



A revised classification of the amphibian reproductive modes

CARLOS HENRIQUE LUZ NUNES-DE-ALMEIDA^{1,2},
CÉLIO FERNANDO BATISTA HADDAD³ & LUÍS FELIPE TOLEDO¹

¹Laboratório de História Natural de Anfíbios Brasileiros (LaHNAB), Departamento de Biologia Animal, Instituto de Biologia, Unicamp, Caixa Postal 6109, 13083-970, Campinas, São Paulo, Brazil

²Programa de Pós-Graduação em Biologia Animal, Instituto de Biologia, Unicamp, Campinas, São Paulo, Brazil

³Departamento de Biodiversidade e Centro de Aquicultura (CAUNESP), Instituto de Biociências, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil

Corresponding author: LUÍS FELIPE TOLEDO, e-mail: toledosapo@gmail.com

Manuscript received: 22 February 2021

Accepted: 25 June 2021 by STEFAN LÖTTERS

Abstract. Amphibian reproductive modes (RMs) have been extensively described and applied to amphibian biology studies. However, due to new behavioural observations and past system inconsistencies we found it necessary to review the current classification and redefine the sets of characters which define amphibian RMs. We suggest the use of 11 characters that include phases from egg to early development (including or not including larval stages) and we do not include behavioural aspects that are in general hard to identify, such as parental care, except those related to feeding and incubation. Based on 2,171 amphibian species (roughly a fourth of the species known), we built a dichotomous tree with 74 different possible RMs for amphibians – almost twice the number of the previous classification categories. This system could possibly be applied to other vertebrates as well and therefore facilitate comparisons across different taxa.

Key words. Anura, Caudata, Gymnophiona, reproduction, behaviour, reproductive strategies, breeding biology.

Introduction

Terrestrial vertebrates or tetrapods currently include more than 32,000 extant species that have diverged from an ancestral tetrapod that abandoned an obligate aquatic lifestyle and subsequently diversified in terrestrial environments (INGER 1957, LONG & GORDON 2004). During this evolutionary transition, tetrapods also diversified their reproduction, specifically their reproductive modes (RMs) (LONG & GORDON 2004), making breeding biology one of the most studied aspects of vertebrates' natural history. Such research themes 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 concept of 'reproductive mode' only first appeared in a study of the reproductive biology of fishes in the mid 20th century (BREDER JR. & ROSEN 1966). Based on that, SALTHER & DUELLMAN (1973) defined the RM as a combination of traits that includes oviposition site, ovum and clutch characteristics, rate and duration of development, stage and size of hatchlings, and type of parental care, if any. Hence, RM 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 between vertebrate clades, because researchers naturally focus on the reproductive traits present within their clades of study (COLLIAS 1964, SHINE 1983, BRONSON 1989, HADDAD & PRADO 2005a). Currently, there is no standard classification system that applies to all groups of tetrapods. It is in fact only for amphibians that a standard classification system is commonly accepted and used, which describes how and where eggs are fertilized and where embryos and larvae live. If this amphibian classification system were extended to other tetrapod groups, it would advance in the comprehension of the diversity and evolution of RMs in a broader (phylogenetic or comparative) sense. However, before extending this concept to other vertebrates, a detailed re-evaluation of the current system must take place.

RMs have been well characterized in amphibians, perhaps because of their diversity and complexity. BOULENGER (1886) proposed a classification of RMs (without of course using the term RM; see above) 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 reproduc-

tive traits, the resolution of RM categories increased by including additional traits. SALTHER (1969) classified and described three RMs for salamanders (Caudata). Just a few years later, SALTHER & DUELLMAN (1973) added ovum and clutch characteristics, rate and duration of larval development, stage at hatching, and presence/absence of parental care. This review was pivotal because it promptly stimulated interest and resulted in a considerable increase in studies of amphibian RMs and their specific components (SALTHER & MECHAM 1974, LAMOTTE & LESCURE 1977, MC-DIARMID 1978, WAKE 1982) – a development that could also happen with other tetrapods if a similar system were available. 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 (2005a, 2005b) reviewed anuran RMs and increased the list to include 39 RMs, including three rearrangements of known modes and seven new modes described for anurans of the Brazilian Atlantic forest. 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, MALAGOLI et al. 2021).

