330	1	1	-
Placentaria	5,080	10%	96%	524	3	1	2
Tetrapoda	**35,346**	**17%**	**95%**	**6,200**	**116**	**5**	**82**

Table 1. Tetrapod reproductive modes (RM) information summary. Total number of known species [based on Frost (2018) for amphibians; HBW & BirdLife International (2017) for birds; Uetz (2018) for reptiles; and Wilson & Reeder (2018) for synapsids], percentage of species included in our study, percentage of represented families, number of RMs, maximum number of RMs for a single species, and number of unique RMs for each group.

FIGURE LEGENDS

Figure 1. Dichotomous reproductive character and state key of Tetrapoda with 116 different reproductive modes. Letters indicate groups: Anura (A), Caudata (B), Gymnophiona (C), Rhynchocephalia (D), Amphisbaenia (E), Lizards (F), Serpentes (G), Cryptodira (H), Pleurodira (I), Crocodylia (J), Aves Paleognathae (K), Aves Neognathae non-Passeriformes (L), Aves Neognathae Passeriformes (M), Monotremata (N), Marsupialia (O), and Placentaria (P). Numbers on a top row and lower left indicate the 10 trait categories. IMO = Insect mound, FLV = Floating vegetation, SGD = Subaquatic ground, SPBR = Subaquatic plant branch/root, SCH = Subaquatic chamber, WFC = Water-filled container. RMs 1-40.

Figure 2. Dichotomous reproductive character and state key of Tetrapoda with 116 different reproductive modes. Letters indicate groups: Anura (A), Caudata (B), Gymnophiona (C), Rhynchocephalia (D), Amphisbaenia (E), Lizards (F), Serpentes (G), Cryptodira (H), Pleurodira (I), Crocodylia (J), Aves Paleognathae (K), Aves Neognathae non-Passeriformes (L), Aves Neognathae Passeriformes (M), Monotremata (N), Marsupialia (O), and Placentaria (P). Numbers on the top row and lower left indicate the 10 trait categories. IMO = Insect mound, FLV = Floating vegetation, SGD = Subaquatic ground, SPBR = Subaquatic plant branch/root, SCH = Subaquatic chamber, WFC = Water-filled container. RMs 41-78.

Figure 3. Dichotomous reproductive character and state key of Tetrapoda with 116 different reproductive modes. Letters indicate groups: Anura (A), Caudata (B), Gymnophiona (C), Rhynchocephalia (D), Amphisbaenia (E), Lizards (F), Serpentes (G), Cryptodira (H), Pleurodira (I), Crocodylia (J), Aves Paleognathae (K), Aves Neognathae non-Passeriformes (L), Aves Neognathae Passeriformes (M), Monotremata (N), Marsupialia (O), and Placentaria (P). Numbers on the top row and lower left indicate the 10 trait categories. IMO = Insect mound, FLV = Floating vegetation, SGD = Subaquatic ground, SPBR = Subaquatic plant branch/root, SCH = Subaquatic chamber, WFC = Water-filled container. RMs 79-116.

Figure 4. Heat map with the number (upper diagonal) and percentage (lower diagonal) of shared reproductive modes (RM) among tetrapod groups. The gray diagonal indicates the total number of RMs per group.

Figure 5. Diversity of anuran, bird and reptile egg laying microhabitat: *Fritziana goeldii* with eggs on its back (A), *Aptenodytes forsteri* with an egg holded apart from ground on its feet (B), *Natrix natrix* eggs on the ground (C), *Nyctidromus albicollis* eggs on the ground (D), *Ptychozoon nicobarensis* eggs on a tree trunk (E), and *Gygis alba* egg layed on a tree branch (F).

Figure 6. Froth nests of amphibians and birds: *Ololygon rizibilis* bubble nest, made by the female jumping in the middle of the spawn (A); *Chiasmocleis leucosticta* bubble nest made by the release of air bubbles through the parents' nostrils (B); *Physalaemus olfersii* foam nest on water, made by the movements of the males' legs (C); *Physalaemus spiniger* foam nest on bromeliad axil, made by the movements of the males' legs on the mucus secreted by the female (D); *Chiromantis xerampelina* foam nest on tree branch, produced by movement of the parents's legs on the mucus secreted by the female (E); *Aerodramus fuciphagus* saliva nest attached to a wall (F).

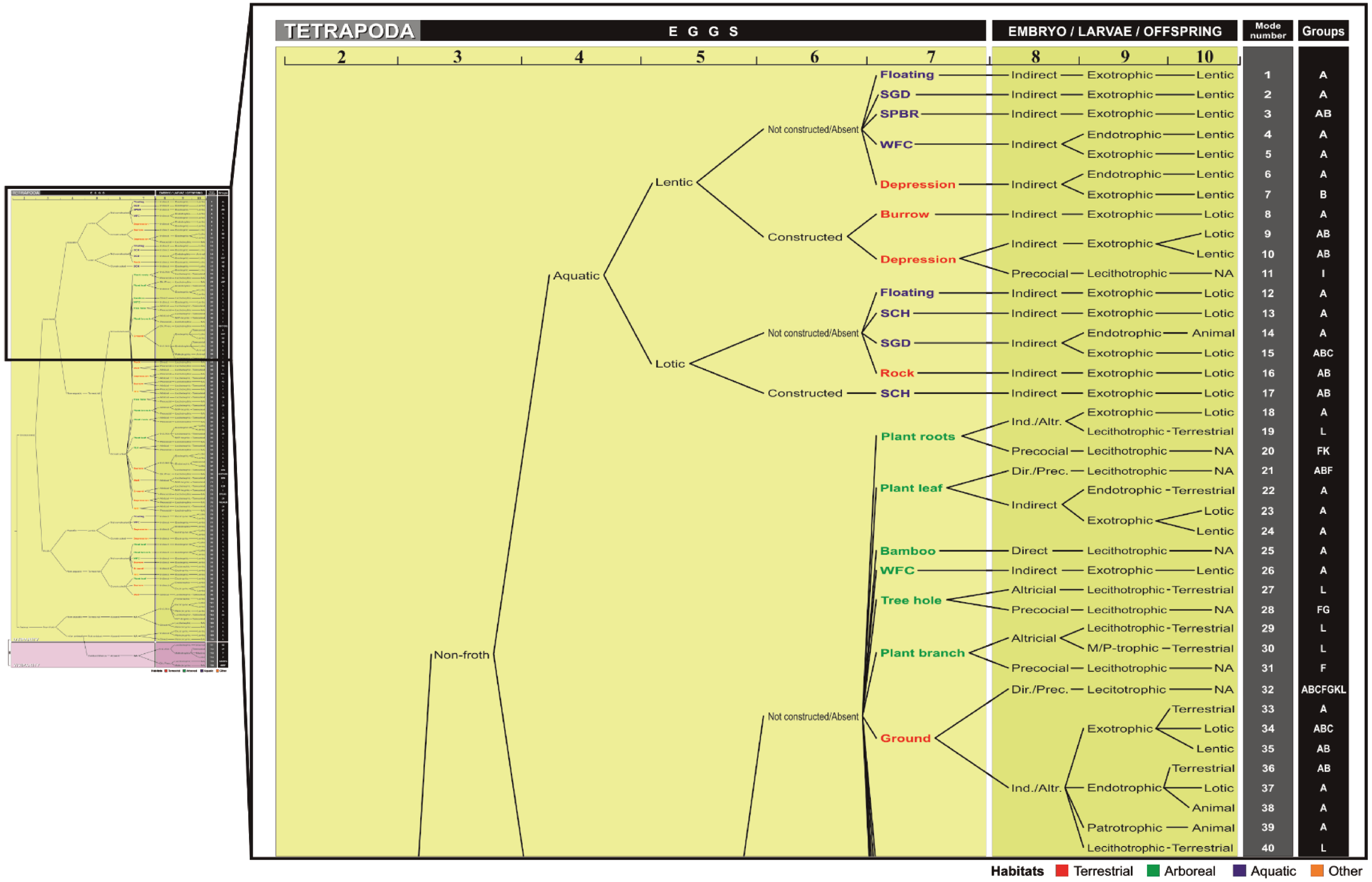
Figure 7. The most generalized RM of amphibians (eggs and exotrophic tadpoles in still water bodies) proposed in previous classification was split into three new RMs: RM 1 represented by *Boana crepitans* (A) and *Elachistocleis cesarii* (B); RM 2 represented by *Rhinella icterica* (C) and *Boana marginata* (D); RM 3 represented by *Boana prasina* (E) and *Ambystoma maculatum* (F).

Figure 8. Plant leaf nests of anurans and birds: *Dendropsophus haddadi*, indirect development (A); *Florisuga fusca*, altricial (B); *Eleutherodactylus coqui*, direct development (C); and *Icterus cucullatus*, altricial (D).

Figure 9. Anuran eggs laid on water-filled containers: *Phrynobatrachus guineensis* tadpoles hatched from eggs laid inside the water accumulated in a snail shell (A), and eggs attached to a tree hole where tadpoles will develop (B), eggs of *Ololygon alcatraz* in the water accumulated in a bromeliad (C), *Kalophrynus palmatissimus* tadpoles hatched from eggs laid inside the water accumulated in a bamboo internode (D), adult *Microhyla borneensis* perched on a tropical pitcher plant *Nepenthes ampullaria*, where it lays eggs (E), adult *Adelphobates castaneoticus* perched on a fruit capsule of the Brazil nut *Bertholletia excelsa*, where it lays eggs (F).

FIGURES

Figure 1



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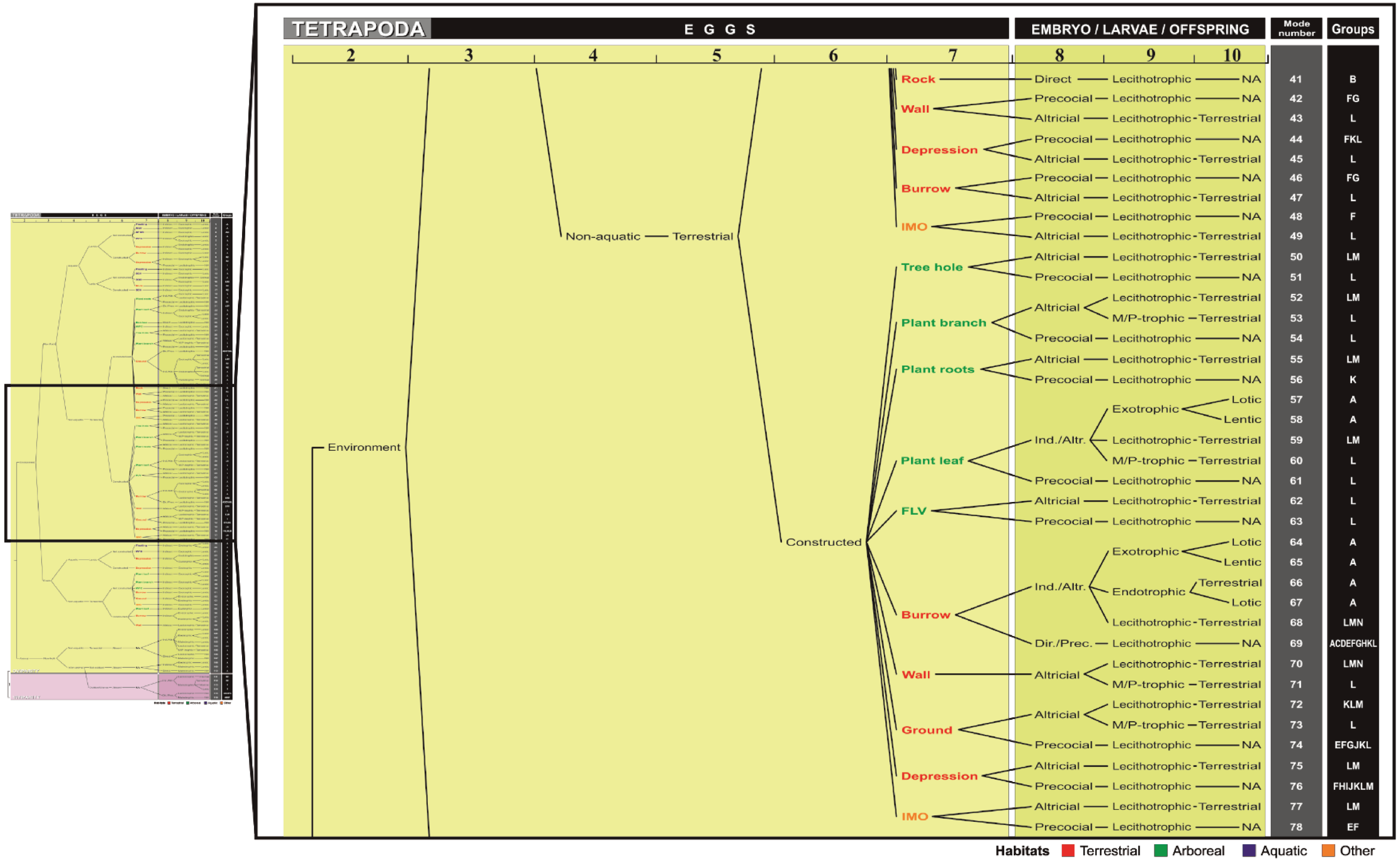

TETRAPODA
E G G S
EMBRYO / LARVAE / OFFSPRING
Mode number
Groups
2 3 4 5 6 7 8 9 10
Environment
Non-aquatic — Terrestrial
Constructed
Rock — Direct — Lecithotrophic — NA 41 B
Wall — Precocial — Lecithotrophic — NA 42 FG
Altricial — Lecithotrophic - Terrestrial 43 L
Depression — Precocial — Lecithotrophic — NA 44 FKL
Altricial — Lecithotrophic - Terrestrial 45 L
Burrow — Precocial — Lecithotrophic — NA 46 FG
Altricial — Lecithotrophic - Terrestrial 47 L
IMO — Precocial — Lecithotrophic — NA 48 F
Altricial — Lecithotrophic - Terrestrial 49 L
Tree hole — Altricial — Lecithotrophic - Terrestrial 50 LM
Precocial — Lecithotrophic — NA 51 L
Plant branch — Altricial — Lecithotrophic - Terrestrial 52 LM
M/P-trophic — Terrestrial 53 L
Precocial — Lecithotrophic — NA 54 L
Plant roots — Altricial — Lecithotrophic - Terrestrial 55 LM
Precocial — Lecithotrophic — NA 56 K
Plant leaf — Ind./Altr. — Exotrophic — Lotic 57 A
Lentic 58 A
Lecithotrophic - Terrestrial 59 LM
M/P-trophic — Terrestrial 60 L
Precocial — Lecithotrophic — NA 61 L
FLV — Altricial — Lecithotrophic - Terrestrial 62 L
Precocial — Lecithotrophic — NA 63 L
Burrow — Ind./Altr. — Exotrophic — Lotic 64 A
Lentic 65 A
Endotrophic — Terrestrial 66 A
Lotic 67 A
Lecithotrophic - Terrestrial 68 LMN
Dir./Prec. — Lecithotrophic — NA 69 ACDEFGHKL
Wall — Altricial — Lecithotrophic - Terrestrial 70 LMN
M/P-trophic — Terrestrial 71 L
Ground — Altricial — Lecithotrophic - Terrestrial 72 KLM
M/P-trophic — Terrestrial 73 L
Precocial — Lecithotrophic — NA 74 EFGJKL
Depression — Altricial — Lecithotrophic - Terrestrial 75 LM
Precocial — Lecithotrophic — NA 76 FHIJKLM
IMO — Altricial — Lecithotrophic - Terrestrial 77 LM
Precocial — Lecithotrophic — NA 78 EF
Habitats Terrestrial Arboreal Aquatic Other

Figure 3

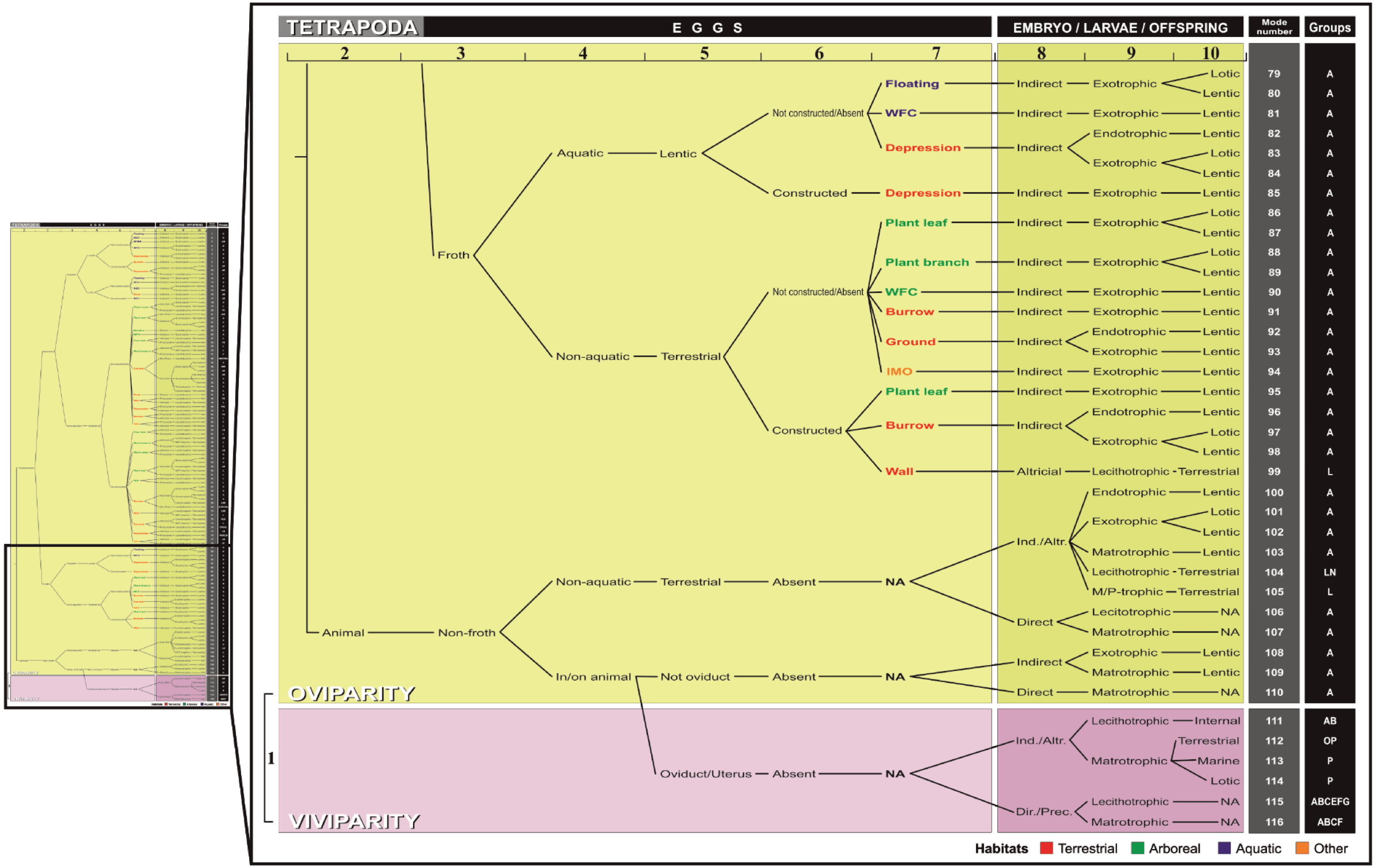
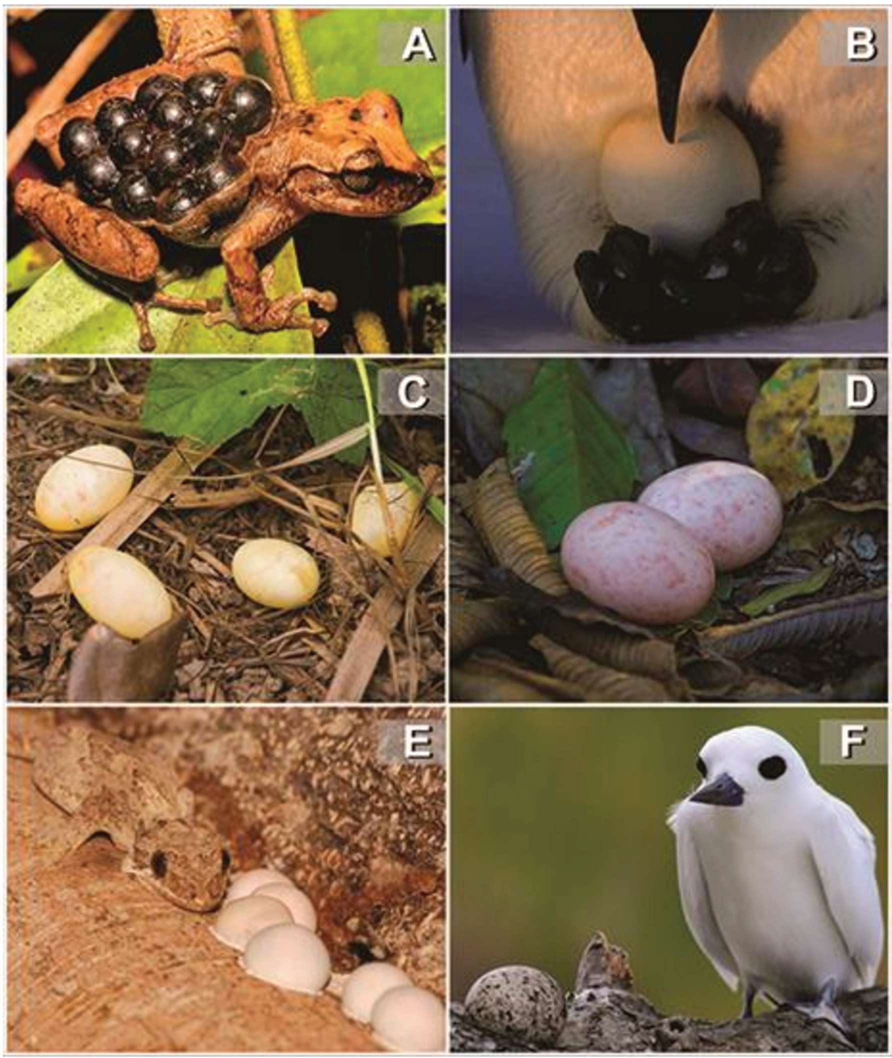

TETRAPODA
E G G S
EMBRYO / LARVAE / OFFSPRING
Mode number
Groups
2 3 4 5 6 7 8 9 10
Aquatic — Lentic
Not constructed/Absent
Floating — Indirect — Exotrophic — Lotic / Lentic — 79 A; 80 A
WFC — Indirect — Exotrophic — Lentic — 81 A
Depression — Indirect — Endotrophic — Lentic — 82 A; Exotrophic — Lotic / Lentic — 83 A; 84 A
Constructed — Depression — Indirect — Exotrophic — Lentic — 85 A
Froth
Non-aquatic — Terrestrial
Plant leaf — Indirect — Exotrophic — Lotic / Lentic — 86 A; 87 A
Plant branch — Indirect — Exotrophic — Lotic / Lentic — 88 A; 89 A
WFC — Indirect — Exotrophic — Lentic — 90 A
Burrow — Indirect — Exotrophic — Lentic — 91 A
Ground — Indirect — Endotrophic — Lentic — 92 A; Exotrophic — Lentic — 93 A
IMO — Indirect — Exotrophic — Lentic — 94 A
Constructed
Plant leaf — Indirect — Exotrophic — Lentic — 95 A
Burrow — Indirect — Endotrophic — Lentic — 96 A; Exotrophic — Lotic / Lentic — 97 A; 98 A
Wall — Altricial — Lecithotrophic - Terrestrial — 99 L
Animal — Non-froth
Non-aquatic — Terrestrial — Absent — NA
Ind./Altr. — Endotrophic — Lentic — 100 A; Exotrophic — Lotic / Lentic — 101 A; 102 A; Matrotrophic — Lentic — 103 A; Lecithotrophic - Terrestrial — 104 LN; M/P-trophic — Terrestrial — 105 L
Direct — Lecitotrophic — NA — 106 A; Matrotrophic — NA — 107 A
In/on animal — Not oviduct — Absent — NA
Indirect — Exotrophic — Lentic — 108 A; Matrotrophic — Lentic — 109 A
Direct — Matrotrophic — NA — 110 A
OVIPARITY
1
Oviduct/Uterus — Absent — NA
Ind./Altr. — Lecithotrophic — Internal — 111 AB; Matrotrophic — Terrestrial — 112 OP; Marine — 113 P; Lotic — 114 P
Dir./Prec. — Lecithotrophic — NA — 115 ABCEFG; Matrotrophic — NA — 116 ABCF
VIVIPARITY
Habitats Terrestrial Arboreal Aquatic Other

Figure 4

Reproductive Modes n = 116	Amphibia	Lepidosauria	Testudines	Archosauria	Synapsida
Amphibia	71	5	1	2	0
Lepidosauria	5.7	16	1	4	0
Testudines	1.3	5.3	3	0	0
Archosauria	1.8	7.5	0	37	3
Synapsida	0	0	0	7	6

Figure 5



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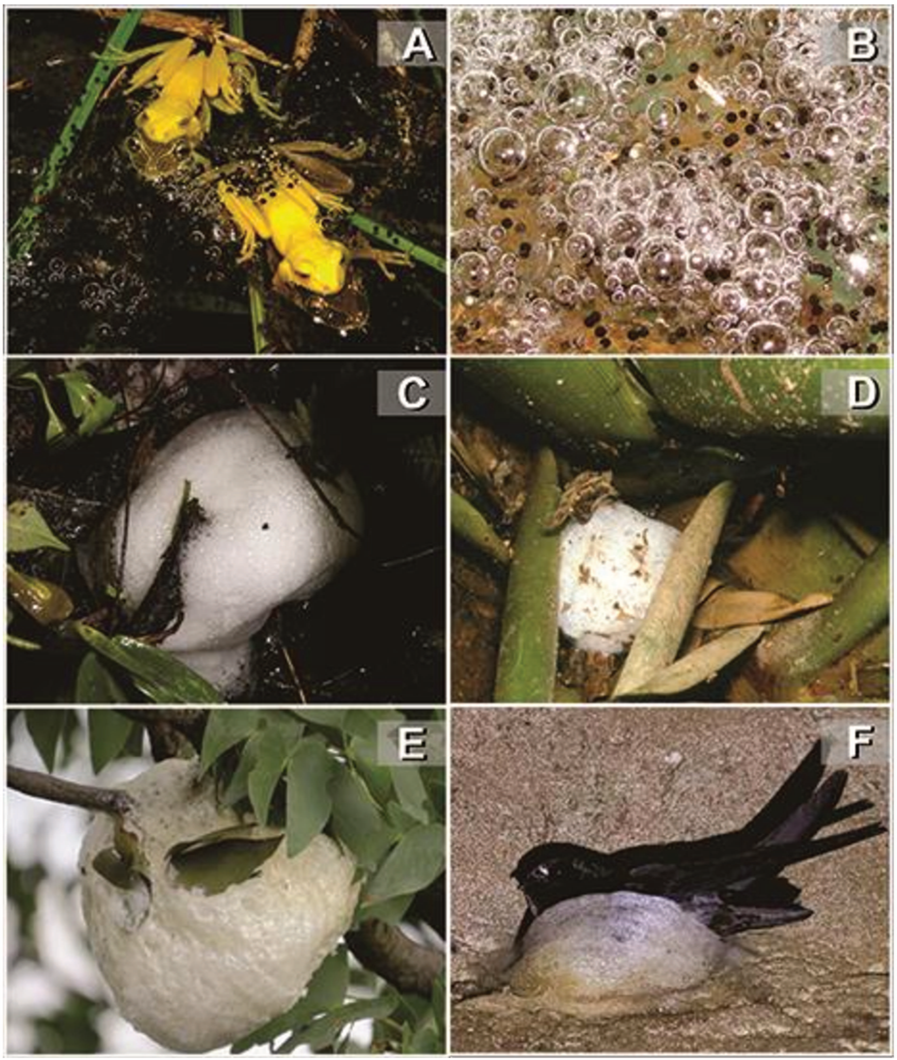

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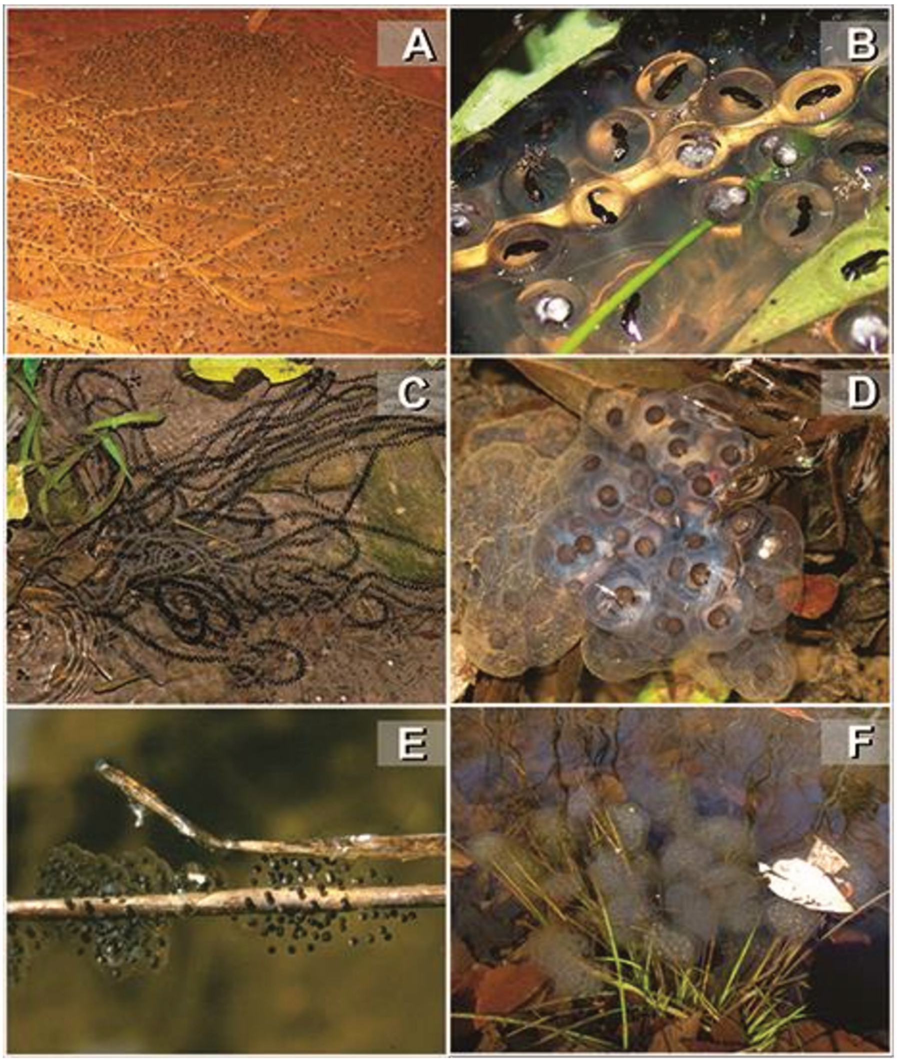

Figure 8

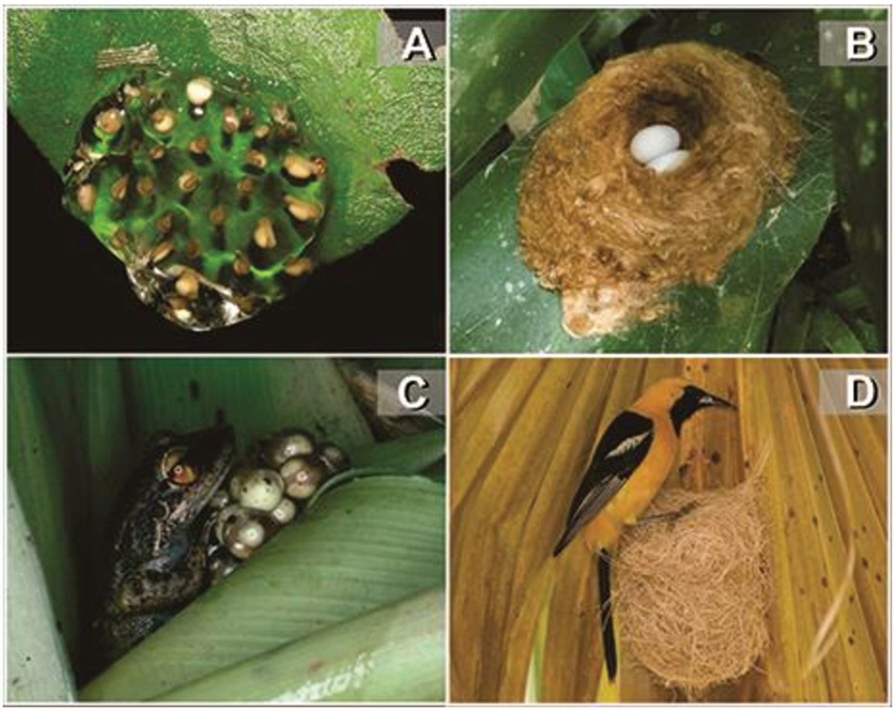

Figure 9

SUPPLEMENTARY MATERIAL

Appendix I. Description of reproductive modes of tetrapods

Appendix II. Definitions and Abbreviations

Figure S1. Reproductive character key for Amphibia with 71 Reproductive Modes (RM) and previous classifications of Haddad & Prado (2005a; b), Duellman & Trueb (1996) and Boulenger (1886). The RM number follows those from Figure 6. Numbers on the top row and lower left indicate the 10 trait categories.

Figure S2. Reproductive character key of Amniota with 51 RMs. The RM number follows those from Figure 6. Numbers on the top row and lower left indicate the 10 traits categories.

Figure S3. Dichotomous reproductive character and state key of Tetrapoda with 116 different reproductive modes. Letters indicate groups: Anura (A), Caudata (B), Gymnophiona (C), Rhynchocephalia (D), Amphisbaenia (E), Lizards (F), Serpentes (G), Cryptodira (H), Pleurodira (I), Crocodylia (J), Aves Paleognathae (K), Aves Neognathae non-Passeriformes (L), Aves Neognathae Passeriformes (M), Monotremata (N), Marsupialia (O), and Placentaria (P). Numbers on a top row and lower left indicate the 10 traits categories. IMO = Insect mound, FLV = Floating vegetation, SGD = Subaquatic ground, SPBR = Subaquatic plant branch/root, SCH = Subaquatic chamber, WFC = Water-filled container.

Table S1. Database for the reproductive modes (RMs) of 6,200 tetrapod species.

Appendix I

Description of reproductive modes of tetrapods

1) Oviparity

1.1) Eggs in environment

Mode 1 – Nest absent, non-froth floating eggs laid in lentic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 2 – Nest absent, non-froth subaquatic eggs laid on bed of lentic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 3 – Nest absent, non-froth subaquatic eggs laid on plants, branches, or roots in lentic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 4 – Non-froth eggs laid in water-filled container nest. Offspring with indirect development, endotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 5 – Non-froth eggs laid in water-filled container nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 6 – Non-froth eggs laid in depression nest. Offspring with indirect development, endotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 7 – Non-froth eggs laid in depression nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 8 – Non-froth eggs laid in constructed burrow nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 9 – Non-froth eggs laid in constructed depression nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 10 – Non-froth eggs laid in constructed depression nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 11 – Non-froth eggs laid in constructed depression nest in lentic water. Offspring with precocial development, lecithotrophic nutrition. Known only for turtles.

Mode 12 – Nest absent, non-froth floating eggs laid in lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 13 – Non-froth eggs laid in subaquatic chamber nest in lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 14 – Nest absent, non-froth subaquatic eggs laid on bed of lotic water. Offspring with indirect development, endotrophic nutrition, and larvae develop in/on parents. Known only for amphibians.

Mode 15 – Nest absent, non-froth subaquatic eggs laid on bed of lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 16 – Non-froth eggs laid on rock nest in lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 17 – Non-froth eggs laid in constructed subaquatic chamber nest in lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 18 – Terrestrial non-froth eggs laid in plant root nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 19 – Terrestrial non-froth eggs laid in plant root nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known only for birds.

Mode 20 – Terrestrial non-froth eggs laid in plant root nest. Offspring with precocial development, lecithotrophic nutrition. Known for lizards and birds.

Mode 21 – Terrestrial non-froth eggs laid on plant leaf nest. Offspring with direct or precocial development, lecithotrophic nutrition. Known for amphibians and lizards.

Mode 22 – Terrestrial non-froth eggs laid on plant leaf nest. Offspring with indirect development, endotrophic nutrition, and larvae with terrestrial development. Known only for amphibians.

Mode 23 – Terrestrial non-froth eggs laid on plant leaf nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 24 – Terrestrial non-froth eggs laid on plant leaf nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 25 – Terrestrial non-froth eggs laid in bamboo nest. Offspring with direct development, lecithotrophic nutrition. Known only for amphibians.

Mode 26 – Terrestrial non-froth eggs laid in water-filled container nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 27 – Terrestrial non-froth eggs laid in tree hole nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known only for birds.

Mode 28 – Terrestrial non-froth eggs laid in tree hole nest. Offspring with precocial development, lecithotrophic nutrition. Known for lizards and snakes.

Mode 29 – Terrestrial non-froth eggs laid on plant branch nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known only for birds.

Mode 30 – Terrestrial non-froth eggs laid on plant branch nest. Offspring with altricial development, matrotrophic or patrotrophic nutrition, and terrestrial development. Known only for birds.

Mode 31 – Terrestrial non-froth eggs laid on plant branch nest. Offspring with precocial development, lecithotrophic nutrition. Known only for lizards.

Mode 32 – Nest absent, terrestrial non-froth eggs laid on ground. Offspring with direct or precocial development, lecithotrophic nutrition. Known for amphibians, lizards, snakes, and birds.

Mode 33 – Nest absent, terrestrial non-froth eggs laid on ground. Offspring with indirect development, exotrophic nutrition, and terrestrial development larvae. Known only for amphibians.

Mode 34 – Nest absent, terrestrial non-froth eggs laid on ground. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 35 – Nest absent, terrestrial non-froth eggs laid on ground. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 36 – Nest absent, terrestrial non-froth eggs laid on ground. Offspring with indirect development, endotrophic nutrition, and terrestrial development larvae. Known only for amphibians.

Mode 37 – Nest absent, terrestrial non-froth eggs laid on ground. Offspring with indirect development, endotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 38 – Nest Absent, terrestrial non-froth eggs laid on ground. Offspring with indirect development, endotrophic nutrition, and larvae develop in/on parents. Known only for amphibians.

Mode 39 – Nest absent, terrestrial non-froth eggs laid on ground. Offspring with indirect development, patrotrophic nutrition, and larvae develop in/on parents. Known only for amphibians.

Mode 40 – Nest absent, terrestrial non-froth eggs laid on ground. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known only for birds.

Mode 41 – Terrestrial non-froth eggs laid on rock nest. Offspring with direct development, lecithotrophic nutrition. Known only for amphibians.

Mode 42 – Terrestrial non-froth eggs laid on wall nest. Offspring with precocial development, lecithotrophic nutrition. Known for lizards and snakes.

Mode 43 – Terrestrial non-froth eggs laid on wall nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known only for birds.

Mode 44 – Terrestrial non-froth eggs laid in depression nest. Offspring with precocial development, lecithotrophic nutrition. Known for lizards and birds.

Mode 45 – Terrestrial non-froth eggs laid in depression nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known only for birds.

Mode 46 – Terrestrial non-froth eggs laid in burrow nest. Offspring with precocial development, lecithotrophic nutrition. Known for lizards and snakes.

Mode 47 – Terrestrial non-froth eggs laid in burrow nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known only for birds.

Mode 48 – Terrestrial non-froth eggs laid in insect mound nest. Offspring with precocial development, lecithotrophic nutrition. Known only for lizards.

Mode 49 – Terrestrial non-froth eggs laid in insect mound nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known only for birds.

Mode 50 – Terrestrial non-froth eggs laid in constructed tree hole nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known only for birds.

Mode 51 – Terrestrial non-froth eggs laid in constructed tree hole nest. Offspring with precocial development, lecithotrophic nutrition. Known only for birds.

Mode 52 – Terrestrial non-froth eggs laid on constructed plant branch nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known only for birds.

Mode 53 – Terrestrial non-froth eggs laid on constructed plant branch nest. Offspring with altricial development, matrotrophic or patrotrophic nutrition. Known only for birds.

Mode 54 – Terrestrial non-froth eggs laid on constructed plant branch nest. Offspring with precocial development, lecithotrophic nutrition. Known only for birds.

Mode 55 – Terrestrial non-froth eggs laid in constructed plant root nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known only for birds.

Mode 56 – Terrestrial non-froth eggs laid in constructed plant root nest. Offspring with precocial development, lecithotrophic nutrition. Known only for birds.

Mode 57 – Terrestrial non-froth eggs laid in constructed plant leaf nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 58 – Terrestrial non-froth eggs laid in constructed plant leaf nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 59 – Terrestrial non-froth eggs laid in constructed plant leaf nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known only for birds.

Mode 60 – Terrestrial non-froth eggs laid in constructed plant leaf nest. Offspring with altricial development, matrotrophic or patrotrophic nutrition, and terrestrial development. Known only for birds.

Mode 61 – Terrestrial non-froth eggs laid in constructed plant leaf nest. Offspring with precocial development, lecithotrophic nutrition. Known only for birds.

Mode 62 – Terrestrial non-froth eggs laid in constructed floating vegetation nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known only for birds.

Mode 63 – Terrestrial non-froth eggs laid in constructed floating vegetation nest. Offspring with precocial development, lecithotrophic nutrition. Known only for birds.

Mode 64 – Terrestrial non-froth eggs laid in constructed burrow nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 65 – Terrestrial non-froth eggs laid in constructed burrow nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 66 – Terrestrial non-froth eggs laid in constructed burrow nest. Offspring with indirect development, endotrophic nutrition, and terrestrial development. Known only for amphibians.

Mode 67 – Terrestrial non-froth eggs laid in constructed burrow nest. Offspring with indirect development, endotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 68 – Terrestrial non-froth eggs laid in constructed burrow nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known for birds and monotremes.

Mode 69 – Terrestrial non-froth eggs laid in constructed burrow nest. Offspring with precocial development, lecithotrophic nutrition. Known for amphibians, amphisbaenids, lizards, snakes, turtles, and birds.

Mode 70 – Terrestrial non-froth eggs laid on constructed wall nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known for birds and monotremes.

Mode 71 – Terrestrial non-froth eggs laid on constructed wall nest. Offspring with altricial development, matrotrophic or patrotrophic nutrition, and terrestrial development. Known only for birds.

Mode 72 – Terrestrial non-froth eggs laid on constructed ground nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known only for birds.

Mode 73 – Terrestrial non-froth eggs laid on constructed ground nest. Offspring with altricial development, matrotrophic or patrotrophic nutrition, and terrestrial development. Known only for birds.

Mode 74 – Terrestrial non-froth eggs laid on constructed ground nest. Offspring with precocial development, lecithotrophic nutrition. Known for amphisbaenids, lizards, snakes, crocodiles, and birds.

Mode 75 – Terrestrial non-froth eggs laid in constructed depression nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known only for birds.