These classifications are useful because they allow comparative and evolutionary studies. 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 oviposition coupled with the parental care of covering eggs with mud. In addition, these classifications help comparative evolutionary studies on the evolutionary sequence of RMs and the selective mechanisms that lead to their diversification (GOMEZ-MESTRE et al. 2012, PEREIRA et al. 2015, ZAMUDIO et al. 2016). Finally, they can also be used to classify species into ecological guilds in conservation-orientated studies (e.g., BECKER et al. 2007, SANTORO & BRANDÃO 2014, SHABRANI & DAS 2015).

In spite of being useful to various fundamental research topics, some quantitative parameters that were included in the original definition of RM (SALTHER & DUELLMAN 1973), like time of development of larvae, female body size, egg size and clutch size, have almost never been used in later studies (for an exception see GAITONDE & GIRI 2014). In addition, there are some inconsistencies in the use of RM characters. For example, in the list of RMs by HADDAD & PRADO (2005a), 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 impractical, as this information is lacking for many species, difficult to obtain, and in some cases facultative and variable between individuals (MARTINS 1993, WELLS 2007, VÁGI et al. 2020). Therefore, based on the current amphibian classification, we are proposing the exclusion of female size, egg size, clutch size, and time of larval development (as previously included by SALTHER &

DUELLMAN 1973), avoiding the use of parental care, but the inclusion of a trait that has only recently been applied to anurans, i.e., the presence/absence of nest construction (ZAMUDIO et al. 2016), which is easily obtained information and clearly befits modern phylogenies (e.g., FAIVOVICH et al. 2010a).

To improve and facilitate future ecological studies, the possible consequences of such a new system has to be discussed. In addition, our proposed reclassification of RMs can be remodelled (it is not static) and in future can be extended to other animal groups, enabling broader, especially ecological, comparisons. Based on the proposed classification system, future studies will be able to test for phylogenetic signals in RMs. For example, most species of the genus *Scinax* (Anura, treefrogs) lay their eggs in ponds. Alternatively, the species of the *S. perpusillus* clade (FAIVOVICH et al. 2010b) lay their eggs in bromeliad phytothelma, while individuals belonging to species in the *S. catharinae* clade may lay their eggs both in bromeliads and ponds (TOLEDO et al. 2012).

Besides testing for phylogenetic signals in RMs, it is also possible to reconstruct RMs’ ancestral states. This has been done with increasing frequency in recent times, for example, considering the type of development (direct or indirect) in amphibians (PORTIK & BLACKBURN 2016, CAMPOS et al. 2019), reproduction type (oviparity or viviparity) in squamates (WATSON et al. 2014), or nest types in birds (FANG et al. 2018). Most studies tend to analyze binary state characters, though, and few have tried to examine the whole set of traits related to RMs in such reconstructions (e.g., PORTIK & BLACKBURN 2016). Deeper analyses of groups with a large diversity of RMs would make for interesting cases in future evolutionary studies.

Thus, the aim of our natural history-based study is to develop a simpler and more cohesive definition of the RMs of amphibians and to provide a basis for a future classification of other vertebrate lineages.

Survey methodology

Set of characters of reproductive modes

After reviewing the literature on amphibian reproductive biology, we selected the most common set of characters traditionally used for the classification of amphibian RMs, incorporated newly assessed traits (such as nest construction) to improve the classification, and defined their categories and subcategories hierarchically from eggs to offspring. We thereby redefine the concept of the RM as a combination of 11 reproductive traits: (1) reproduction type, (2) oviposition macrohabitat, (3) spawning type, (4) oviposition substrate, (5) egg-surrounding medium, (6) nest construction, (7) oviposition microhabitat, (8) embryonic development, (9) embryonic nutrition, (10) larval and newborn nutrition, and (11) place of larval development. These traits are mostly physical, and we did not consider purely behavioural aspects, such as courtship, amplexus/copulation, and parental care, or temporal

aspects, such as egg or embryo development time (as previously suggested). With these traits we built a (mostly) dichotomous RM tree. The different traits and their states are presented below and defined in greater detail in Supplementary document S1; we provided some representative examples to promptly relate a trait to a known species or amphibian clade.

(1) Reproduction type

a. Oviparity – Embryos in the oviduct provided with yolk. After oviposition, the embryonic development continues outside the female body, within extra-embryonic membranes (egg) that may include gelatinous capsules.

b. Viviparity – No oviposition takes place. The female gives birth to larvae, as in the anuran *Limnonectes larvaepartus* (ISKANDAR et al. 2014) or to a miniature edition of the adults, with the omission of free-living larvae. These offspring pre-develop in their mother's body and are born once their yolk reserves are exhausted, and there is no other form of nourishment from the mother (e.g., anurans of the genus *Nectophrynoides*: WAKE 2015). The term ovoviviparity is here included in the viviparity category, as was suggested by BLACKBURN (1992, 1999, 2000), because the terms lecithotrophy and matrotrophy, used in conjunction with the reproduction mode viviparity, obstruct a sensible use of the term ovoviviparity.

(2) Oviposition macrohabitat

a. Environment – Eggs are deposited in the environment, as in species of the Brachycephaloidea clade, and sometimes nests, as in *Micrixalus saxicola* (GURURAJA 2010).

b. Animal – Eggs develop in or on the body of one of the parents, as in *Gastrotheca* spp. and *Rheobatrachus silus* (DUELLMAN 2015, TYLER & CARTER 1981) (Fig. 1A).

(3) Spawning type

a. Froth (as defined by ALTIG & MCDIARMID 2007) – Eggs are deposited in one of two types of froth nest: foam and bubble nests:

i. Foam nests in amphibians are produced by the parents executing beating motions with their limbs on the mucus excreted from the female's oviducts, so that it is mixed with air (e.g., in the families Leptodactylidae and Rhacophoridae). Foam nests can be built on the water surface, on the ground, in burrows, on leaves, or on branches (CRUMP 2009) (Figs 1B–C).

ii. Bubble nests are produced by the female frog effecting jumping motions in the process of spawning, trapping air bubbles in the mucus excreted from the female's oviducts (e.g., *Scinax rizibilis*: HADDAD et al. 1990). Alternatively, both anuran parents may expel bubbles from their nares under the aquatic spawn so that these become trapped in the mucus (e.g., *Chiasmocleis leucosticta*: HADDAD & HÖDL 1997) (Figs 1D–E).

Froth nests are a specialized feature for amphibians that could be considered constructed nests, but according to SIMON and PACHECO (2005), they are not. See further explanations under “Nest construction”.

b. Non-froth – Eggs are not deposited in froth nests, and spawning takes place without the production of foam or bubbles (Fig. 1F).

(4) Oviposition substrate

a. Aquatic – Eggs are deposited in the water, as is observed in most amphibians (e.g., *Ambystoma gracile*, *Itapotihyla langsdorffii*, *Scinax angrensis*, *Rhinella icterica*, *Proceratophrys appendiculata*, *Taricha tosa*) (PETRANKA 1998, HARTMANN et al. 2010) (Fig. 2).

b. Non-aquatic – Eggs are deposited on the ground, rocks, or bushes as reported, for example, from *Eurycea quadridigitata* and *Limnonectes palavanensis* (PETRANKA 1998, SHABRANI & DAS 2015).

c. In/on animal – Eggs stay in different parts of the body of the parents. In amphibians, the eggs may be incubated in the oviduct, as in *Nectophrynoides* spp. and *Mertensiella* spp., or in the dorsal tissue, as in *Pipa* spp., or in specialized anatomical structures, as in the dorsal pouch of *Gastrotheca* spp. (LUTZ 1947, WELLS 2007, DUELLMAN 2015).