Mode 76 – Terrestrial non-froth eggs laid in constructed depression nest. Offspring with precocial development, lecithotrophic nutrition. Known for lizards, turtles, crocodiles, and birds.

Mode 77 – Terrestrial non-froth eggs laid in constructed insect mound nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known only for birds.

Mode 78 – Terrestrial non-froth eggs laid in constructed insect mound nest. Offspring with precocial development, lecithotrophic nutrition. Known for amphisbaenids and lizards.

Mode 79 – Nest absent, froth floating eggs laid in lentic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 80 – Nest absent, froth floating eggs laid in lentic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 81 – Froth eggs laid in water-filled container nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 82 – Froth eggs laid in depression nest. Offspring with indirect development, endotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 83 – Froth eggs laid in depression nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 84 – Froth eggs laid in depression nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 85 – Froth eggs laid in constructed depression nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 86 – Terrestrial froth eggs laid on plant leaf nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 87 – Terrestrial froth eggs laid on plant leaf nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 88 – Terrestrial froth eggs laid on plant branch nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 89 – Terrestrial froth eggs laid on plant branch nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 90 – Terrestrial froth eggs laid in water-filled container nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 91 – Terrestrial froth eggs laid in burrow nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 92 – Nest absent, terrestrial froth eggs laid on ground. Offspring with indirect development, endotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 93 – Nest absent, terrestrial froth eggs laid on ground. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 94 – Terrestrial froth eggs laid in insect mound nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 95 – Terrestrial froth eggs laid in constructed plant leaf nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 96 – Terrestrial froth eggs laid in constructed burrow nest. Offspring with indirect development, endotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 97 – Terrestrial froth eggs laid in constructed burrow nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 98 – Terrestrial froth eggs laid in constructed burrow nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 99 – Terrestrial froth eggs laid on wall nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known only for birds.

1.2) Eggs kept in/on the animal

Mode 100 – Terrestrial non-froth eggs, absent nest. Offspring with indirect development, endotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 101 – Terrestrial non-froth eggs, absent nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water. Known only for amphibians.

Mode 102 – Terrestrial non-froth eggs, absent nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 103 – Terrestrial non-froth eggs, absent nest. Offspring with indirect development, matrotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 104 – Terrestrial non-froth eggs, absent nest. Offspring with altricial development, lecithotrophic nutrition, and terrestrial development. Known for birds and monotremes.

Mode 105 – Terrestrial non-froth eggs, absent nest. Offspring with altricial development, matrotrophic or patrotrophic nutrition, and terrestrial development. Known only for birds.

Mode 106 – Terrestrial non-froth eggs, absent nest. Offspring with direct development, lecithotrophic nutrition. Known only for amphibians.

Mode 107 – Terrestrial non-froth eggs, absent nest. Offspring with direct development, matrotrophic nutrition. Known only for amphibians.

Mode 108 – Non-froth eggs kept in/on the animal, absent nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 109 – Non-froth eggs kept in/on the animal, absent nest. Offspring with indirect development, matrotrophic nutrition, and larvae develop in lentic water. Known only for amphibians.

Mode 110 – Non-froth eggs kept in/on the animal, absent nest. Offspring with direct development, matrotrophic nutrition. Known only for amphibians.

2) Viviparity

Mode 111 – Non-froth eggs kept in the animal, absent nest. Offspring with indirect development, lecithotrophic nutrition, and internal development. Known only for amphibians.

Mode 112 – Non-froth eggs kept in the animal, absent nest. Offspring with altricial development, matrotrophic nutrition, and terrestrial development. Known only for mammals.

Mode 113 – Non-froth eggs kept in the animal, absent nest. Offspring with altricial development, matrotrophic nutrition, and marine development. Known only for mammals.

Mode 114 – Non-froth eggs kept in the animal, absent nest. Offspring with altricial development, matrotrophic nutrition, and lentic water development. Known only for mammals.

Mode 115 – Non-froth eggs kept in the animal, absent nest. Offspring with direct development, lecithotrophic nutrition. Known for amphibians, amphisbaenid, lizards, snakes.

Mode 116 – Non-froth eggs kept in the animal, absent nest. Offspring with precocial development, matrotrophic nutrition. Known for amphibians and lizards.

Appendix II

Definitions and abbreviations

1) DEFINITIONS

Altricial – Applied to offspring development of birds, except Aves Paleognatha group, and all synapsids (Monotremata, Marsupialia and Placentaria), where the young are borne or hatched with their eyes closed, without the ability of swimming, walking, or flying, and rely on their parents, siblings, or family for feeding. This occurs until the independence of their parents; in the case of synapsids, until weaning.

Animal – This term is related to the macro-habitat where eggs are laid, when eggs are kept in or moved on the body of one of the parents. Besides this, it is applied to offspring development with indirect or altricial development on the body of one of the parents.

Aquatic – Related to eggs that are laid in the water.

Bamboo – Term applied to the microhabitat of the spawning, where eggs are laid inside the internodes of bamboo without water.

Bubble nest – A film or layers of eggs supported by few larger bubbles trapped by the undersurface of the mucus secreted by the female's oviduct, and produced by jumping of female frogs in the middle of the spawning. Alternatively, both anuran parents expel bubbles from the nares under the spawn and the air bubbles become trapped in the mucus.

Burrow – Term applied to the microhabitat where eggs are laid. In this case, eggs are laid in a subterranean burrow, dug or not by parents.

Constructed nest – A structure prepared by some vertebrates, which can be considered as any kind of environmental modification for the function of incubating eggs and raising their offspring.

Depression – Ground depression that can be dug by adult vertebrates. This is also termed basin in previous studies.

Direct development – Applied to offspring development without larval stage, and is observed in amphibians where eggs hatch into juvenile morphs.

Endotrophic – This term is used in offspring nutrition, where the larvae obtain their entire developmental energy from vitellogenic yolk. This category is applied only to indirect developing amphibians.

Environment – Term applied to the microhabitat where eggs are laid. Eggs are laid in the environment, in or outside nests.

Exotrophic – This term is used in offspring nutrition, where the larvae obtain energy by oral consumption of food, when the vitellogenic yolk runs out. We applied this category only to indirect developing amphibians.

Floating – Eggs are laid on the water surface, in froth or non-froth nests.

Floating vegetation (FLV) – Term applied to the microhabitat where eggs are laid. In this case, eggs are laid on floating vegetation in constructed nests.

produced by movement of the legs of the parents on the fluid of eggs jelly layer,

Foam nest – Foam nests are produced by amphibians and birds. In amphibians, eggs are embedded in many small bubbles, produced by limbs motion (beating) of parents on the mucus secreted by the female's oviduct, which is mixed with air. In birds, the pure saliva of some species of the genus *Aerodromus* produces it.

Froth – Related to nest type. There are two types of froth nest: foam and bubble nests (defined above). Froth nests are not considered constructed nests.

Ground – Term applied to the microhabitat where eggs are laid. In this case, eggs are laid on the soil.

In/on animal – Related to eggs laying substrate. In this case, eggs are kept in different parts of the body of the parents. For example, eggs are kept in the uterus of synapsids and in the oviduct of squamates and amphibians. In amphibians, the eggs may also be incubated in the dorsum and legs of adults. In birds, the penguin *Aptenodytes forsteri* incubates its egg on its feet.

Indirect development – Applied to offspring development with larval stage. It is observed in most of the amphibians, where eggs hatch into larvae (tadpoles in anurans).

Insect mound (IMO) – Term applied to microhabitat where eggs are laid. It can be terrestrial or arboreal, made by wasps, termites or ants. Eggs are usually laid in holes dug by birds.

Internal – Applied to offspring development. This is only applied to indirect or altricial viviparous animals. In amphibians eggs hatch inside the parents into tadpoles and complete their development as froglets inside the male's hip pouch, eggs are swallowed and hatch into tadpoles and complete the development as froglets inside the mother's stomach, or eggs are hatched as tadpoles that develop inside the male's vocal sacs. In most marsupials, eggs develop in the uterus and, after hatching the larval development is completed inside a marsupium.

Lecithotrophic – This term is used for offspring nutrition. The embryos obtain energy from the vitellogenic yolk, as amphibians with direct development, turtles, lepidosaurians, birds and monotreme mammals.

Lentic water – This term is used in relationship to eggs surrounding medium. Larvae develop in still/lentic water, such as lakes, ponds or swamps. The term is also related to offspring development, when larvae develop in still/lentic water, such as lakes, ponds or swamps, including fossorial larvae that develop under the sand bed, gravel bed, or mud. Water filled container (below) also may contain lentic water.

Lotic water – This term is used in relationship to eggs surrounding medium. Eggs are laid in flowing waters, such as rivulets, creeks, streams or rivers, as reported for many amphibians. The term is also related to offspring development. Larvae that develop in flowing waters, such as rivulets, streams or rivers, as in amphibians, including larvae that are developed under the sand bed, gravel bed, or mud.

Marine water – Applied to offspring development medium. Offspring can develop in marine water, such as in cetacean mammals.

Marsupium – Marsupium is applied for most marsupials and marsupial frogs (Hemiphractidae), and refers to a body pouch where eggs, tadpoles, froglets or developing offspring and juvenile marsupials are kept.

Matrotrophic – Related to offspring nutrition. Embryos or nestlings obtain energy not only by vitellogenic yolk, but supplemented by nourishment derived from the mother.

This category is applied to direct developing amphibians, all synapsids, and birds that feed their offspring with milk.

Milk – Milk is a lipid rich material produced by secretion of epithelial cells of the esophagus or crop, used by birds to feed their offspring. It can be observed in birds of the families Columbidae and Phoenicopteridae, and in emperor penguins.

Nest – Adapted from Simon and Pacheco (2005), nest is any place selected by the parent (or both parents) for laying its eggs, regardless of how much (if any) digging, cleaning, lining, or building it requires.

Nest absent – When there is no nest used during egg or embryo development stages. Nests (constructed or not) used for parental care of altricial offspring, as observed in many synapsids such as gorillas, coatis, squirrels, and rats, are not considered in this classification.

Non-aquatic – Related to egg laying substrate. Eggs are laid out of the water, as on the ground, rocks, trees, scrubs, or grass.

Non-froth nest – Eggs are laid in non-frothy nests, without the production of foam, bubbles or saliva.

Not constructed nest – A structure used by some vertebrates, not built by them and for the function of incubating eggs and raising their offspring.

Not oviduct – This term is related to eggs surrounding medium. Eggs are embedded in dorsum or dorsal pouches of amphibians. They can also be laid on feet of the parents, as observed in birds, *Aptenodytes forsteri*.

Offspring development – For amphibians the terms direct and indirect development are recognizable discrete categories, referring to the absence or presence of larval stage, respectively. For amniotes, the terms precocial and altricial are extremes of a continuum, referring to offsprings' with different levels of parental dependency. Therefore, we define the boundary between these two categories (precocial and altricial) as the ability of the young to survive without parents or other adult collaboration in locomotion and feeding. We maintained both nomenclatures, but they were treated as equivalent states for Reproductive Modes classification: direct/precocial *vs.* indirect/altricial.

Oviduct/uterus – This term is related to eggs surrounding medium. Eggs develop in a specialized portion of the oviduct, being nourished by yolk, by tissue of the oviduct, or other substances secreted by the parent, as reported for amphibians, squamates and synapsids.

Oviparity – Embryos in the oviduct provided with yolk. After egg laying, the embryonic development continues outside the female body, within complex extraembryonic membranes (egg) that may include gelatinous capsules or hard shells. Known for amphibians, lepidosaurians, archosaurians, and monotremes.

Patrotrophic – This term is used in offspring nutrition. Embryos or nestlings obtain energy not only by vitellogenic yolk, but also through paternal provision of nutrients. We applied this category to amphibians and birds that produce milk.

Plant branch – Term applied to the microhabitat where eggs were laid. In this case, eggs are laid on sticks, branches, or trunks of trees and shrubs.

Plant leaf – Term applied to the microhabitat where eggs were laid. In this case, eggs are laid on or underneath leaves of trees, shrubs, and grass, either rolled (constructed nest) or not.

Plant root – Term applied to the microhabitat where eggs were laid. In this case, eggs are laid on or between tree roots.

Precocial – Applied to offspring development. This term is applied to lepidosaurians and birds. In this case, a young does not depend of its parents. For example, birds of the family Megapodidae present high level of precocity, where the chicks are hatched with feathers on their bodies and already able to fly.

Rock – Term applied to the microhabitat where eggs were laid. In this case, eggs are laid on or underneath rocks.

Subaquatic chamber (SCH) – Term applied to the microhabitat where eggs were laid. In this case, eggs are laid in a chamber inside the water.

Subaquatic ground (SGD) – Term applied to the microhabitat where eggs were laid. In this case, eggs are laid on the bed of lentic or lotic water bodies.

Subaquatic plant branch or root (SPBR) – Term applied to the microhabitat where eggs were laid. In this case, eggs are laid on or attached to subaquatic plant branches or roots.

Terrestrial – This term is related to eggs surrounding medium. Eggs are laid on terrestrial environment, as reported for amphibians, birds, lepidosaurians, and monotremes. It can also be related to offspring development. Offspring develop on terrestrial environment, as in amphibians, birds and all synapsids.

Tree hole – Term applied to the microhabitat where eggs were laid. In this case, eggs are laid in natural or constructed cavities in trees or logs.

Viviparity – Occurs when egg laying is absent (= oviparity). The parent may give birth to larvae, as in the anurans or developed offspring (several vertebrate groups). In this last case, after exhaustion of vitellogenic yolk, embryos feed on oviductal material, as secretions, as in snakes and mammals, or on ovum in the ovary to complete their development, and the offspring are born after the yolk is exhausted and there is no other form of nourishment from the mother, as in some amphibians.

Wall – Term applied to the microhabitat where eggs were laid. In this case, eggs are laid on rocky cliffs, ravines, cave walls, and rock stacks in the sea.

Water-filled container (WFC) – Term applied to the microhabitat where eggs were laid. Amphibians lay eggs in Phytotelmata and fruit capsules on the ground that accumulate water. WFC are also holes in branches, trunks and logs, including bamboo internodes. This state also includes snail shells (Gastropoda) containing water.

2) ABBREVIATIONS

Dir./Prec. – Direct or precocial development

FLV – Floating vegetation

IMO – Insect mound

Ind./Altr. – Indirect or altricial development

M/P-trophic – Matrotrophic or patrotrophic nutrition

SCH – Subaquatic chamber

SGD – Subaquatic ground

SPBR – Subaquatic plant branch or root

WFC – Water-filled container

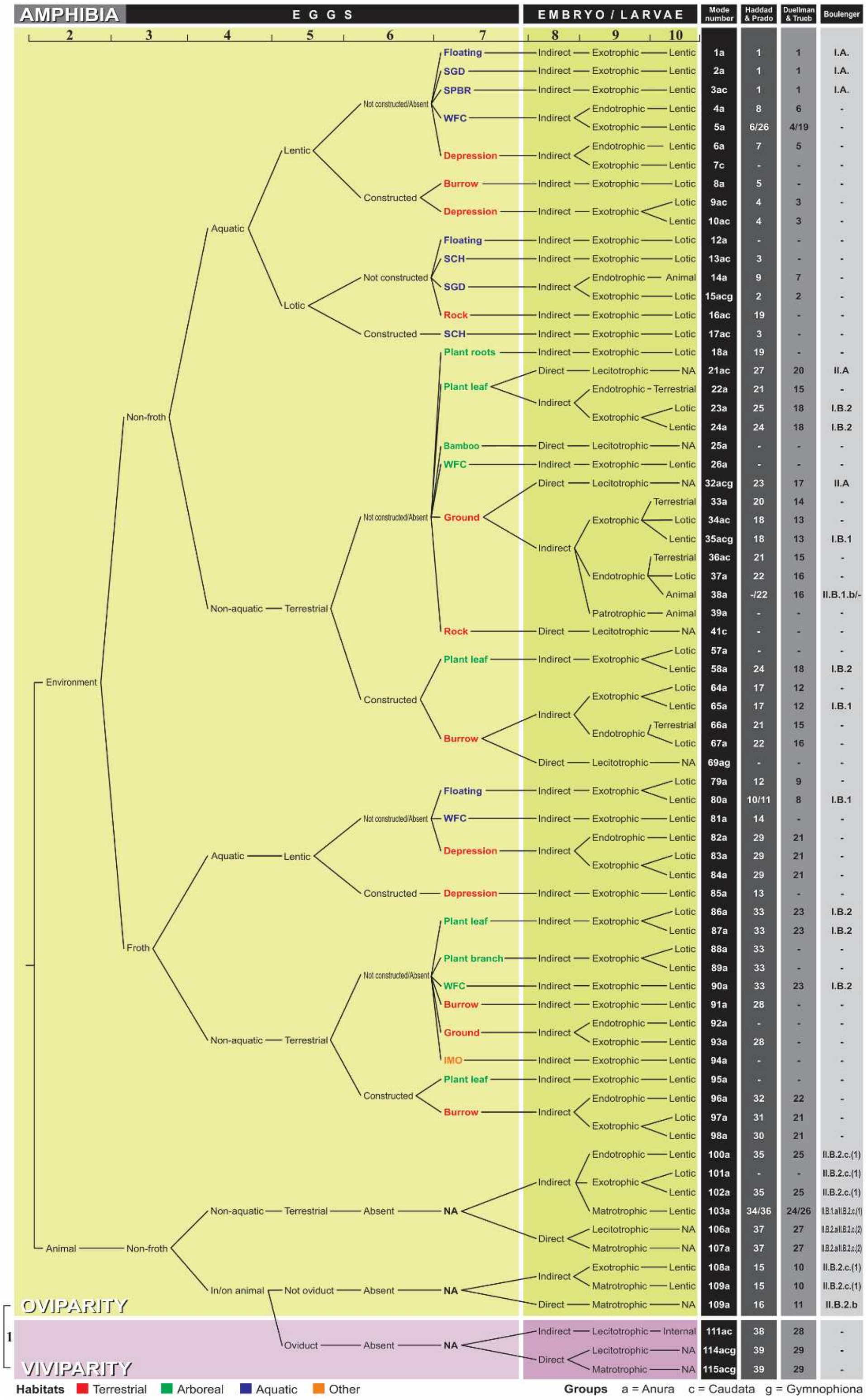

Figure S1. Reproductive character key for Amphibia with 71 Reproductive Modes (RM) and previous classifications of Haddad & Prado (2005a; b), Duellman & Trueb (1996) and Boulenger (1886). The RM number follows those from Figure 6. Numbers on a top row and lower left indicate the 10 traits categories.

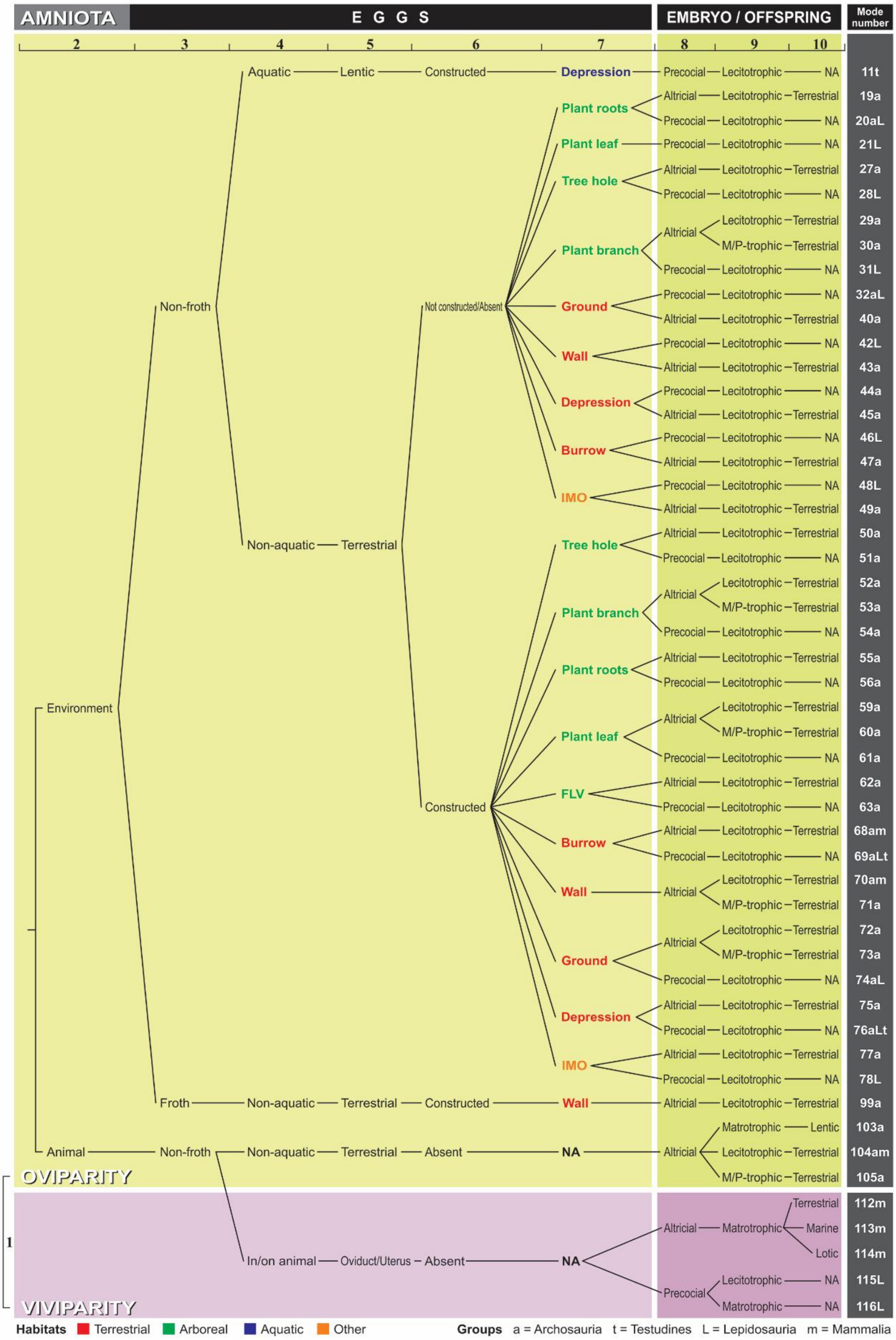

Figure S2. Reproductive character key of Amniota with 51 RMs. The RM number follows those from Figure 6. Numbers on a top row and lower left indicate the 10 traits categories.

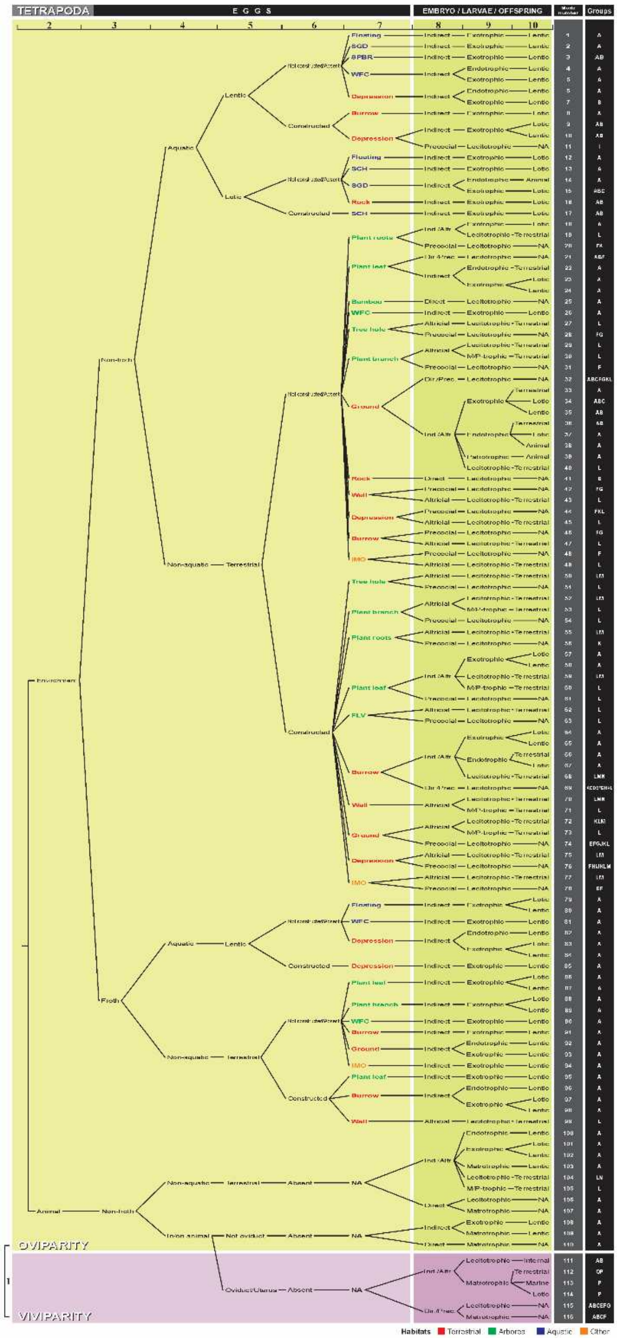

Figure S3. Dichotomous reproductive character and state key of Tetrapoda with 116 different reproductive modes. Letters indicate groups: Anura (A), Caudata (B), Gymnophiona (C), Rhynchocephalia (D), Amphisbaenia (E), Lizards (F), Serpentes (G), Cryptodira (H), Pleurodira (I), Crocodylia (J), Aves Paleognathae (K), Aves Neognathae non-Passeriformes (L), Aves Neognathae Passeriformes (M), Monotremata (N), Marsupialia (O), and Placentaria (P). Numbers on a top row and lower left indicate the 10 traits categories. IMO = Insect mound, FLV = Floating vegetation, SGD = Subaquatic ground, SPBR = Subaquatic plant branch/root, SCH = Subaquatic chamber, WFC = Water-filled container.

Capítulo 2. REPRODUCTIVE MODES OF FISHES: AN OVERVIEW

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ABSTRACT

Fish as a group includes approximately 34,000 living species, more species than all other groups of vertebrates combined. Such diversity should be followed by great variety in breeding strategies. However, although suggested to be quite diverse, their reproductive modes (RMs) were never reviewed. Therefore, after a comprehensive review we classified the RMs of fishes based on a recent classification method applied for tetrapods. Based on a sample of over 4,000 fish species, including Agnatha, Chondrichthyes and Osteichthyes, we identified 52 different RMs. Agnatha had three RMs, Chondrichthyes six RMs, and Osteichthyes 52 RMs, including 43 exclusive RMs. The commonest RM (RM 1) was marine pelagic spawn, found in at least 1,660 fish species. Freshwater fishes had 53 % more RMs than marine fishes. In comparison to other vertebrate groups, the number of RMs presented by fishes agrees with the number of examined species. On the other hand, we found that Amphibia (especially Anura), is an outlier, as we found more RMs than it would be expected by the regression analysis. We found 156 RMs for Craniata, of which only nine RMs were shared between fishes and tetrapods. This new classification may serve as a basis for expanding the knowledge of fish breeding biology and could be used for future comparative ecological and evolutionary studies.

Key words: Agnatha, Breeding Behavior, Chondrichthyes, Natural History, Osteichthyes, Reproductive Strategies.

INTRODUCTION

Fishes represent a phenetic and paraphyletic group that includes more than a half of the extant vertebrate species richness, with approximately 34,000 described species (Froese & Pauly 2017). This group can be divided into three subgroups: jawless (Agnatha: hagfishes and lampreys – paraphyletic), cartilaginous (Chondrichthyes: chimaeras, rays and sharks – monophyletic), and bony fishes (Osteichthyes – paraphyletic) (Helfman *et al.* 2009; Nelson *et al.* 2016). Fishes dwell in all types of aquatic environments, including oceans, estuaries, lakes, rivers, streams and temporary ponds. They thrive in oceanic waters with subzero temperatures in both north and south poles, and in the tropics or deserts with temperatures higher than 50 ºC. Fishes may live from abyssal depths to highland lakes (Wootton & Smith 2015; Pough *et al.* 2016) and, thus, they are the most worldwide-distributed vertebrate group.

The great habitat variety occupied by fishes may be a result of the huge species richness of the group. This high diversity can be explained by numerous events of adaptive radiations, which promoted astonishing morphological variations that allowed fishes to explore a multitude of niches (Skúlason & Smith 1995). The best-publicized case of adaptive radiation is found among Cichlidae, which had a recent explosive speciation in Africa, where hundreds of species coexist in the Great Lakes of African East (Takahashi & Koblmüller 2011; Brawand *et al.* 2014). The evolution of these species was shaped by isolation when the lakes dried up, resulting in an evolutionary parallelism (Skúlason & Smith 1995; Turner *et al.* 2001; Brawand *et al.* 2014). Besides this, ecological factors also contributed to their diversification, such as predation risk, seasonal temperature variation, food availability, ecological opportunity, and strong sexual selection (Balon 1975; Snorrason & Skúlason 2004; Wagner *et al.* 2012).

All these events linked to speciation probably lead to diverse reproductive strategies. Laying pelagic eggs (e.g., the tuna *Thunnus maccoyii*, and the scad *Trachurus murphyi*: Hauser & Ward 1998; Miller & Kendall 2009) probably is the commonest reproductive mode (RM *sensu* C. H. L. Nunes-de-Almeida, C. F. B. Haddad and L. F. Toledo, in prep.; or reproductive guild, as in Balon 1975). However, fishes may build very elaborate nests on a lake bottom (e.g., the tilapia *Oreochromis macrochir*: Helfman *et al.* 2009), produce bubble nests (e.g., the electric eel *Electrophorus electricus*, the armored catfish *Hoplosternum littorale*, the swamp eel *Monopterus albus*: Andrade & Abe 1997; Assunção & Schwassmann 1995; Chivers 1999). There are fishes that spawn in terrestrial environments, such as the splash tetra *Copella arnoldi* that lays eggs on plant leafs out of water (Martin *et al.* 2004), and gobies that dig a burrow in the sand of the sea shore and spawn inside dry chambers (Martin *et al.* 2004; Wootton & Smith 2015). Alternatively, there are several viviparous species (e.g., the seaperch *Embiotoca lateralis*, the wobbegong shark *Orectolobus wardi*, the guppy *Poecilia wingei*, and the facultative egg-laying and live-bearing killifish *Tomeurus gracilis*: Dulvy & Reynolds 1997; Poeser *et al.* 2005; Benedito 2015; Wootton & Smith 2015).

The reproductive diversity of fishes is so outstanding that some authors have even suggested that this group presents more RMs than any other vertebrate group (e.g., Helfman *et al.* 2009; Wootton & Smith 2015). Still, it is difficult to make such statement without a standardized system of RMs classification, applied to all groups. Providentially, a straightforward method was recently proposed in a study of tetrapods (C. H. L. Nunes-de-Almeida, C. F. B. Haddad and L. F. Toledo, in prep.). In this review, the concept of RMs is redefined, which is a combination of 10 traits: reproduction type, egg laying macro-habitat, secretion use, egg laying substrate, medium surrounding eggs, nest construction, egg laying microhabitat, offspring development, offspring nutrition, and place of offspring development. Thus, we hereby use the same classification method for fishes, which would enable comparisons among all vertebrate groups.

METHODS

Set of Characters of reproductive modes

After a literature review on fish reproductive biology, and based on the tetrapod RM classification system (C. H. L. Nunes-de-Almeida, C. F. B. Haddad and L. F. Toledo, in prep.), we selected the same 10 traits used for tetrapods, their categories and subcategories, following a hierarchical order from egg, to embryo/larva, to offspring. These traits are mostly physical (as egg deposition site) and we did not consider some behavioral aspects such as migration, courtship, copulation, and parental care. The different traits and their states are presented below, and we illustrate them with some representative examples.

(1) Reproduction type

c. Oviparity – Ovules with yolk in ovaries or oviducts. After spawning fertilization, embryonic development continues outside of the female body, within complex extraembryonic membranes (eggs) that may include gelatinous capsules or coriaceous shells (e.g., the killifish *Kryptolebias marmoratus*, the skate *Leucoraja erinacea*, and the lamprey *Petromyzon marinus*: Bristow 1992; Callard *et al.* 1995; Furness 2016) (Figure 1).

d. Viviparity – This occurs when egg laying (as in oviparity) is absent. Offspring develop within the ovaries or oviducts. After exhaustion of vitellogenic yolk, embryos feed on oviductal material (secretions, fragments of the oviduct) or on ova in the ovary to complete their development (e.g., the shark *Carcharodon carcharias*, the gambusia *Gambusia geiseri*, the rockfish *Sebastes ovalis*, the electric ray *Torpedo panthera*, and the eelpout *Zoarces viviparus*: Dulvy & Reinolds 1997; Marsh-Matthews *et al.* 2001; Miller & Kendall 2009; Wootton & Smith 2015). The term ovoviviparity is here included in the viviparity category, as suggested by Blackburn (1992), because the terms lecithotrophy and matrotrophy, used in conjunction with the reproduction mode viviparity, hampers the use of the term ovoviviparity (Figure 2E, F).

(2) Egg laying macrohabitat

a. Environment – Eggs are laid in the milieu, in or out of nests, as in cartilaginous species (e.g., the dogshark *Galeus melastomos* and the chimaera *Harriotta raleighana*: Dulvy & Reinolds 1997; Finucci *et al.* 2017), and bony fishes (e.g., the bass *Micropterus dolomieu*, and the mudskipper *Periophthalmus modestus*: Martin *et al.* 2004; Wootton & Smith 2015).
b. Animal – Eggs in or on the body of one of the parents, (e.g., the sharks *Mustelus lenticulatus* and *Nebrius ferrugineus*: Compagno 1984; Boomer *et al.* 2013) and bony fishes (e.g., the guppy *Poecilia wingei*, the catfish *Genidens barbus*, and the nurseryfish *Kurtus gulliveri*: Breder Jr. & Rosen 1966; Poeser *et al.* 2005; Helfman *et al.* 2009) (Figure 2).

(3) Nest type

a. Froth – Spawn in frothy nest with bubbles expelled from mouth to water surface, parents carry eggs to bubbles (e.g., the fighting fish *Betta splendens*, the electric eel *Electrophorus electricus*, the armored catfish *Hoplosternum littorale*, and the gourami *Trichogaster labiosa*: Braddock & Braddock 1959; Assunção & Schwassmann 1995; Axelrod *et al.* 1996; Carvalho *et al.* 2009). Froth nest is not considered a constructed nest (see below) (Figure 3E; 4D).
b. Non-froth – Spawn in non-frothy nests, without the production of bubbles.

(4) Egg laying substrate

a. Aquatic – Eggs surrounded by water, represented by the vast majority of fishes (e.g., the perch *Archoplites interruptus* and the catshark *Scyliorhinus haeckeli*: Matheus 1965; Mabraganã *et al.* 2011).

b. Non-aquatic – Eggs are laid on plant leaves or burrows (e.g., the splash tetra *Copella arnoldi* and the mudskipper *Scartelaos tenuis*: Martin *et al.* 2004; Wootton & Smith 2015).

c. In/on animal – Eggs are incubated in different parts of the body of the parents, such as mouth, belly, throat, head, and ventral and dorsal pouch (Oppenheimer 1970; Wootton & Smith 2015), or in different parts of the zoogenic substrate, such as anemones, ascidians, coral, crabs, fishes, molluscans, tunicates, and sponges (Balon 1975, 1981; Helfman *et al.* 2009) (e.g., the snailfish *Careproctus zispi*, the arawana *Osteoglossum bicirrhosum*, the guppy *Poecilia reticulata*: Oppenheimer 1970; Szpilman 1992; Helfman *et al.* 2009; Benedito 2015) (Figure 2).

(5) Eggs surrounding medium

a. Lentic – Eggs are laid in still water, such as lakes, ponds or swamps (e.g., the chromide *Etroplus maculatus*, the giant cichlid *Boulengerochromis microlepis*: Konings 1988; Oppenheimer 1970).

b. Lotic – Spawn occurs in flowing waters, such as rivulets, creeks, streams or rivers (e.g., the stoneroller *Campostoma anomalum*, the minnow *Pimephales promelas*, the freshwater ray *Potamotrygon constellata*: Miller 1962; McMillan & Smith 1974; Thorson *et al.* 1983).

c. Marine – Spawn occurs in the marine environment (e.g., the machete *Elops affinis*, the ratfish *Hydrolagus colliei*: Breder Jr. & Rosen 1966; Whitehead and Rodriguez-Sanchez 1995; Conrath & Musick 2012).

d. Terrestrial – Eggs are laid on terrestrial environments, such as on terrestrial plants, logs or rocks (e.g., the characin *Brycon petrosus*, the splash tetra *Copella arnoldi*, the mudskipper *Scartelaos gigas*: Kramer 1978; Martin *et al.* 2004; Wootton & Smith 2015) (Figure 1F).

e. Not oviduct – Eggs are embedded in different parts of the body of the parents, such as mouth, belly, throat, head, and ventral and dorsal pouch (e.g., the seahorse *Hippocampus kuda*, the nurseryfish *Kurtus gulliveri*: Lin *et al.* 2006; Helfman *et al.* 2009; Wootton & Smith 2015). This trait includes mouth brooding fishes (e.g., the bullseye *Apogonichthyoides nigripinnis*, the armored catfish *Loricariichthys chanjoo*, the jawfish *Opistognathus aurifrons*: Leong 1967; Carvalho *et al.* 2009; Otero *et al.* 2013).

f. Oviduct – Eggs are developed in a specialized portion of the oviduct, including species whose embryos depend solely on yolk reserves (e.g., the buntingi *Adrianichthys poptae*, the sawfish *Pristis pristis*: Balon 1981; Dulvy & Reynolds 1997), those with oophagous embryos (e.g., the shark *Lamna nasus*, the killifish *Tomeurus gracilis*: Compagno 2001; Benedito 2015), and those with embryos that depend on nourishment through placental analogues (e.g., the top minnow *Belonesox belizanus*, the shark *Carcharhinus porosus*, the killifish *Heterandria formosa*, the ray *Urolophus aurantiacus*: Michael 1993; Dulvy & Reynolds 1997; Wootton & Smith 2015) (Carrier *et al.* 2004).

g. Zoogenic substrate – Spawn occurs in different parts of the body in other species of aquatic animals (see 4.c.) (e.g., the snailfish *Careproctus abbreviatus*, the blenny *Paraclinus marmoratus*: Balon 1975, 1981; Helfman *et al.* 2009) (Figure 2C, D).

(6) Nest construction

As defined by Simon and Pacheco (2005), nest is any place selected by a bird for laying its eggs, regardless of how much digging, cleaning, lining, or building it performs. We extend this definition to all groups of vertebrates (C. H. L. Nunes-de-Almeida, C. F. B. Haddad and L. F. Toledo, in prep.).

a. Constructed – Defined as all sorts of environmental modification (Figure 4).

b. Not constructed – Nest used by a fish, which did not build it (e.g., murenids that nest in rocky cavities not dug by them) (Figure 1B to F).

c. Absent – Pelagic spawning (Figure 1A).

(7) Egg laying microhabitat

a. Pelagic – Eggs are laid in the water column (e.g., the sablefish *Anoplopoma fimbria*, the crocodile toothfish *Champsodon snyderi*, the gizzard shad *Konosirus punctatus*: Kimura *et al.* 1999; Shao *et al.* 2002; Muñoz 2010) (Figure 1A).

b. Subaquatic chamber (SCH) – Eggs are laid in a chamber (e.g., the midshipman *Porichthys notatus*, the prickleback *Xiphister mucosus*: Martin *et al.* 2004; Martin 2014).

c. Sand beach – Eggs are laid on the seashore (e.g., the stickleback *Gasterosteus aculeatus*, the goby *Lythrypnus zebra*: Lombardi 1998; Martin *et al.* 2004) or in natural banks of flowing water (e.g., the characin *Brycon petrosus*: Martin *et al.* 2004) (Figure 3D).

d. Floating – Eggs are laid in a free-floating froth nest on the surface of water bodies (e.g., the African pikes *Hepsetus cuvieri*, *Hepsetus odoe*: Baensch & Riehl 1985).

e. Depression – Eggs are laid in a sandy or muddy depression, dug or not, covered or not (e.g., the damselfish *Pomacentrus nagasakiensis* and the tilapia *Sarotherodon melanotheron*: Mertz & Barlow 1966; Moyer 1975) (Figure 4A).

f. Ground – Eggs are laid on the sea bottom or flowing waterbed with muddy or sandy substrates, or pebbly bottoms (attached on bottom structures) (e.g., the lamprey *Geotria australis*, the prochilod *Prochilodus lineatus*, the damselfish *Stegastes lividus*: Monette & Renaud 2005; Helfman *et al.* 2009; Benedito 2015).

g. Burrow – Eggs are laid in a subterranean burrow dug or not by parents (e.g., the mudskippers *Periophthalmus modestus*, *Scartelaos gigas*: Martin *et al.* 2004) (Figure 3C; 4F).

h. Mound – Eggs are laid on constructed mounds (e.g., the minnow *Exoglossum maxillingua*, the chub *Nocomis biguttatus*, the tilapia *Oreochromis macrochir*: Helfman *et al.* 2009) (Figure 4B, C).

i. Rock – Eggs are laid on or underneath rocks, crevices, cave walls, which may be in the sea, lentic or lotic water bodies (e.g., the blind tetra *Astyanax jordani*, the herring *Clupea pallasii*, the horn shark *Heterodontus francisci*: Compagno 2001; Miller & Kendall 2009; Wootton & Smith 2015).

j. Floating vegetation (FLV) – Eggs are laid in constructed nests or froth nests in floating vegetation (e.g., the aba *Gymnarchus niloticus*, the bonytongue *Heterotis niloticus*, the armored catfish *Hoplosternum littorale*: Andrade & Abe 1997; Lombardi 1998; Petr 2000).

k. Plant leaf – Eggs are laid on algal beds, aquatic plants, branches of terrestrial plants, or logs in the water (e.g., the chimaera *Callorhinchus callorynchus*, the snakehead *Channa punctata*, the inanga *Galaxias maculatus*: Conrath & Musick 2012; Martin 2014; Wootton & Smith 2015) (Figure 1E; F).

l. Plant root – Eggs are laid in or on plant roots (e.g., the perch *Archoplites interruptus*, the blenny *Lupinoblennius paivai*: Mathews 1965; Sazima & Carvalho-Filho 2003) (Figure 3F).

(8) Offspring development

a. Indirect – This describes development with a larval stage (including fry) (Balon 1999).

b. Direct – This describes development without a larval stage. Recorded for most cartilaginous fishes (Balon 1999).

(9) Offspring nutrition

a. Endotrophic – This is the condition where larvae obtain their entire developmental energy from vitellogenic yolk (Balon 1999) (e.g., the acara *Aequidens vittatus*, the lionfish *Dendrochirus brachypterus*: Riehl & Patzner 1998; Helfman *et al.* 2009).

b. Exotrophic – The condition where the larvae obtain energy by oral consumption of food, when the vitellogenic yolk runs out (Balon 1999) (e.g., the shark *Galeocerdo cuvier*, the killifishes *Leptolebias aureoguttatus*, *Nothobranchius torgashevi*: Szpilman 1992; Bini 2012; Dorn *et al.* 2014).

c. Matrotrophic – Embryos that obtain energy not only by vitellogenic yolk, but supplemented by nourishment derived from the mother (Pough *et al.* 2016) (e.g., the discus *Symphysodon discus*, the freshwater ray *Potamotrygon motoro*: Oppenheimer 1970; Thorson *et al.* 1983).