(5) Medium surrounding the eggs

a. Lentic – Eggs are deposited in still water, such as lakes, ponds, or swamps, as has been reported for many amphibians (HADDAD & PRADO 2005a).

b. Lotic – Eggs are deposited in flowing waters, such as rivulets, creeks, streams, or rivers, as is observed in many amphibians (e.g., all hyloidid and many centrolenid and ranid species: MCDIARMID & ALTIG 1999, HADDAD & PRADO 2005a).

c. Terrestrial – Eggs are deposited in a terrestrial environment, as has been reported for several amphibians (e.g., LIMA et al. 2013).

d. Non-oviductal – Eggs are embedded for development in the dorsum or dorsal pouches, such as in the family Hemiphractidae (MCDIARMID & ALTIG 1999, DUELLMAN 2015).

e. Oviductal/uterine – Eggs develop in a specialized portion of the oviduct, being nourished by yolk, by tissue of the oviduct, or other nutritious substances secreted by the female, as has been reported from *Dermophis mexicanus* and *Nimbaphrynoides occidentalis* (WAKE & DICKIE 1998, WELLS 2007, LODÉ 2012, WAKE 2015).

(6) Nest construction

We hereby define a nest as any spatially delimited place selected by amphibians to deposit eggs, which may or may not include the parents digging, cleaning, lining, or building.

a. Constructed nest – A nest created by all sorts of environmental modification, except froth nests (see above).

b. Adopted nest – A nest used but not constructed by an amphibian.

c. No nest – Eggs are not deposited in a nest.

(7) Oviposition microhabitat

a. Floating – Eggs are deposited on the surface of lentic water, in froth, or in a non-froth nest, as has been observed