(10) Place of offspring development

a. Lentic – Larvae or embryos are developed in still water, such as lakes, ponds or swamps (e.g., the snakehead *Channa striata*, the mbuna *Maylandia zebra*, the smelt *Osmerus eperlanus*: Alikunhi 1953; Dando 1984; Kornfield & Smith 2000).

b. Lotic – Larvae or embryos are developed in flowing waters, such as rivulets, streams or rivers (e.g., the bullhead *Cottus gobio*, the carp *Ctenopharyngodon idella*, the minnow *Cyprinodon variegatus*: Mertz & Barlow 1966; Mills 1991; Wootton & Smith 2015).

c. Marine – Larvae or embryos are developed in marine environment (e.g., the hake *Merluccius albidus*, the electric ray *Narcine brasiliensis*, the tuna *Thunnus orientalis*: Breder & Springer 1940; Pauly & Pullin 1988; Miller & Kendall 2009).

PROPOSED ANALYSES SYSTEM

We collect information for 4,037 fish species (Table S1). All these species had their RMs classified in accordance with the proposed system, and then we compared fishes with other tetrapod clades: Amphibia, Squamata, Testudines, Archosauria, and Mammalia. To test the existence of the relationship between RMs and number of analyzed species, a linear regression was performed using Statistica 7.1 (Stasoft 2005) and we considered the regression significant if $P < 0.05$.

We used the software Past 3.15 to run a similarity test with all Craniata groups. We used classical clustering, using paired group algorithm (UPGMA), with Euclidean distance and boot n = 1,000 (Hammer *et al.* 2001).

RESULTS

Based on our sample we identified 52 different RMs for fishes (Figure 5; Table S1). Out of the 4,037 fish species, 16 species were Agnatha, 185 Chondrichthyes, and 3,836 Osteichthyes; 39 % of the families of all groups were represented. Agnatha had three RMs, Chondrichthyes had six RMs, and Osteichthyes had 52 RMs, of which nine were non-exclusive and 43 were exclusive to this latter group. The commonest RM (RM 1), occurred in 41 % (1,662 species) of the analyzed species and 41 % (136 families) of analyzed families (Table S1). Seven RMs were rare in our analysis, so far recorded for a single teleost species each: RMs 11, 17, 20, 34, 36, 41, and 47 (Figure 6). Almost 97 % of the species had only one RM (Table S1). On the other hand, the characin *Brycon petrosus* was the species that showed more RMs, with five different RMs: it can lay eggs out of water in humid places on river banks (RM 20), on rocks on river margins (RM 25), in the water it lays eggs on the ground and plant leaves (RMs 22 and 27), or lays pelagic eggs (RM 29) (Balon 1990; Martin *et al.* 2004).

Even if marine fishes were represented by more species in our analysis (62 % of the studied species), freshwater fishes had more RMs (73 % of RMs more than marine species). Most teleosts (2,301 spp.; 60 % of teleosts) are marine that lay numerous small pelagic eggs. Freshwater teleosts (1,548; 40 % of teleosts), on the other hand, mostly lay large non-planktonic eggs (Pough *et al.* 2016). The majority of freshwater fishes (1,313 spp.; 85 % of freshwater species) spawn in lotic waters. In this environment, a great number of species lay eggs on the bottom, in depressions, in subaquatic chambers, on plant leaves, on rocks (214 spp.; 16 % of freshwater fishes) (Figure 7). Among marine fishes, RM 1 was the commonest mode, in which eggs are fertilized externally, have a high fertility rate, and there is no parental care involved (Angelini & Ghiara 1984).

Out of the 52 RMs found for fishes, freshwater fishes had a total of 38 RMs. The RM 22 occurs in the majority (523 out of 1,552 species; 34 %) of the analyzed freshwater fishes. Marine fishes exhibited 18 RMs, with RM 1 displayed by most species (1,662 out of 2,485 species; 67 %). A few species spawn both in marine, brackish, and freshwater environments, as exemplified by the glass perchlet *Ambassis interrupta* (Coates 1990). Among freshwater fishes, 85 % of the species (1,317 spp.) spawns in lotic water, with 21 RMs, and 15 % of the species (235 spp.) spawns in lentic water, with 13 RMs (Figure 7).

Ten RMs are shared among fishes and tetrapods: RMs 13, 17, 22, 23, 25, 29, 33, 36, 40, and 52 (Figure 5). We found a positive relationship between RMs richness and the number of analyzed species. Thus, we performed a regression analysis, including fishes and all other groups of vertebrates. Most were within the 95% confidence interval, except for amphibians that did not present MRs more than predicted by the number of species analyzed (Figure 8).

Combining this study and the previous Tetrapoda RMs classification (Nunes-de-Almeida, Haddad and Toledo, in prep.), we were able to list 158 RMs for Craniata as follows. Agnatha had 3 RMs, Chondrichthyes 6, Osteichthyes 52, Anura 69, Caudata 16, Gymnophiona 6, Rhynchocephalia 1, Squamata 16, Cryptodira 2, Pleurodira 2, Crocodilia 2, Aves Paleognatha 8, Aves Neognatha Non-Passeriformes 35, Aves Neognatha Passeriformes 10, Monotremata 3, Marsupialia 1, and Eutheria 3 reproductive modes. About the maximum number of Craniata groups per a particular RMs, RM 32 was recorded in Anura, Caudata, Gymnophiona, Squamata, Aves Paleognatha, and Aves Neognatha Non-Passeriformes, whereas RM 116 was found in Chondrichthyes, Osteichthyes, Anura, Caudata, Gymnophiona, and Squamata (Table S2). In fishes and amphibians, 9 % of RMs are similar (Table S2). The similarity test using Euclidean algorithm was based on a matrix with 158 RMs and 17 Craniata groups. This test distributed the groups by number of RMs per group (Figure S1).

DISCUSSION

According to our data, the number of analyzed freshwater fish species is 1,552 (38 %) and it is considerably smaller than that of marine fish species, 2,485 (62 %). On the other hand, the oceans covering about 70 % of the Earth surface, while freshwater is nearly 1 % of the planet surface (Helfman *et al.* 2009, Pough *et al.* 2016, Nelson *et al.* 2016). These numbers notwithstanding, we found a higher number of RMs among freshwater fish species, than the number of RMs of marine fish species. An explanation may be the higher complexity of freshwater environments, including small to large lentic and lotic waterbodies, e.g., the huge Amazon and the Nile rivers, subterranean lakes in caves, besides a variety of wetlands, temporary water puddles and streams (Helfman *et al.* 2009, Pough *et al.* 2016, Nelson *et al.* 2016). Such variety may provide different opportunities to diversify fish RMs.

Bony fish (Osteichthyes) alone are the group with the greatest number of species among the Craniata (Helfman *et al.* 2009; Pough *et al.* 2016; Nelson *et al.* 2016). The aforementioned fish group presents an outstanding reproductive variation, including sex determination by the environment, flexible gender system with hermaphroditism, temporary dimorphism, diverse fertilization modes, promiscuity and polygamy, and great variation of parental care (Wootton & Smith 2015). Based on such variation, Wootton and Smith (2015) and Helfman *et al.* (2009) stated that fishes are the group with the highest diversity of RMs among vertebrates. However, according to our analysis, amphibians, especially driven by anurans, present more RMs than fishes. Amphibians are unique among Craniata in the sense that they thrive between aquatic and terrestrial environment, allowing them to explore even more egg laying or embryo development sites (Wells 2007). Besides sharing some RMs with fishes, as they may have aquatic eggs (Wells 2007; Pough *et al.* 2016), amphibians present non-aquatic eggs and direct developing species, sharing other modes with Amniota.

Similary to some groups of fish with larval stages (e.g., lampreys, eels, flatfishes, some gobies: Dufour *et al.* 2012), most amphibian eggs are laid in the water and hatch into gill-breathing aquatic larvae. The larvae undergo metamorphosis and reach terrestrial life, and as adults they return to the water to lay their eggs (Hickman *et al.* 2016). Viviparity originated more than 160 times among vertebrates, including bony and cartilaginous fishes, amphibians, mammals, and reptiles (Blackburn 1999). However, in fishes and amphibians, the similarity among RMs could be explained by the presence of aquatic eggs, however, anamniotic eggs are not suitable for terrestrial environments (Pough *et al.* 2016; Hickman *et al.* 2016).

Some of the less usual RMs are quite similar to common RMs, as exemplified by the splashing tetra *Copella arnoldi* spawns on plant leaves out of the water (RM 36), whereas many other fish species lay eggs on plant leaves in the water (RM 27). This may lead to the conjecture that RM 36 derived from RM 27. Other example would be the characin *Brycon petrosus* that spawns on sand banks out of water (RM 20), a mode that could be derived from spawning in riverbeds (RM 22). Laying eggs out of the water is probably an adaptation that reduces predation risk and a sexual selection (Helfman *et al.* 2009; Pough *et al.* 2016; Zamudio *et al.* 2016).

The classification method shown here is straightforward, using only 10 characteristics, mostly obtained easily. Thus, this method may stimulate further research on the highly diverse breeding biology of fishes. As this method was applied to tetrapods (C. H. L. Nunes-de-Almeida, C. F. B. Haddad and L. F. Toledo, in prep.) it allows some initial comparisons. We hope that the database hereby will be useful for future studies of vertebrate natural history, ecology and evolution.

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TABLE

Table 1 Summary of fish reproductive modes (RMs). Total number of described species obtained from FishBase (Froese & Pauly 2018).

Taxon / group	Number of known species	Percentage of represented species	Percentage of represented families	Number of species with RM information	Number of RMs	Maximum number of RMs for one species	Maximum number of exclusive RMs
Fish	**33,970**	**12%**	**39%**	**4,037**	**52**	**5**	**43**
Agnatha	**129**	**12%**	**100%**	**16**	**3**	**1**	**0**
Chondrichthyes	**1,282**	**14%**	**96%**	**185**	**6**	**3**	**0**
Holocephali	56	9%	100%	5	2	2	0
Elasmobranchii	1,226	15%	98%	180	6	3	0
Selachimorpha	692	16%	100%	112	6	3	0
Batoidea	534	13%	89%	68	4	2	0
Osteichthyes	**32,559**	**12%**	**43%**	**3,836**	**52**	**5**	**43**
Sarcopterygii	8	75%	100%	6	4	2	0
Actinopterygii	32,551	12%	58%	3,830	52	5	40
*Other Actinopterygii	49	51%	100%	25	6	2	2
Teleostei	32,463	12%	57%	3,811	50	5	36
Ostariophysi	10,318	6%	54%	606	27	5	16
Acanthopterygii	17,061	15%	41%	2,627	42	3	19
**Other Teleostei	5,084	11%	10%	578	17	2	1

*Other groups of Actinopterygii clade, except Teleostei. **Other groups of Teleostei clade, except Ostariophysi and Acanthopterygii.

FIGURES LEGENDS

Figure 1. Diversity of fish spawns on not constructed nests: the snapper *Lutjanus bohar* displays pelagic spawn (A); the clownfish *Amphiprion percula* spawns on hard substrates at the base of sea anemones (Actiniaria) (B); the hornshark *Heterodontus galeatus*, seen here eating the egg case of another hornshark, attaches egg cases to algae and other substrates (C); an egg case of the catshark *Scyliorhinus canicula* tied to coral branches (D); the angelfish *Pterophyllum scalare* spawns on leaves of aquatic plant (E); splash tetra *Copella arnoldi* pair spawns on plant leaf out of water (F).

Figure 2. Different types of reproductive strategies: the cardinalfish *Apogon aureus* mouthbrooding (A); the nurseryfish *Kurtus gulliveri* carrying egg cluster attached to its forehead bony hook (B); the goby *Pleurosicya mossambica* laying eggs on the tunicate *Polycarpa* sp. (C); female bitterling *Rhodeus amarus* lays eggs in zoogenic (animal) substrate, the mussel *Unio tumidus* (D); the viviparous guppy *Poecilia wingei* (E) and the shark *Negaprion brevirostris* (F) give birth to fully formed young.

Figure 3. Different types of reproductive strategies: the seahorse *Hippocampus abdominalis* is an internal brooder (A); the seadragon *Phyllopteryx taeniolatus* is an external brooder (B); the mudskipper *Periophthalmus modestus* spawns on the wall of a tunnel excavated out of water (burrow) (C); the grunion *Leuresthes tenuis* spawns on sand beaches or gravel beaches during extreme high tides (D); the fighting fish *Betta splendens* spawning in floating bubble secretion nest (E); the blenny *Lupinoblennius paivai* spawns in tunnels excavated by mollusks in mangrove roots (F).

Figure 4. Diversity of fish spawns in constructed nests: the tilapia *Oreochromis mossambicus* in ground excavated nest (depression) (A); the pufferfish *Torquigener albomaculosus* in elaborate mound nest (B); the sand-sifter *Lethrinops macrophthalmus* in crater-like mound nest (C); the armored catfish *Hoplosternum littorale* secretes a dome-shaped bubble nest, habitually among plants (D); the chub *Nocomis effusus* spawns in accumulated gravel mound called trough (E); the shrimpgoby *Myersina nigrivirgata*

spawns in ground burrow (F).

Figure 5. Dichotomous reproductive character and state key of fishes with 52 different reproductive modes (RMs). Numbers are proposed modes, in light gray modes shared with tetrapods. Letters indicate groups: Agnatha (A), Chondrichthyes (B), "Osteichthyes" (C), Anura (D), Caudata (E), Gymnophiona (F), and Squamata (G). Numbers on a top row and lower left indicate the 10 traits categories. FLV = Floating vegetation, SCH = Subaquatic chamber.

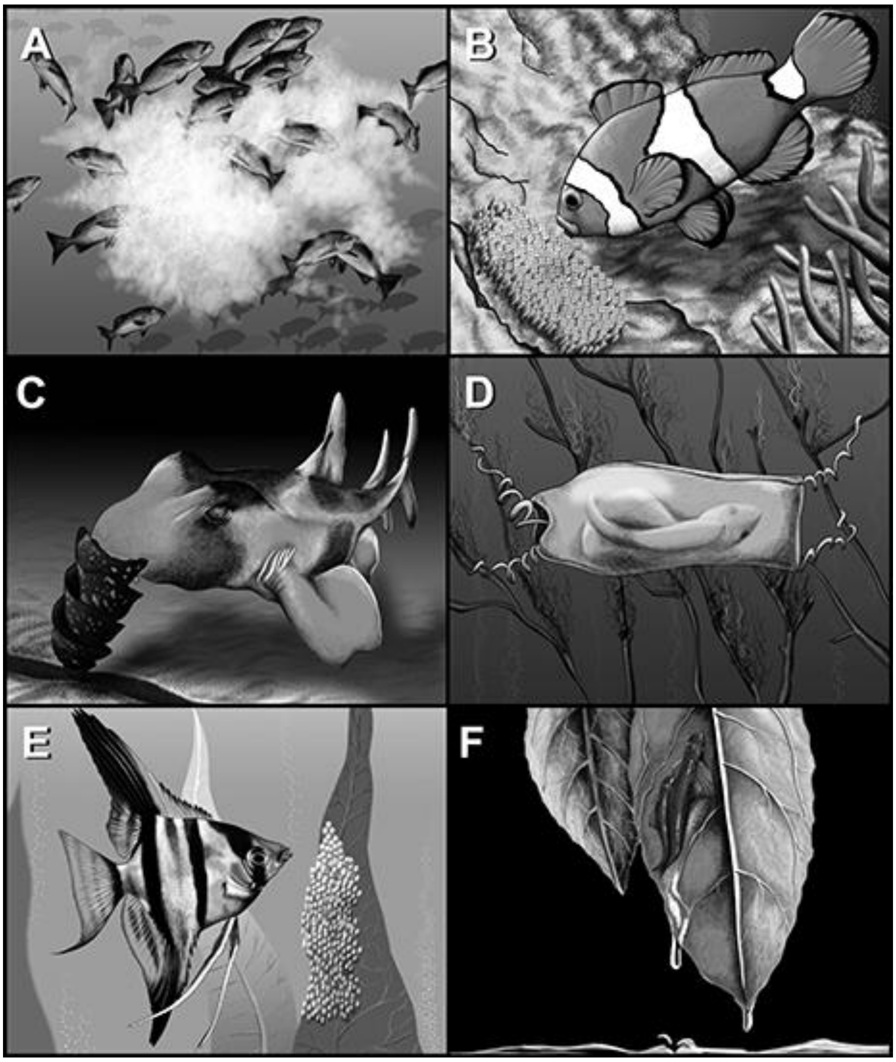
Figure 6. Number of species per RM (in logarithmic scale), colors according to spawning habitat.

Figure 7. Variation of RMs and sampled fish species per spawning habitat.

Figure 8. Linear regression between number of RMs and number of sampled vertebrate species: Amphibia, Testudines, Lepidosauria, Archosauria, and Synapsida. The shaded gray area signifies 95 % confidence interval of the linear regression ($F_{(1,4)} = 10.29$; $r^2 = 0.72$; $P = 0.03$).

FIGURES

Figure 1



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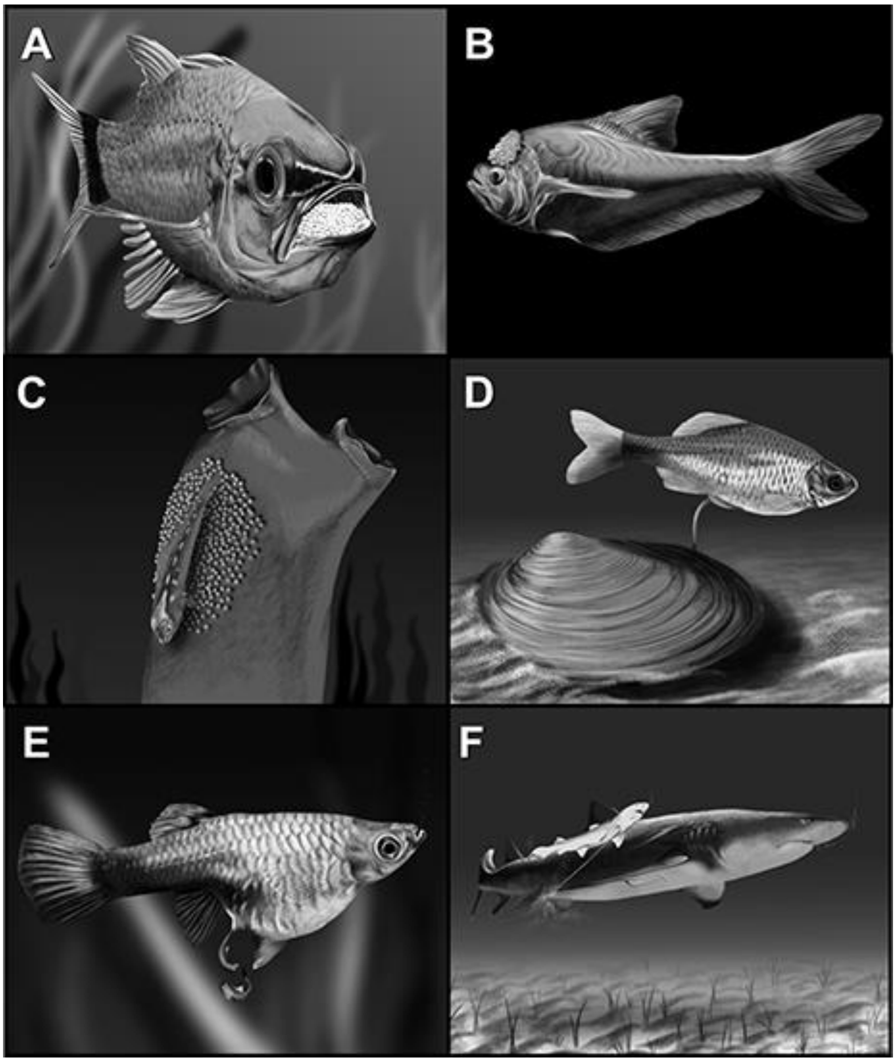
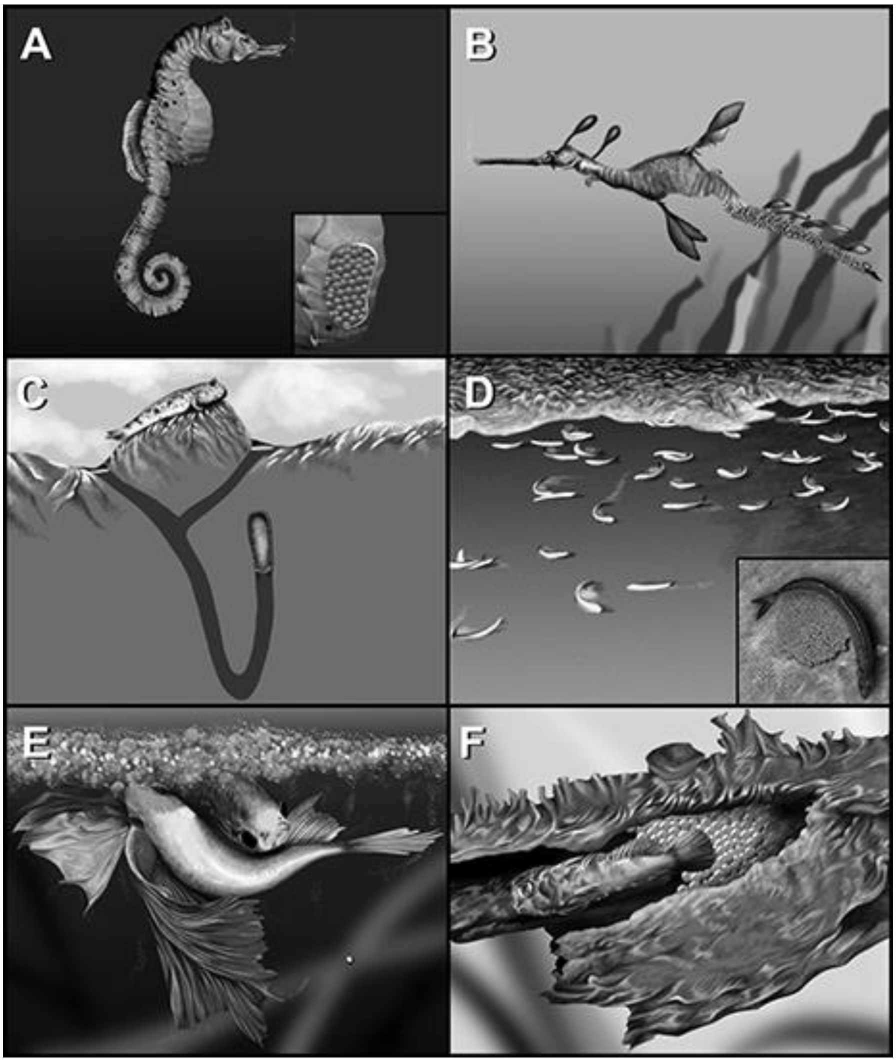


Figure 3



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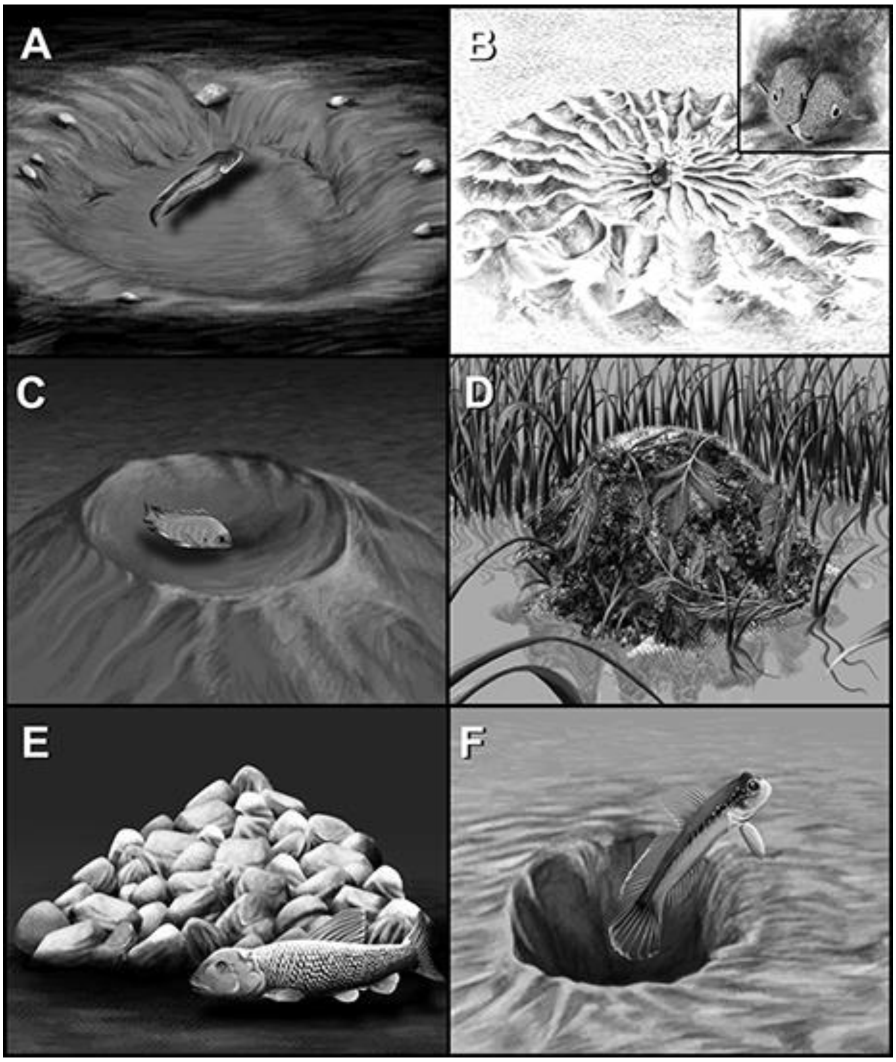

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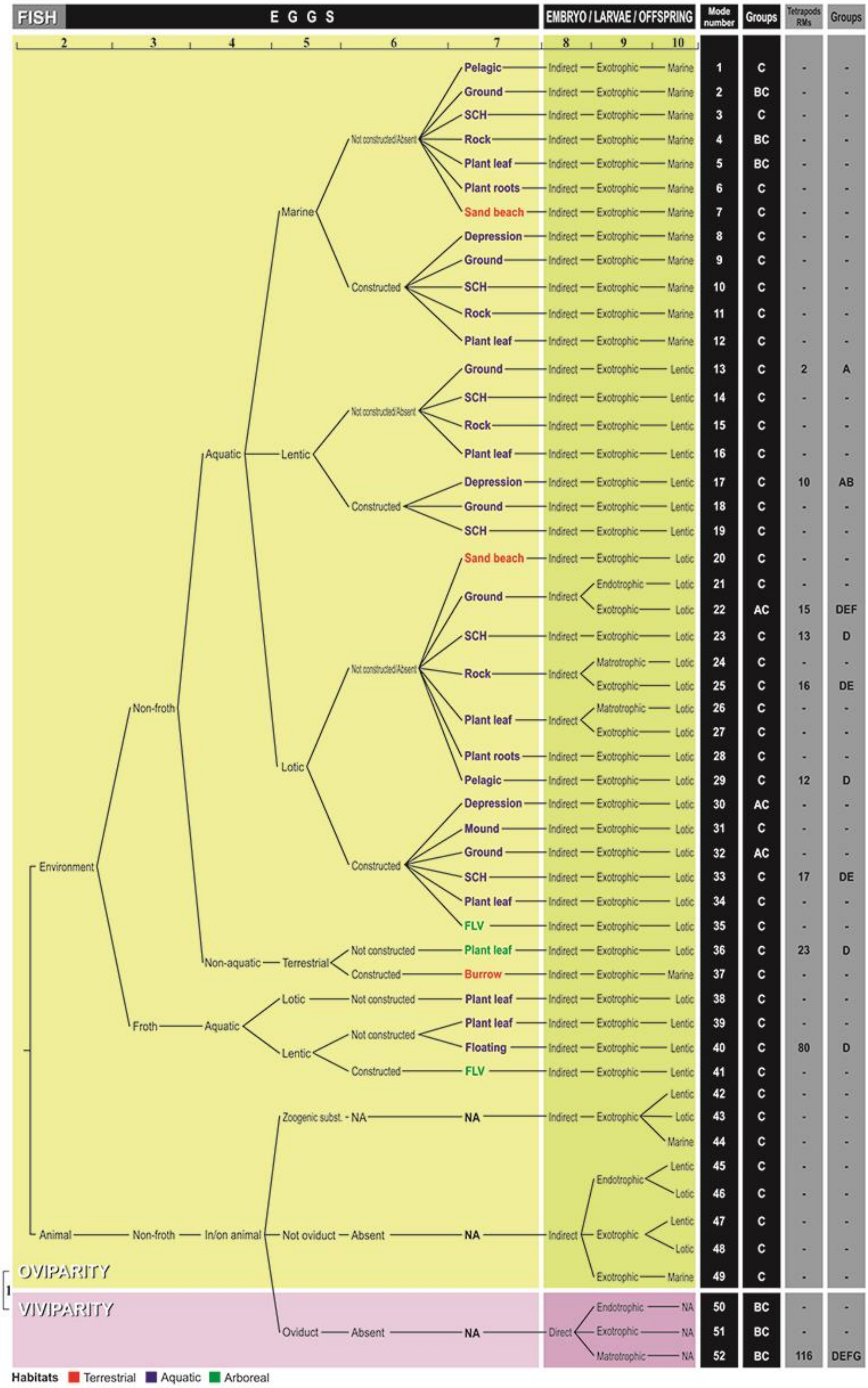

FISH
E G G S
EMBRYO / LARVAE / OFFSPRING
Mode number
Groups
Tetrapods RMs
Groups
2 3 4 5 6 7 8 9 10
Environment
Animal
Non-froth
Froth
Aquatic
Non-aquatic
In/on animal
Marine
Lentic
Lotic
Terrestrial
Zoogenic subst. - NA
Not oviduct — Absent
Oviduct — Absent
Not constructed/Absent
Constructed
Not constructed
Pelagic
Ground
SCH
Rock
Plant leaf
Plant roots
Sand beach
Depression
Mound
FLV
Burrow
Floating
NA
Indirect
Direct
Exotrophic
Endotrophic
Matrotrophic
Marine
Lentic
Lotic
OVIPARITY
VIVIPARITY
1 C - -
2 BC - -
3 C - -
4 BC - -
5 BC - -
6 C - -
7 C - -
8 C - -
9 C - -
10 C - -
11 C - -
12 C - -
13 C 2 A
14 C - -
15 C - -
16 C - -
17 C 10 AB
18 C - -
19 C - -
20 C - -
21 C - -
22 AC 15 DEF
23 C 13 D
24 C - -
25 C 16 DE
26 C - -
27 C - -
28 C - -
29 C 12 D
30 AC - -
31 C - -
32 AC - -
33 C 17 DE
34 C - -
35 C - -
36 C 23 D
37 C - -
38 C - -
39 C - -
40 C 80 D
41 C - -
42 C - -
43 C - -
44 C - -
45 C - -
46 C - -
47 C - -
48 C - -
49 C - -
50 BC - -
51 BC - -
52 BC 116 DEFG
Habitats Terrestrial Aquatic Arboreal

Figure 6

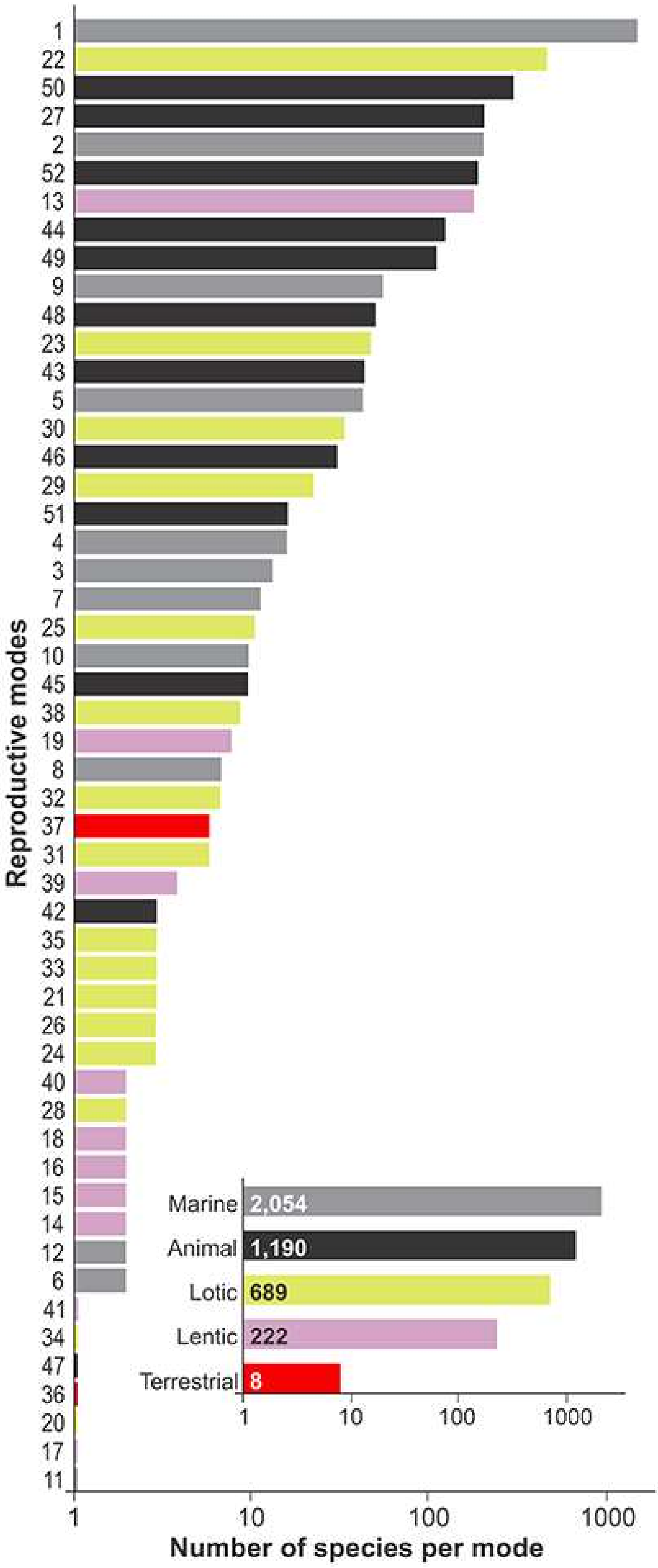

Reproductive modes
1
22
50
27
2
52
13
44
49
9
48
23
43
5
30
46
29
51
4
3
7
25
10
45
38
19
8
32
37
31
39
42
35
33
21
26
24
40
28
18
16
15
14
12
6
41
34
47
36
20
17
11
Marine 2,054
Animal 1,190
Lotic 689
Lentic 222
Terrestrial 8
1
10
100
1000
Number of species per mode

Figure 7

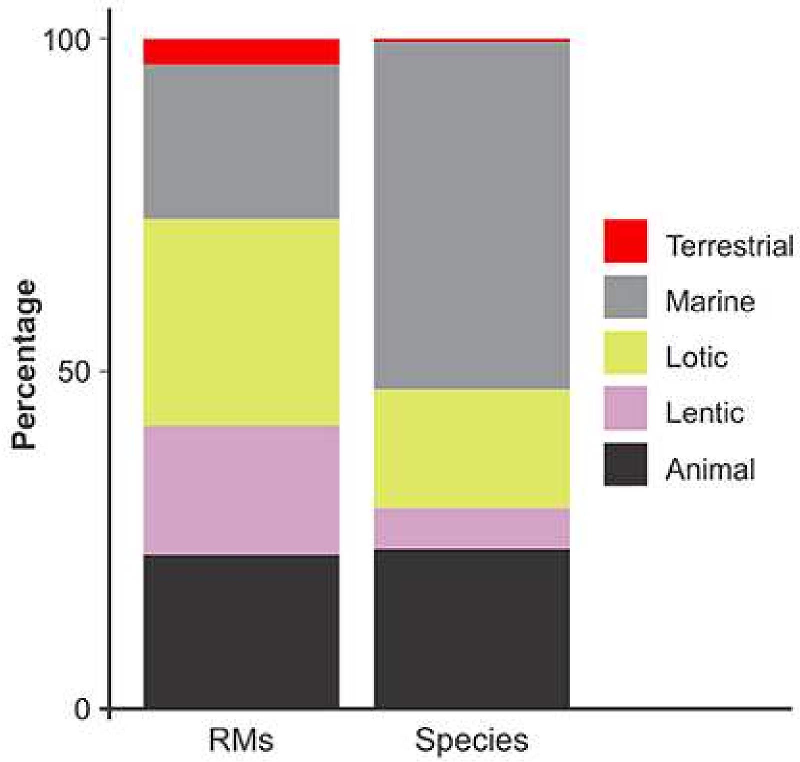
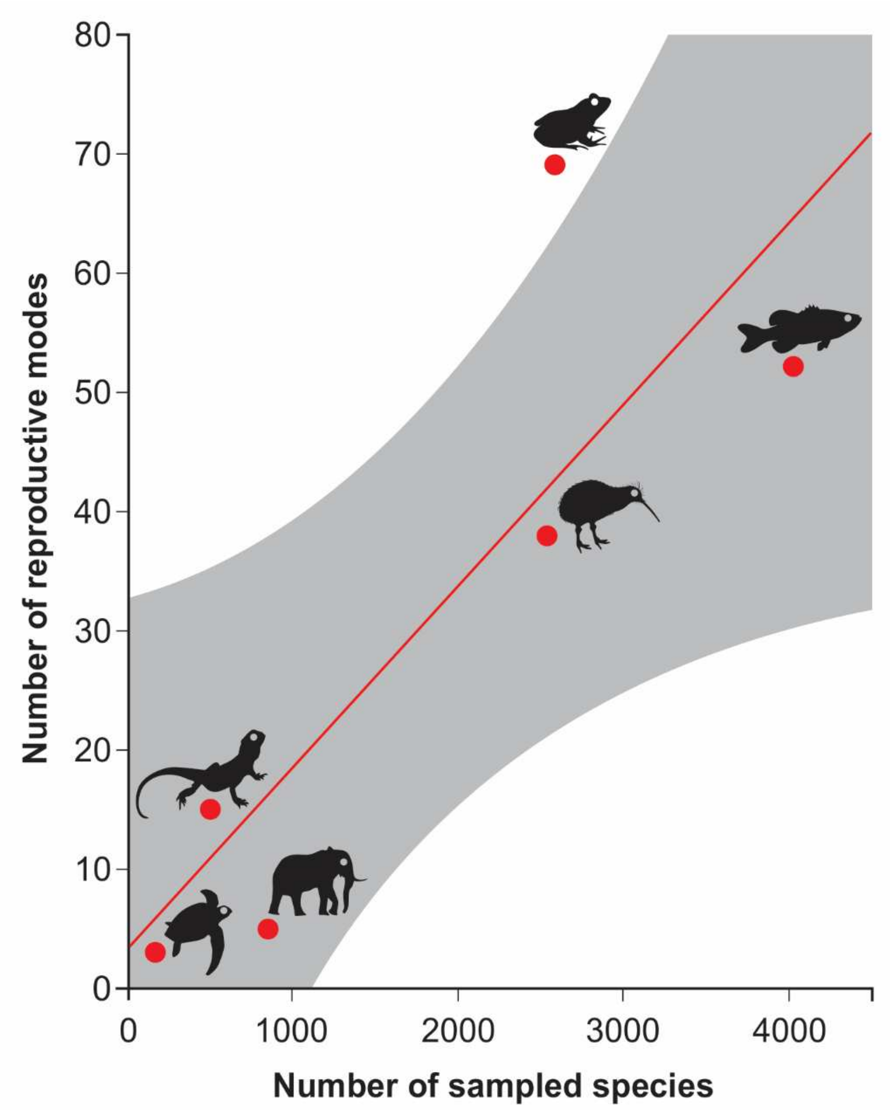

100
50
0
Percentage
RMs
Species
Terrestrial
Marine
Lotic
Lentic
Animal

Figure 8



80
70
60
50
40
30
20
10
0
Number of reproductive modes
0
1000
2000
3000
4000
Number of sampled species

SUPPLEMENTARY MATERIAL

Appendix I. Description of reproductive modes of tetrapods.

Appendix II. Definitions and Abbreviations.

Figure S1. Hierarchical cluster of Craniata RMs, using paired group algorithm (UPGMA), Euclidean similarity index, and 1,000 bootstrap randomizations, cophenetic correlation coefficient 0.98. Number of RMs per group in parenthesis.

Table S1. Database for the reproductive modes (RMs) of 4,037 fish species.

Table S2. Reproductive modes of Craniata and number of groups per RM.

Appendix I

Description of reproductive modes of aquatic vertebrates

1) Oviparity

1.1) Eggs in environment

Mode 1 – Nest absent, non-froth pelagic eggs laid in marine water. Offspring with indirect development, exotrophic nutrition, and larvae develop in marine water.

Mode 2 – Nest absent, non-froth subaquatic eggs laid on bed of marine water. Offspring with indirect development, exotrophic nutrition, and larvae develop in marine water.

Mode 3 – Non-froth subaquatic eggs laid in subaquatic chamber nest in marine water. Offspring with indirect development, exotrophic nutrition, and larvae develop in marine water.

Mode 4 – Non-froth subaquatic eggs laid on rock nest in marine water. Offspring with indirect development, exotrophic nutrition, and larvae develop in marine water.

Mode 5 – Non-froth subaquatic eggs laid on plant leaf nest in marine water. Offspring with indirect development, exotrophic nutrition, and larvae develop in marine water.

Mode 6 – Non-froth subaquatic eggs laid on plant roots nest in marine water. Offspring with indirect development, exotrophic nutrition, and larvae develop in marine water.

Mode 7 – Nest absent, non-froth eggs laid on sand beach of marine water. Offspring with indirect development, exotrophic nutrition, and larvae develop in marine water.

Mode 8 – Non-froth subaquatic eggs laid in constructed depression nest in marine water. Offspring with indirect development, exotrophic nutrition, and larvae develop in marine water.

Mode 9 – Non-froth subaquatic eggs laid in constructed nest on bed of marine water. Offspring with indirect development, exotrophic nutrition, and larvae develop in marine water.

Mode 10 – Non-froth subaquatic eggs laid in constructed chamber nest in marine water. Offspring with indirect development, exotrophic nutrition, and larvae develop in marine water.

Mode 11 – Non-froth subaquatic eggs laid in constructed rock nest in marine water. Offspring with indirect development, exotrophic nutrition, and larvae develop in marine water.

Mode 12 – Non-froth subaquatic eggs laid in constructed plant leaf nest in marine water. Offspring with indirect development, exotrophic nutrition, and larvae develop in marine water.

Mode 13 – Nest absent, non-froth subaquatic eggs laid on bed of lentic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water.

Mode 14 – Non-froth eggs laid in subaquatic chamber nest in lentic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water.

Mode 15 – Non-froth subaquatic eggs laid on rock nest in lentic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water.

Mode 16 – Non-froth subaquatic eggs laid on plant leaf nest in lentic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water.

Mode 17 – Non-froth subaquatic eggs laid in constructed depression nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water.