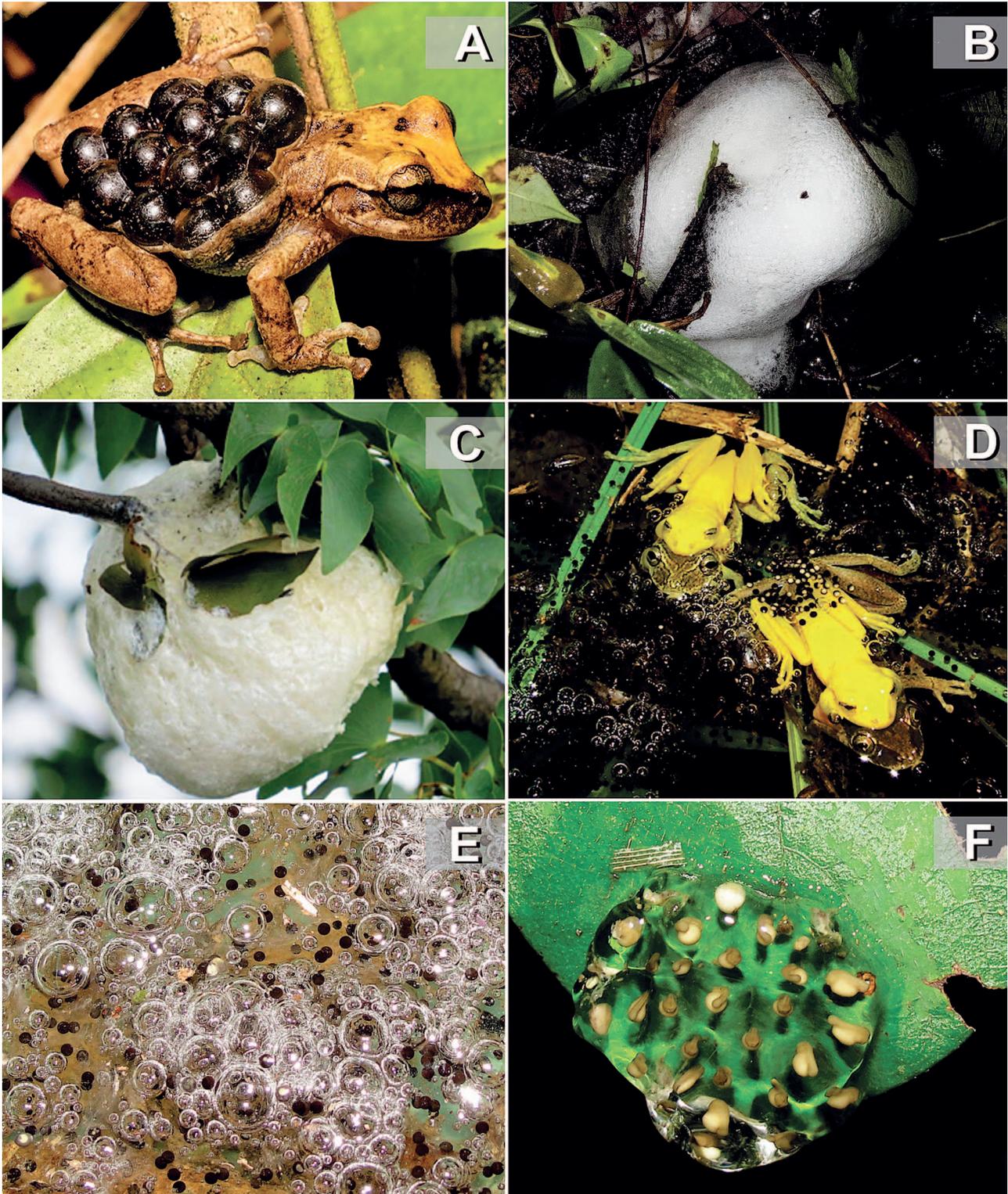


Figure 1. Diversity of anuran oviposition: *Fritziana goeldii* with eggs on its back (A), *Physalaemus olfersii* foam nest on water, whipped up with the legs by the male (B), *Chiromantis xerampelina* foam nest on a tree branch, produced by the parents moving their legs in the mucus excreted by the female (C), *Scinax rizibilis* bubble nest, made by the female effecting jumps while spawning (D), *Chiasmocleis leucosticta* bubble nest made by releasing air bubbles from the parents' nostrils (E), and a plant leaf nest of *Dendropsophus haddadi* (F).