Mode 18 – Non-froth subaquatic eggs laid in constructed nest on bed of lentic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water.

Mode 19 – Non-froth eggs laid in constructed subaquatic chamber nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water.

Mode 20 – Nest absent, non-froth eggs laid on sand beach of lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water.

Mode 21 – Nest absent, non-froth subaquatic eggs laid on bed of lotic water. Offspring with indirect development, endotrophic nutrition, and larvae develop in lotic water.

Mode 22 – Nest absent, non-froth subaquatic eggs laid on bed of lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water.

Mode 23 – Non-froth eggs laid in subaquatic chamber nest in lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water.

Mode 24 – Non-froth eggs laid on rock nest in lotic water. Offspring with indirect development, matrotrophic nutrition, and larvae develop in lotic water.

Mode 25 – Non-froth eggs laid on rock nest in lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water.

Mode 26 – Non-froth eggs laid on plant leaf nest in lotic water. Offspring with indirect development, matrotrophic nutrition, and larvae develop in lotic water.

Mode 27 – Non-froth eggs laid on plant leaf nest in lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water.

Mode 28 – Non-froth eggs laid on plant roots nest in lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water.

Mode 29 – Nest absent, non-froth floating eggs laid in lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water.

Mode 30 – Non-froth subaquatic eggs laid in constructed depression nest in lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water.

Mode 31 – Non-froth subaquatic eggs laid in constructed mound nest in lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water.

Mode 32 – Non-froth subaquatic eggs laid in constructed nest on bed of lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water.

Mode 33 – Non-froth eggs laid in constructed subaquatic chamber nest in lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water.

Mode 34 – Non-froth subaquatic eggs laid in constructed plant leaf nest in lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water.

Mode 35 – Non-froth subaquatic eggs laid in constructed floating vegetation nest in lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water.

Mode 36 – Terrestrial non-froth eggs laid on plant leaf nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water.

Mode 37 – Terrestrial non-froth eggs laid in burrow nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in marine water.

Mode 38 – Nest absent, froth eggs laid on plant leaf nest in lotic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water.

Mode 39 – Nest absent, froth eggs laid on plant leaf nest in lentic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentictic water.

Mode 40 – Nest absent, froth floating eggs laid in lentic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water.

Mode 41 – Froth floating eggs laid in constructed floating vegetation in lentic water. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water.

1.2) Eggs kept in/on the animal

Mode 42 – Non-froth eggs laid on zoogenic substrate. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water.

Mode 43 – Non-froth eggs laid on zoogenic substrate. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water.

Mode 44 – Non-froth eggs laid on zoogenic substrate. Offspring with indirect development, exotrophic nutrition, and larvae develop in marine water.

Mode 45 – Non-froth eggs kept in the animal, absent nest. Offspring with indirect development, endotrophic nutrition, and larvae develop in lentic water.

Mode 46 – Non-froth eggs kept in the animal, absent nest. Offspring with indirect development, endotrophic nutrition, and larvae develop in lotic water.

Mode 47 – Non-froth eggs kept in the animal, absent nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lentic water.

Mode 48 – Non-froth eggs kept in the animal, absent nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in lotic water.

Mode 49 – Non-froth eggs kept in the animal, absent nest. Offspring with indirect development, exotrophic nutrition, and larvae develop in marine water.

2) Viviparity

Mode 50 – Non-froth eggs kept in the animal, absent nest. Offspring with direct development, endotrophic nutrition.

Mode 51 – Non-froth eggs kept in the animal, absent nest. Offspring with direct development, exotrophic nutrition.

Mode 52 – Non-froth eggs kept in the animal, absent nest. Offspring with direct development, matrotrophic nutrition.

Appendix II

Definitions and abbreviations

1) DEFINITIONS

Animal – This term is related to the macro-habitat where eggs are laid, when eggs are kept in or moved on the body of one of the parents.

Aquatic – Related to eggs that are laid in the water.

Bubble nest – Bubbles are expelled from mouth to water surface, parents carry eggs to bubbles.

Burrow – Term applied to the microhabitat where eggs are laid. In this case, eggs are laid in a subterranean burrow, dug or not by parents.

Constructed nest – A structure prepared by some vertebrates, which can be considered as any kind of environmental modification for the function of incubating eggs and raising their offspring.

Depression – Term applied to the microhabitat where eggs are laid. Eggs are laid in a sandy or muddy depression, dug or not, covered or not.

Direct development – Applied to offspring development without larval stage, this describes development without a larval stage.

Endotrophic – This term is used in offspring nutrition, where the larvae obtain their entire developmental energy from vitellogenic yolk.

Environment – Term applied to the macro-habitat where eggs are laid. Eggs are laid in the milieu, in or out of nests.

Exotrophic – This term is used in offspring nutrition, where the larvae obtain energy by oral consumption of food, when the vitellogenic yolk runs out.

Floating – Term applied to the microhabitat where eggs are laid. Eggs are laid in a free-floating froth nest on the surface of water bodies.

Floating vegetation (FLV) – Term applied to the microhabitat where eggs are laid. In this case, eggs are laid in constructed nests or froth nests in floating vegetation.

Froth – Related to nest type, made with bubbles. Froth nests are not considered constructed nests.

Ground – Term applied to the microhabitat where eggs are laid. In this case, eggs are laid on the sea bottom or flowing waterbed with muddy or sandy substrates, or pebbly bottoms.

In/on animal – Related to eggs laying substrate. In this case, eggs are incubated in different parts of the body of the parents. For example, eggs are incubated in the mouth, belly, throat, head, and ventral and dorsal pouch in bonny fishes, or in different parts of the zoogenic substrate, such as anemones, ascidians, coral, crabs, fishes, molluscans, tunicates, and sponges. Some cartilaginous and bonny fishes incubate their eggs on oviduct.

Indirect development – Applied to offspring development with larval stage. This describes development with a larval stage.

Lentic water – This term is used in relationship to eggs surrounding medium. Larvae develop in still/lentic water, such as lakes, ponds or swamps. The term is also related to offspring development, when larvae develop in still/lentic water, such as lakes, ponds or swamps.

Lotic water – This term is used in relationship to eggs surrounding medium. Eggs are laid in flowing waters, such as rivulets, creeks, streams or rivers. The term is also related to offspring development. Larvae that develop in flowing waters, such as rivulets, streams or rivers.

Marine water – This term is used in relationship to eggs surrounding medium. Eggs are laid in the marine environment. The term is also related to offspring development medium.

Matrotrophic – Related to offspring nutrition. Embryos or nestlings obtain energy not only by vitellogenic yolk, but supplemented by nourishment derived from the mother.

Mound – Term applied to microhabitat where eggs are laid. Eggs are laid on constructed mounds.

Nest – Adapted from Simon and Pacheco (2005), nest is any place selected by the parent (or both parents) for laying its eggs, regardless of how much (if any) digging, cleaning, lining, or building it requires.

Nest absent – When there is no nest used during egg laying.

Non-aquatic – Related to egg laying substrate. Eggs are laid out of the water, as on plant leaf, or burrow.

Non-froth nest – Eggs are laid in non-frothy nests, without the production of bubbles.

Not constructed nest – A structure used by some vertebrates, not built by them and for the function of incubating eggs and raising their offspring.

Not oviduct – This term is related to eggs surrounding medium. Eggs are embedded in different parts of the body of the parents, such as mouth, belly, throat, head, and ventral and dorsal pouch.

Oviduct – This term is related to eggs surrounding medium. Eggs are developed in a specialized portion of the oviduct, including species whose embryos depend solely on yolk reserves, those with oophagous embryos, and those with embryos that depend on nourishment through placental analogues.

Oviparity – Ovules with yolk in ovaries or oviducts. After spawning fertilization, embryonic development continues outside of the female body, within complex extraembryonic membranes (eggs) that may include gelatinous capsules or coriaceous shells.

Pelagic – Term applied to the microhabitat where eggs were laid. Eggs are laid in the water column.

Plant leaf – Term applied to the microhabitat where eggs were laid. In this case, eggs are laid on algal beds, aquatic plants, branches of terrestrial plants, or logs in the water.

Plant root – Term applied to the microhabitat where eggs were laid. In this case, eggs are laid on algal beds, aquatic plants, branches of terrestrial plants, or logs in the water.

Rock – Term applied to the microhabitat where eggs were laid. In this case, eggs are laid on or underneath rocks, crevices, cave walls, which may be in the sea, lentic or lotic water bodies.

Sand beach – Term applied to the microhabitat where eggs were laid. Eggs are laid on the seashore or in natural banks of flowing water.

Subaquatic chamber (SCH) – Term applied to the microhabitat where eggs were laid. In this case, eggs are laid in a chamber inside the water.

Terrestrial – This term is related to eggs surrounding medium. Eggs are laid on terrestrial environment, as plants, logs or rocks.

Viviparity – This occurs when egg laying (as in oviparity) is absent. Offspring develop within the ovaries or oviducts. After exhaustion of vitellogenic yolk, embryos feed on oviductal material (secretions, fragments of the oviduct) or on ova in the ovary to complete their development, as in some cartilaginous and bony fishes.

Zoogenic substrate – This term is related to eggs surrounding medium. Eggs are embedded in different parts of the body in other species of aquatic animals.

2) ABBREVIATIONS

FLV – Floating vegetation

SCH – Subaquatic chamber

Zoogenic subst. – Zoogenic substrate

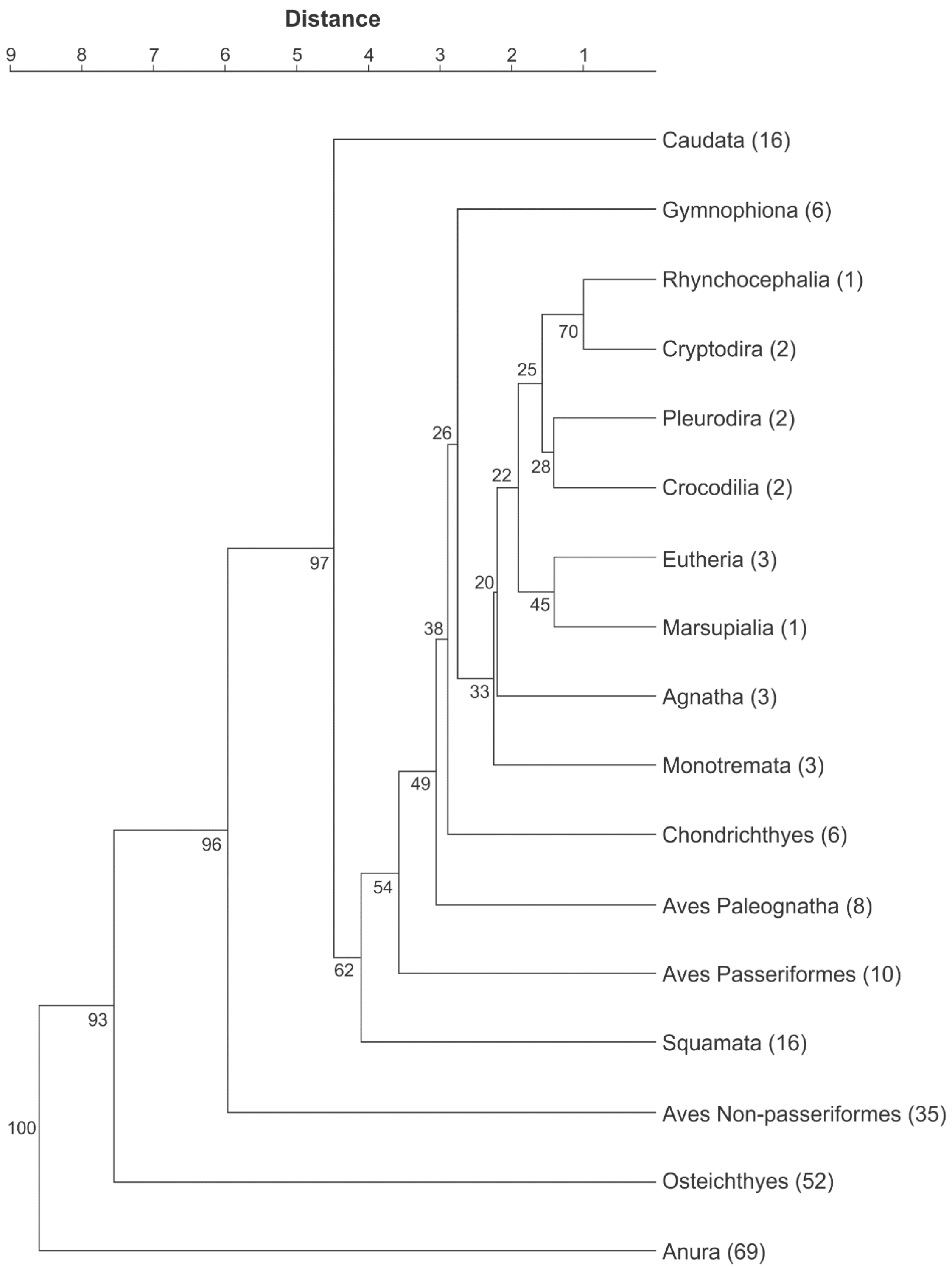


Figure S1. Hierarchical cluster of Craniata RMs, using paired group algorithm (UPGMA), Euclidean similarity index, and 1,000 bootstrap randomizations, cophenetic correlation coefficient 0.98. Number of RMs per group in parenthesis.

Capítulo 3. SPATIAL RELATIONSHIP BETWEEN AMPHIBIAN DIVERSITY AND THEIR REPRODUCTIVE MODES

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ABSTRACT

Amphibians are the vertebrate group with the higher diversity of reproductive modes (RMs). Such great diversity was never explained. However, one possible and straightforward explanation is that species richness is directly related to the diversity of RMs. Brazil is quite suitable to test such hypothesis as it houses over 1,000 amphibian species, and where is located the Atlantic forest, previously reported as an area of great RMs diversity. To test that, we mapped both the diversity of amphibian species and the RMs diversity in Brazil. The Atlantic forest presented high RMs diversity when compared to other drier grasslands or warmer rainforest (Amazonia) biomes. We detected an overall linear and positive relationship between RMs diversity and amphibian species richness. We then estimated a reproductive mode diversity relative index (RMDRI), merging both datasets (species richness and RM diversity), revealing that the relationship between species richness and RM diversity varies among biomes. I.e., some regions present less RMs than expected by the direct relationship. Therefore, we conclude that the major driver of RMs diversity is correlated with the local species richness, but in some areas, other factors may be influencing such relationship, as climatic conditions and breeding microhabitat availability.

Key words: Anura, Caudata, Gymnophiona, reproduction, reproductive strategies, breeding biology, species richness.

INTRODUCTION

Many studies on amphibian biology focus on their reproductive modes (RMs) (e.g., Boulenger, 1886; Salthe & Duellman, 1973; Duellman & Trueb, 1986; Haddad & Prado, 2005; CHAPTER 1). RM is a set of characters and their states representing all reproduction strategies (Salthe & Duellman, 1973; Duellman & Trueb, 1986; Haddad & Prado, 2005). Amphibians have the highest number, 71 (CHAPTER 1), of RMs among all vertebrate classes (CHAPTER 2). These RMs are observed all over the globe, but the Atlantic forest has been cited as a region of unexpected high number of RMs (Haddad & Prado, 2005).

Studies on the Atlantic forest have shown that the diversity of amphibian RMs is related to complex topography that provides different microhabitats and barriers, which allowed a high diversification of RMs (Haddad & Prado, 2005; Toledo *et al.*, 2014). According to Haddad & Prado (2005) and da Silveira Vasconcelos *et al.*, (2010), high humidity also correlates with the RMs diversity because it reduces the risk of desiccating eggs and tadpoles that develop out of water. Toledo *et al.* (2014) argue that elevation and latitudinal variation are not correlated to amphibian rare species richness. On the other hand, da Silveira Vasconcelos *et al*. (2010) said that elevation is correlated positively to anuran species richness. However, no study actually tested this or one quite straightforward hypothesis, that amphibian species richness is directly related to RM diversity.

Many studies have related species richness with behavioral richness. For example, Mitra *et al.* (1996) verified if the species richness was associated with the social system of mating in birds. Nicolakakis *et al.* (2003) argued that the social transmission of new abilities to other members of a bird population can accelerate evolution rates and thus could explain differences in species richness. Altitude and rainfall are positively correlated to anuran RMs, on the other hand, temperature may not be correlated (da Silveira Vasconcelos *et al.*, 2010). Herbivore insect richness was correlated with feeding a single plant species (Novotny *et al.*, 2004). Auster *et al.* (2019) analyzed mixed-species piscivorous fishes groups related on hunting behaviors. Therefore, it is clear that species richness may influence the diversity of behaviors.

Thus, we tested the hypothesis that amphibian species richness is directly related to their RMs diversity. To accomplish that, we performed a spatial analysis comparing the RMs diversity with amphibian species richness in Brazil. In addition, as habitat may influence, we also compared different biomes, expecting that biomes with greater vegetation structure and moisture, i.e., the Tropical rainforests (Atlantic forest and the Amazonia), would have more number RM diversity than less structured and drier grasslands (Caatinga, Cerrado, Pantanal, and Pampas).

METHODS

We did a review for information on amphibian species richness in Brazil. Out of all amphibian species distribution shape files available in the IUCN Red List of Threatened Species website (2018), we had information for the RMs for 1,837 species (see CHAPTER 1). Therefore, with this second set of species, we produced a species richness map for Brazil, as it is a country with more robust data on RM and with more amphibian species in the world (Segalla *et al.*, 2019). Furthermore, we produced a RMs map with the information we have on these species. Then, we rescaled the maps of amphibian species richness and reproductive modes diversity to values from 0 to 1 for each pixel, in order to make them equivalent for the subsequent map algebra. With these resulting maps we produced a map of RMs diversity relative index (RMDRI), resulting from the RMs diversity map subtracted by the amphibian species richness map. Maps were produced in MATLAB (2012) and R Core Team (2012).

From these three maps, we extracted each pixel value and analyzed the six Brazilian biomes (following IBGE definitions and geographical boundaries) independently. We compared biomes with an ANOVA analyses and when significant differences were found, we run a TUKEY *a posteriori* test. These testes were run in R.

Finally, we made a linear regression in Statistica 7.1 (Stasoft, 2005), considering the regression significant if $P < 0.05$, in order to test the relationship between the RMs diversity and amphibian species richness. We then validated the modeled regression by plotting published field datasets in the resulting graph. These data are from previous Neotropical anuran assemblage studies that provided the information of RM diversity and local amphibian species richness (Arzabe, 1999; Pombal Jr. & Haddad, 2005; Prado *et al.* 2005; Moreira *et al.*, 2007; Zina *et al.*, 2007; Da Silva Vieira *et al.*, 2009; Armstrong & Conte, 2010; Hartmann *et al.*, 2010; Bitar *et al.*, 2012; Santoro & Brandão, 2014).

RESULTS

We observed higher values of amphibian species richness for the Atlantic forest when compared to other biomes (Figure 1A, B; $F_{(1,5)} = 12{,}369$; $P < 0.001$). We observed lower values of RM diversity in most grasslands (Cerrado, Pantanal and Pampas) and higher in the tropical rainforests (Atlantic forest and Amazonia) and in one of the driest areas of Brazil (Caatinga) (Figure 1C, D; $F_{(1,5)} = 5{,}289$; $P < 0.001$). We observed mostly negative values for the RMDRI the northernmost biomes (Amazonia and Caatinga) and close to zero values for the other southern biomes (Figure 1E, F; $F_{(1,5)} = 12{,}715$; $P < 0.001$). Finally, we found a positive relationship between RMs diversity and amphibian species richness ($r^2 = 0.32$; $P < 0.001$; Figure 2).

DISCUSSION

The species richness distribution pattern is congruent with other studies that reported the same for Brazil (Buckley & Jetz, 2007; Toledo & Batista, 2012; Jenkins *et al.*, 2013; 2015). However, the RMs diversity did not follow the same pattern of the species richness, probably by the variable elevation and climatic conditions of such different biomes (da Silveira Vasconcelos *et al.*, 2010). As pointed out, humidity may or may not allow the presence of a specific RM in a given area (Haddad & Prado, 2005; Da Silva *et al.*, 2012). Therefore, although we found a general pattern relating species richness and RM diversity, rainfall, relative humidity (or other climatic variable) may influence in the RMDRI. Another factor that may be related to RM diversity is the temperature, as the northern biomes (Amazonia and Caatiga), in spite of constant rainfall at least in the Amazon, presented less RM diversity than the southern biomes (Atlantic forest, Cerrado, Pantanal and Pampa), for which the species richness is highly related to RM diversity (Figure 1E, F). Higher temperatures may relate to higher evaporation, consequently increasing desiccation, on its turn reducing the RMs that involves terrestrial stages of eggs or tadpole development.

In the dryer biomes, there is not so much vegetation structure, hampering the existence of species that reproduce in the arboreal stratum, thus reducing the RM diversity. For example RMs 21, 22, 23, 24, 25, 57, 58, 86, 87, 88, 89, and 95 would not be possible as they depend on vegetation. In the Amazonia, although there is vegetal extractification, there are few bromeliads, diminishing the breeding habitats for arboreal species. On the other hand, in the Atlantic forest, water filled containers (WFC, *sensu* CHAPTER 1) is widespread and abundant. Thus, many species and RMs had opportunity to evolve in that forest. In addition, Pantanal is characterized by severe climatic seasonality, with periods of heavy rains and periods of intense drought (Junk *et al.*, 2006). This condition may restrict the local amphibian species richness and RMs diversity. Moreover, Pantanal vegetation is not as stratified as in the Atlantic forest for example, also diminishing the possible niches for amphibians to evolve.