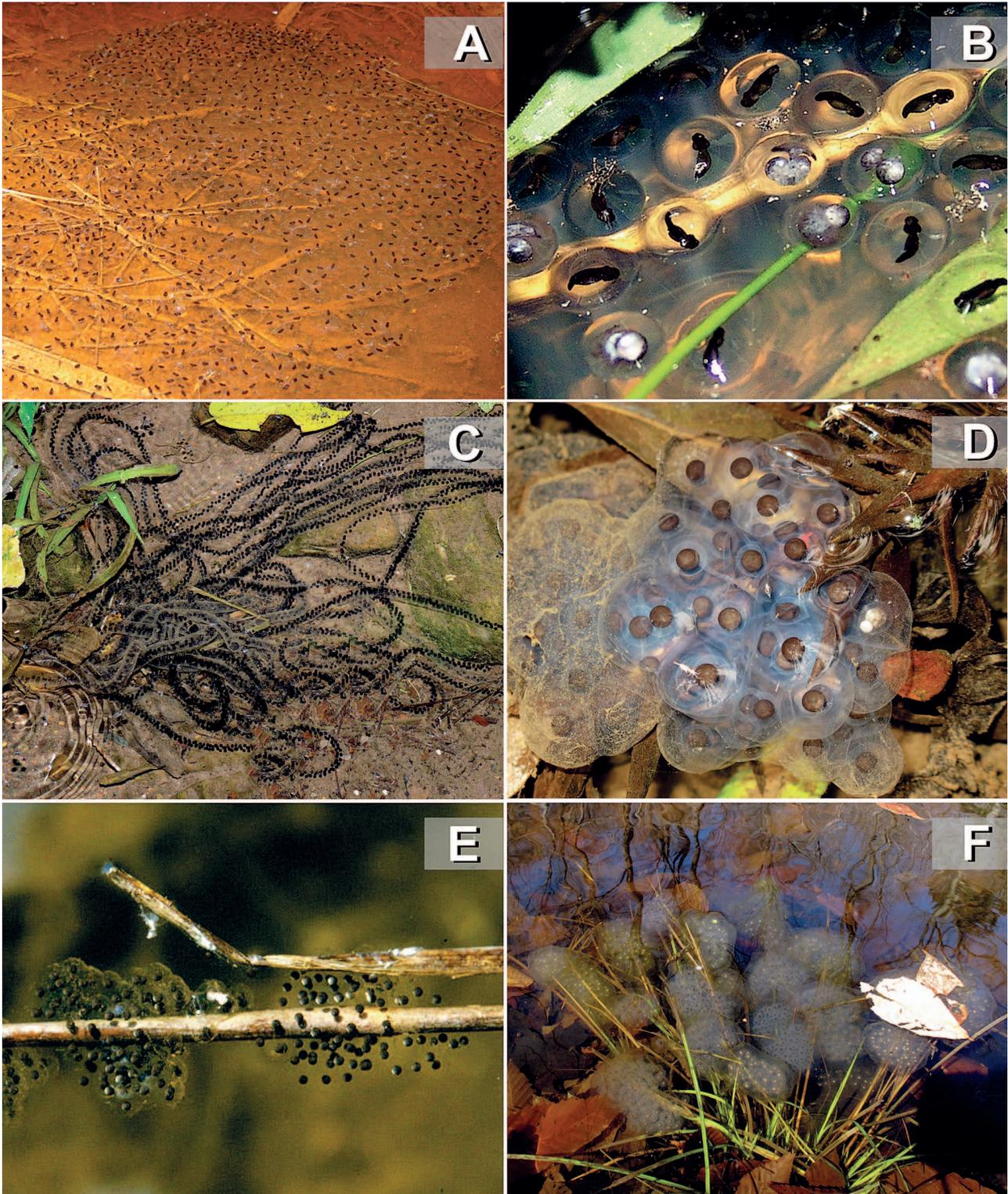


Figure 2. The most general reproductive mode (RM) proposed in previous classifications of amphibians (eggs and exotrophic tadpoles in still water bodies) has been split up here into three new RMs: RM 1 represented by *Boana crepitans* (A) and *Elachistocleis cesarii* (B), RM 2 represented by *Rhinella icterica* (C) and *Boana marginata* (D), RM 3 represented by *Boana prasina* (E), and *Ambystoma maculatum* (F).

in several amphibians (*Boana crepitans*, *Dendropsophus nanus*, *Leptodactylus labyrinthicus*: HADDAD et al. 2013, NASCIMENTO et al. 2015) (Figs 2A–B).

b. Ground – Eggs are deposited on soil, as has been reported for several amphibians (e.g., *Platymantis* spp. and *Stumpffia roseifemoralis*: WELLS 2007).

c. Subaquatic ground (SGD) – Eggs are deposited on the bottom of lentic or lotic water bodies, as has been reported for some amphibians (e.g., *Rhinella diptycha* and *Scinax fuscomarginatus*: HADDAD et al. 2013) (Figs 2C–D).

d. Depression – Eggs are deposited in a depression in the ground, excavated or otherwise, and covered or not. This has occasionally been referred to as a “basin” in the literature. This oviposition microhabitat is observed in amphibians such as *Amphiuma means* and *Boana faber* (PETRANKA 1998, HADDAD & PRADO 2005a).

e. Burrow – Eggs are deposited in a subterranean burrow dug or not by the parents, as is observed in *Xenorhina* spp. and *Microcaecilia dermatophaga* (WELLS 2007, WILKINSON et al. 2013).

f. Subaquatic chamber (SCH) – Eggs are deposited in a submerged chamber in a water body, as has been observed in some amphibians (*Dicamptodon ensatus*, *Hylodes* spp.: PETRANKA 1998, HADDAD & PRADO 2005a).

g. Insect mound (IMO): Terrestrial or arboreal mounds made by termites or ants – Eggs are usually deposited in holes dug by the parental anurans, as has been reported for *Lithodytes lineatus* (SCHLÜTER & REGÖS 1981, SCHLÜTER et al. 2009).

h. Rock – Eggs are laid on or underneath rocks as has been reported for some amphibians (e.g., *Desmognathus* spp. and *Cycloramphus* spp.: PETRANKA 1998, HADDAD & PRADO 2005a).

i. Wall – Eggs are laid on rock cliffs or in the sidewalls of ravines, as is observed in a few anurans, such as *Thoropa* spp. (HADDAD & PRADO 2005a).

j. Plant leaf – Eggs are deposited on the upper or lower side of leaves of trees, shrubs, or blades of grass, with these being either rolled up or folded together (constructed nest) or not. This strategy is observed, for example, in anurans such as *Phyllomedusa* spp. and *Rhacophorus* spp. (HADDAD & PRADO 2005a, MEEGASKUMBURA et al. 2015) (Fig. 1E).