Although we clearly detected a relationship between RMs and species richness we did not tested the influence of climatic conditions in these variables and most importantly in the RMDRI. Therefore, future studies might explore further factors related to the RMs diversity. Finally, as shown in our study, the most species rich biomes are those with the highest diversity of behaviors. This fact would be another argument for the conservation of megadiverse ecosystems.

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Figure legends

Fig. 1. On the left, maps of Brazil showing sampled amphibian species richness (A); sampled diversity of amphibian reproductive modes (C); Reproductive modes diversity relative index (E). On the right, boxplots of amphibian species richness (B), Boxplots of diversity of amphibian reproductive modes (D), and boxplots of reproductive modes diversity relative index (F) for each major Brazilian biome.

Fig. 2. Linear regression between reproductive modes diversity and amphibian species richness in Brazil. The dashed lines represent the 90 % confidence interval of the linear regression ($r^2 = 0.32$; $P = < 0$). Black dots are those extracted from previous studies: Santoro & Brandão (2014) (A); Hartmann *et al.* (2010) (B); Armstrong & Conte (2010) (C); Bitar *et al.* (2012) (D); Da Silva Vieira *et al.* (2009) (E); Arzabe (1999) (F, H); Pombal & Haddad (2005) (G); Prado *et al.* (2005) (I); Zina *et al.* (2007) (J); Moreira *et al.* (2007) (F).

Figure 1

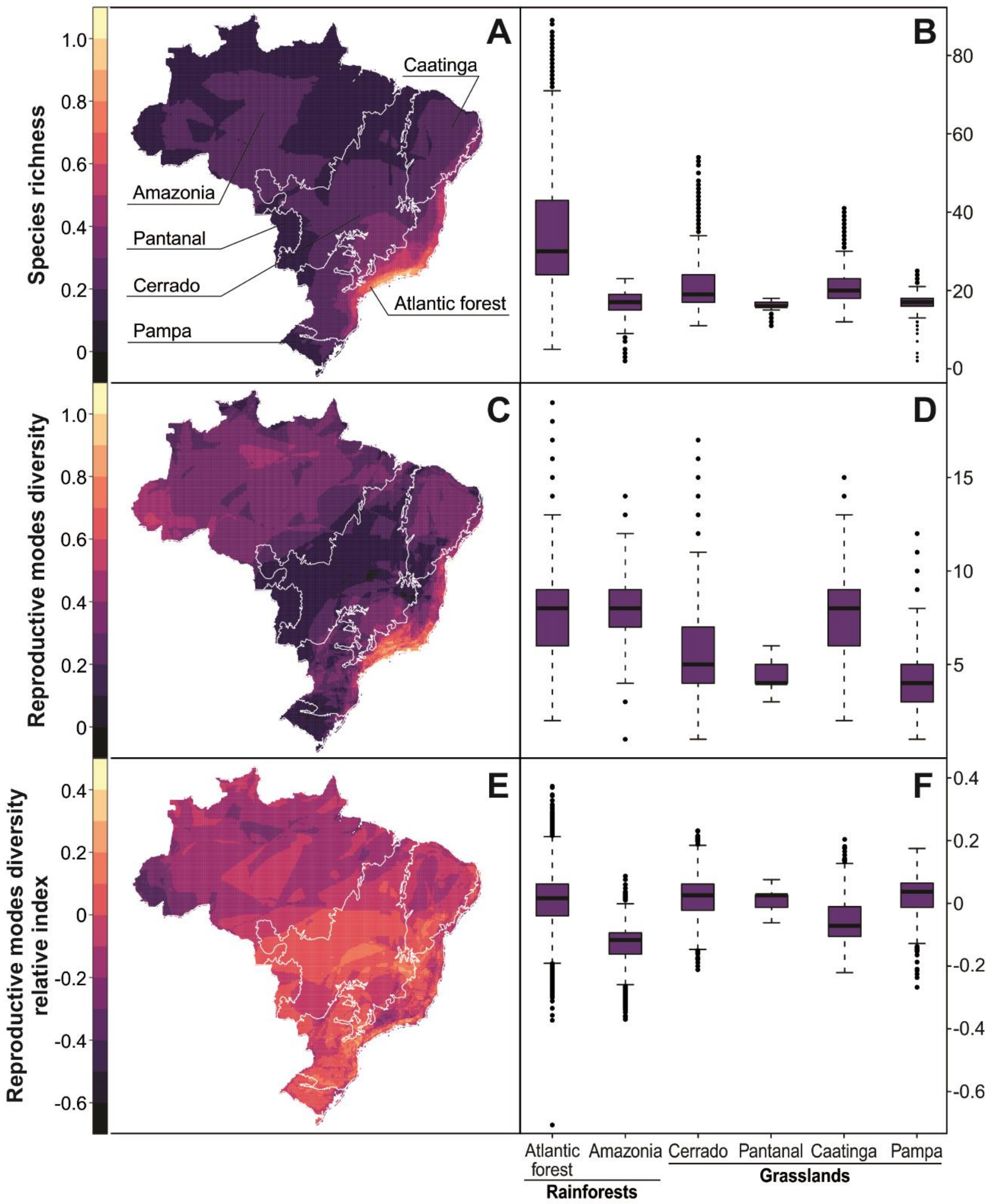
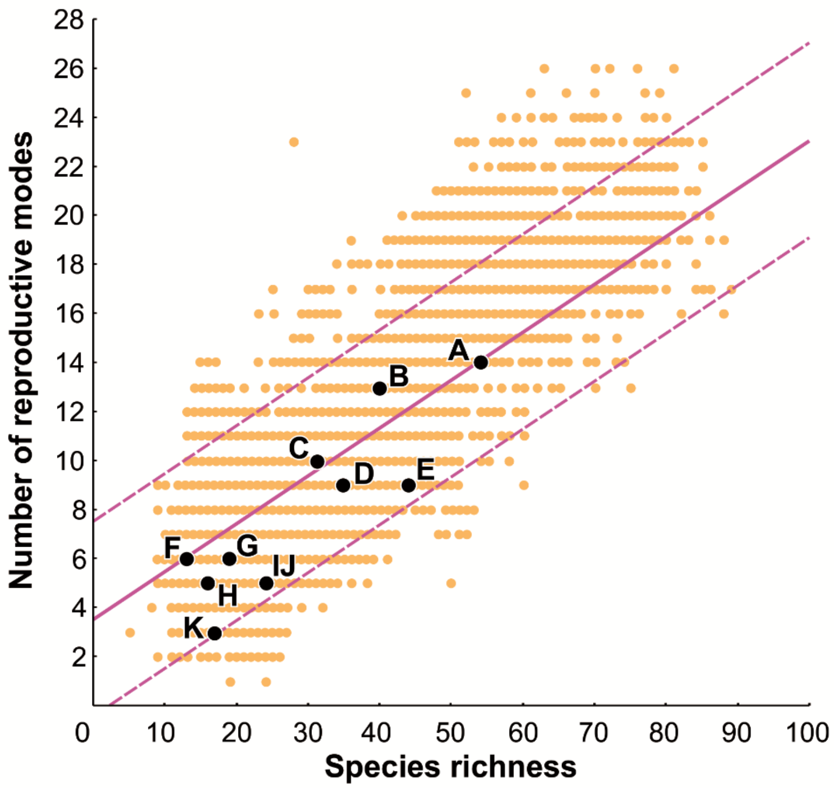

A
B
C
D
E
F
Caatinga
Amazonia
Pantanal
Cerrado
Pampa
Atlantic forest
Species richness
Reproductive modes diversity
Reproductive modes diversity relative index
1.0
0.8
0.6
0.4
0.2
0
80
60
40
20
0
15
10
5
0.4
0.2
0
-0.2
-0.4
-0.6
Atlantic forest
Amazonia
Cerrado
Pantanal
Caatinga
Pampa
Rainforests
Grasslands

Figure 2



Number of reproductive modes
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
10
20
30
40
50
60
70
80
90
100
Species richness
A
B
C
D
E
F
G
H
IJ
K

CONCLUSÕES

Classificação de modos reprodutivos em Craniata

Esse estudo abrangeu 10.237 espécies de vertebrados, entre peixes, anfíbios, répteis, aves e mamíferos, e reconheceu 158 MRs. Para o grupo dos tetrápodes 6.200 espécies foram analisadas e 116 MR classificados. Amphibia, é a classe representada pelo maior número de espécies (2.159 espécies; 35% das espécies; 80% das espécies representadas), e apresentaram o maior número de MRs (71). Anuros (2.001 espécies amostradas) exibiram 69 MRs, das quais 54 foram exclusivos desse grupo, especialmente os MRs de 79 a 98, que incluíram ninhos de espuma, e os MRs de 100 a 103 e de 106 a 110, que incluíram ovos ou larvas transportadas pelos pais. As salamandras (109 espécies amostradas) exibiram 16 MRs, sendo que dois são exclusivos (MR 7 e 41) e cecílias (49 espécies amostradas) exibiram seis MRs, dos quais nenhum foi exclusivo desse grupo.

Em Anura, *Rhacophorus viridis* exibiu quatro MRs diferentes, representando o número máximo de modos conhecidos por uma espécie. Em Caudata, quatro espécies de pletodontídeos, *Desmognathus carolinensis*, *D. ocoee*, *D. orestes* e *Hemidactylium scutatum* exibiram três MRs diferentes. Entre os Gymnophiona, o número máximo de MR foi apenas um. Na chave exclusiva de caracteres reprodutivos para o grupo Amphibia, é possível comparar os MR atuais (71) com os MR das classificações anteriores (Boulenger, 1886; Duellman & Trueb, 1986; Haddad & Prado, 2005).

Com base em 4.041 espécies (65% da amostra total), o grupo Amniota exibiu 51 MRs diferentes, dos quais 36 são exclusivos desse grupo. Dentre esses, 496 MRs foram exibidos em membros do grupo Lepidosauria (2 rincocefálias, 344 serpentes, 150 lagartos e anfisbenídeos), o qual representa 84% das famílias analisadas. Uma única espécie de lagarto, *Gonatodes humeralis*, exibiu cinco MRs diferentes, o que representa o maior número de MRs observado em uma única espécie de tetrápode.

Entre os Testudines, 167 espécies foram analisadas (130 Cryptodira e 37 Pleurodira). Para esse grupo, coletamos dados de todas as famílias, 100%. Os Testudines têm três MRs e o MR 11 é único entre o grupo Amniota, o qual está representado por *Chelodina rugosa*, que põe ovos debaixo d'água, embora o desenvolvimento ocorra apenas quando o ninho está seco, e o desenvolvimento da prole é precoce.

Entre o grupo Archosauria, obtivemos dados sobre 2.519 espécies (23 Crocodilia, 40 Aves Paleognatha, 1.126 Aves Neognatha non-Passeriformes, e 1.330 Aves Neognatha Passeriformes), que representam 99% das famílias analisadas. Archosauria exibiu 37 MRs e o número máximo de MR por uma espécie é quatro (observado em *Strix varia*, *Bubo virginianus*, *Aegotheles cristatus*, *Falco columbarius*, e *Passer domesticus*). As Aves Neognathae non-Passeriformes exibiram 21 MRs exclusivos.

Entre os synapisidas (mamíferos vivos), registramos 859 espécies (5 Monotremata, 330 Marsupialia e 524 Placentaria, o que corresponde a 97% das famílias analisadas). Apenas seis MRs foram listados para esse grupo, dois exclusivos (MRs 113 e 114), e dois foi o número máximo de MRs observado em uma única espécie (*Ornithorhynchus anatinus*).

Descobrimos que Amphibia e Amniota compartilham apenas cinco MRs: Amphibia e Lepidosauria compartilham os MRs 21, 115 e 116; Amphibia, Lepidosauria e Archosauria compartilham o MR 32; Anfíbios, Lepidassúria, Testudines e Archosauria compartilham o MR 69. Entre os Amniota, apenas sete modos foram compartilhados: MRs 20, 44 e 74 compartilhados por Lepidosauria e Archosauria, MRs 68, 70 e 104 compartilhados por Archosauria e Synapsida, e RM 76 compartilhado por Lepidosauria, Testudines e Archosauria. Portanto, descobrimos que menos de 8% (variando de 1,3 a 7,5%) dos MRs são compartilhados entre os principais grupos de tetrápodes.

Com relação ao grupo dos peixes, identificamos 52 MRs. Das 4.037 espécies de peixes, 16 espécies são Agnatha, 185 Chondrichthyes e 3.836 Osteichthyes; 39% das famílias estão representadas. Agnatha tem três MRs, Chondrichthyes tem seis e Osteichthyes tem 52 MRs, dos quais 43 são exclusivos. O MR mais comum (RM 1) ocorreu em 41% (1.662 espécies) das espécies analisadas e 41% (136 famílias) das famílias analisadas. Sete MRs são raros em nossa análise, registrados para uma única espécie cada: MRs 11, 17, 20, 34, 36, 41 e 47. Quase 97% das espécies tinham apenas um MR. Por outro lado, o caracídeo *Brycon petrosus* foi a espécie que apresentou mais MRs, cinco diferentes: ele pode depositar os ovos fora da água em locais úmidos nas margens dos rios (MR 20), em rochas nas margens dos rios (MR 25), na água põe ovos no chão e folhas de plantas (MRs 22 e 27), ou ainda põe ovos pelágicos (MR 29).

Os peixes marinhos são representados por mais espécies em nossa análise (62% das espécies estudadas), por outro lado, os peixes de água doce tem mais MRs (73% de MRs mais que as espécies marinhas). A maioria dos peixes ósseos (2.301 espécies; 60% do total) são marinhos que depositam numerosos e pequenos ovos pelágicos. Os peixes ósseos de água doce (1.548; 40% do total), em sua maioria, depositam ovos grandes e não-planctônicos. A maioria dos peixes de água doce (1.313 espécies; 85% do total) desovam em águas lóticas. Neste ambiente, um grande número de espécies põe ovos no fundo, em depressões, em câmaras subaquáticas, em folhas de plantas, ou em rochas (214 espécies; 16% do total). Entre os peixes marinhos, o MR 1 é o modo mais comum, no qual os ovos são fertilizados externamente, têm alta taxa de fertilidade e não há cuidados parentais envolvidos.

Dos 52 MRs encontrados para peixes, os peixes de água doce tiveram um total de 38 MRs. O MR 22 ocorre na maioria (523 de 1.552 espécies; 34%) dos peixes de água doce analisados. Peixes marinhos exibiram 18 MRs, com o MR 1 exibido pela maioria das espécies (1.662 de 2.485 espécies; 67%). Algumas espécies desovam tanto em ambientes marinhos, salobros e de água doce, como exemplificado pelo *Ambassis interrupta*. Entre os peixes de água doce, 85% das espécies (1.317) desovam em água lótica, com 21 MRs, e 15% das espécies (235) desovam em águas lênticas, com 13 MRs.

Dez RMs são compartilhados entre peixes e tetrápodes: MRs 13, 17, 22, 23, 25, 29, 33, 36, 40 e 52. Encontramos uma relação positiva entre a riqueza de MRs e o número de espécies analisadas. Assim, realizamos uma análise de regressão, incluindo os peixes e todos os outros grupos de vertebrados. A maioria estava dentro do intervalo de confiança de 95%, exceto os anfíbios que não apresentaram mais MRs do que o previsto pelo número de espécies analisadas.

Combinando este estudo e a classificação de MRs de tetrápodes, pudemos classificar 158 MRs para o clado Craniata. Agnatha tem 3 MRs, Chondrichthyes 6, Osteichthyes 52, Anura 69, Caudata 16, Gymnophiona 6, Rhynchocephalia 1, Squamata 16, Cryptodira 2, Pleurodira 2, Crocodilia 2, Aves Paleognatha 8, Aves Neognatha Non-Passeriformes 35, Aves Neognatha Passeriformes 10, Monotremata 3, Marsupialia 1 e Eutheria 3 MRs. Sobre o número máximo de grupos do clado Craniata por MRs, o MR 32 foi registrado em Anura, Caudata, Gymnophiona, Squamata, Aves Paleognatha e Aves Neognatha Non-Passeriformes, enquanto MR 116 foi encontrado para Chondrichthyes, Osteichthyes, Anura, Caudata, Gymnophiona e Squamata. Em peixes e anfíbios, 9% dos MRs são semelhantes. O teste de similaridade usando o algoritmo euclidiano foi baseado em uma matriz com 158 MRs e 17 grupos do clado Craniata.

Relação espacial entre a diversidade de anfíbios e modos reprodutivos

O padrão de distribuição da riqueza de espécies é congruente com outros estudos que relataram o mesmo para o Brasil. Entretanto, a diversidade de MRs não seguiu o mesmo padrão da riqueza de espécies, provavelmente pela variável elevação e condições climáticas de diferentes biomas. A umidade pode ou não permitir a presença de um MR específico em determinada área. Portanto, embora tenhamos encontrado um padrão geral relacionando riqueza de espécies e diversidade de MRs, a umidade relativa do ar (ou outra variável climática) pode influenciar no índice relativo de diversidade de modos reprodutivos. Outro fator que pode estar relacionado à diversidade de MRs é a temperatura, pois os biomas do Norte (Amazônia e Caatiga), apesar da chuva constante, pelo menos na Amazônia, apresentaram menor diversidade de MRs que os biomas do Sul (Mata Atlântica, Cerrado, Pantanal e Pampa), para o qual a riqueza de espécies é altamente relacionada à diversidade de MRs. Temperaturas mais altas podem estar relacionadas à maior evaporação, consequentemente aumentando a dessecação, reduzindo os MRs que envolvem estágios terrestres de ovos ou desenvolvimento de girinos.

Nos biomas mais secos, não há tanta estrutura da vegetação, dificultando a existência de espécies que se reproduzem no estrato arbóreo, reduzindo a diversidade de MRs. Por exemplo, os MRs 21, 22, 23, 24, 25, 57, 58, 86, 87, 88, 89 e 95 não seriam possíveis nesses biomas, pois dependem da vegetação. Na Amazônia, embora haja extratificação vegetal, há poucas bromélias, diminuindo os habitats de reprodução das espécies arbóreas. Por outro lado, na Mata Atlântica, os recipientes naturais com água (WFC, sensu CAPÍTULO 1) são difundidos e abundantes. Assim, muitas espécies e MRs tiveram a oportunidade de evoluir nessa floresta. Além disso, o Pantanal é caracterizado por severa sazonalidade climática, com períodos de fortes chuvas e períodos de seca intensa. Esta condição pode restringir a riqueza de espécies de anfíbios locais e a diversidade de MRs. Além disso, a vegetação pantaneira não é tão estratificada como na Mata Atlântica, por exemplo, diminuindo também os possíveis nichos para os anfíbios evoluírem.

Embora tenhamos detectado claramente uma relação entre MRs e riqueza de espécies, não testamos a influência das condições climáticas nessas variáveis e, mais importante, no índice relativo de diversidade de modos reprodutivos. Portanto, futuros estudos podem explorar outros fatores relacionados à diversidade de MRs. Finalmente, como mostrado em nosso estudo, os biomas mais ricos em espécies são aqueles com maior diversidade de comportamentos. Este fato seria outro argumento para a conservação dos ecossistemas megadiversos.

CONSIDERAÇÕES FINAIS

A importância desse trabalho

Com base no sistema de classificação dos MRs de Craniata proposto, futuros estudos poderão testar sinais filogenéticos em MRs. Por exemplo, a maioria das espécies do gênero *Scinax* (Anura) põe ovos em lagoas, assim como espécies do gênero irmão *Ololygon* que são pertencentes ao grupo *S. perspusillus* e que põe ovos em bromélias, enquanto que indivíduos pertencentes as espécies do grupo *O. catharinae* podem por ovos em ambos substratos, bromélias e lagoas.

Aves da família Megapodidae (aves não-passeriformes), pertencentes ao grupo "Brush turkey" põem ovos somente em depressões cobertas por areia, enquanto que aves do grupo "Scrubfowl", põem ovos em tocas, depressões ou em ambos substratos.

Além de testar o sinal filogenético em MRs, também é possível realizar a reconstrução do estado ancestral do MR. Por exemplo, entre as espécies da família Hirundinidae (Passeriformes), algumas andorinhas constroem seus ninhos com lama fixados em paredes de penhascos, outras escavam tocas, enquanto que outras ainda adotam tocas escavadas (modos ancestrais), outras ainda constroem seus ninhos em ocos de árvores, ocos de cupinzeiros ou utilizam ninhos feito por outras espécies de aves em galhos de árvores.

A reconstrução do estado ancestral na biologia reprodutiva foi anteriormente proposta, mas foi considerado apenas a oviparidade e viviparidade entre os vários gêneros de Squamata. Análises mais profundas de grupos com uma grande diversidade de MRs seriam casos interessantes para futuros estudos evolutivos.

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Anexo

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INFORMAÇÃO

A Comissão de Ética no Uso de Animais da UNICAMP - CEUA/UNICAMP - esclarece que não há necessidade de submeter o projeto intitulado "**Revisão dos modos reprodutivos de Craniata**", de responsabilidade do Prof. Dr. Luís Felipe Toledo (orientador) e do pós-graduando Carlos Henrique Luz Nunes de Almeida, para análise desta Comissão.

Justifica-se por tratar-se de revisão de literatura, não havendo manipulação de animais *in vivo*.

Campinas, 22 de agosto de 2017.

Wagner José Fávaro

Prof. Dr. WAGNER JOSÉ FÁVARO
Presidente da CEUA/UNICAMP

Declaração

As cópias de artigos de minha autoria ou de minha co-autoria, já publicados ou submetidos para publicação em revistas científicas ou anais de congressos sujeitos a arbitragem, que constam da minha Dissertação/Tese de Mestrado/Doutorado, intitulada **Revisão de modos reprodutivos em Craniata**, não infringem os dispositivos da Lei n.° 9.610/98, nem o direito autoral de qualquer editora.

Campinas, 19 de setembro de 2019

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