k. Plant branch – Eggs are deposited on branches, twigs, or the trunks of trees and stems of shrubs, as is observed in *Chiromantis xerampelina* (WELLS 2007).

l. Plant root – Eggs are deposited on or between tree roots, as is observed in some amphibians (e.g., some species of the genus *Cycloramphus*: WELLS 2007).

m. Subaquatic plant branch or root (SPBR) – Eggs are deposited on or around subaquatic plant branches or roots, as is observed in *Melanophryniscus montevidensis* (C. BARDIER, unpubl. data), *Boana prasina*, and *Sphaenorhynchus caramaschii* (Figs 2E–F).

n. Water-filled reservoir (WFR) – Eggs are deposited in plant structures that accumulate water (phytotelmata), such as bromeliads axils or rosettes, as has been noted in *Scinax perpusillus* (MUSCAT et al. 2019), other plants such as *Paepalanthus* spp. and *Eriocaulon ligulatum* by *Melano-*

phryniscus alipioi and *M. biancae* (LANGONE et al. 2008, NADALINE et al. 2019), *Crinum* sp. used by *Anodonthyla* spp., *Cophyla* spp., *Platypelis* spp., and *Plethodontohyla* spp. (GLAW & VENCES 2007, ANDREONE et al. 2010), *Musa* spp. used by *Leptopelis uluguruensis* (BARBOUR & LOVERIDGE 1928), *Pandanus* spp. used by *Pelophryne brevipes* (MALKMUS & DEHLING 2008), pitcher plants like *Nepenthes ampullaria* and *N. bicalcarata* used by *Microhyla* spp. and *Philautus kerangae* (MALKMUS & DEHLING 2008), and the fruit husks of *Bertholletia excelsa* lying on the ground used by *Adelphobates castaneoticus* and *Rhinella castaneotica* (CALDWELL 1993). WFR also includes holes in branches or tree trunks that are used by *Metaphrynella sundana* (MALKMUS & DEHLING 2008), and holes in logs used by *Chaperina fusca* (MALKMUS & DEHLING 2008). Also included in this category are snail shells (Gastropoda) containing water are used by *Phrynobatrachus guineensis* and *Stumpffia achillei* (WELLS 2007, RAKOTOARISON et al. 2017, Fig. 3).

o. Reservoir without water (RWW): tree holes and bamboo internodes without water – Eggs are deposited in natural cavities in trees or logs or those constructed by birds and other animals (HARRISON 1998). This strategy is observed, for example, in *Eleutherodactylus hedricki* (WELLS 2007), and in the case of using the dry internodes of bamboo, by *Raorchestes chalazodes* (SESHADRI et al. 2015).

(8) Embryonic development

a. Indirect – The development with a larval stage, as is observed in most amphibians with eggs from which larvae hatch.

b. Direct – The development without a larval stage, as is observed in species in which embryos run the full course of their development within eggs and hatch as fully formed metamorphs, such as in the Brachycephaloidea clade (PADIAL et al. 2014).

(9) Embryonic nutrition

a. Lecithotrophic – Embryos obtain energy exclusively from vitellogenic yolk reserves (POUGH et al. 2009). We applied this category to direct-developing amphibians such as *Brachycephalus* spp. (POMBAL 1999).

b. Matrotrophic – Embryos that obtain energy not only from vitellogenic yolk reserves, but supplementarily from nourishment derived from the mother (POUGH et al. 2009). We apply this category to some direct-developing amphibians, like *Pipa pipa* and *Pipa carvalhoi* (WELLS 2007; FERNANDES et al. 2011), *Nimbaphrynoides occidentalis* and *Salamandra atra* (SANDBERGER-LOUA et al. 2017). We also include in this category cases of oophagy and embryophagy (= adelphophagy; i.e., intra-oviductal cannibalism), as these sources of energy were also supplemented by the mother, as is the case in *Salamandra atra* (besides direct matrotrophy and lecithotrophy) (WAKE 2015) and *Salamandra salamandra* (BUCKLEY et al. 2017).

(10) Larval and newborn nutrition

a. Endotrophic – Larvae obtain their developmental energy from vitellogenic yolk (MCDIARMID & ALTIG 1999). This

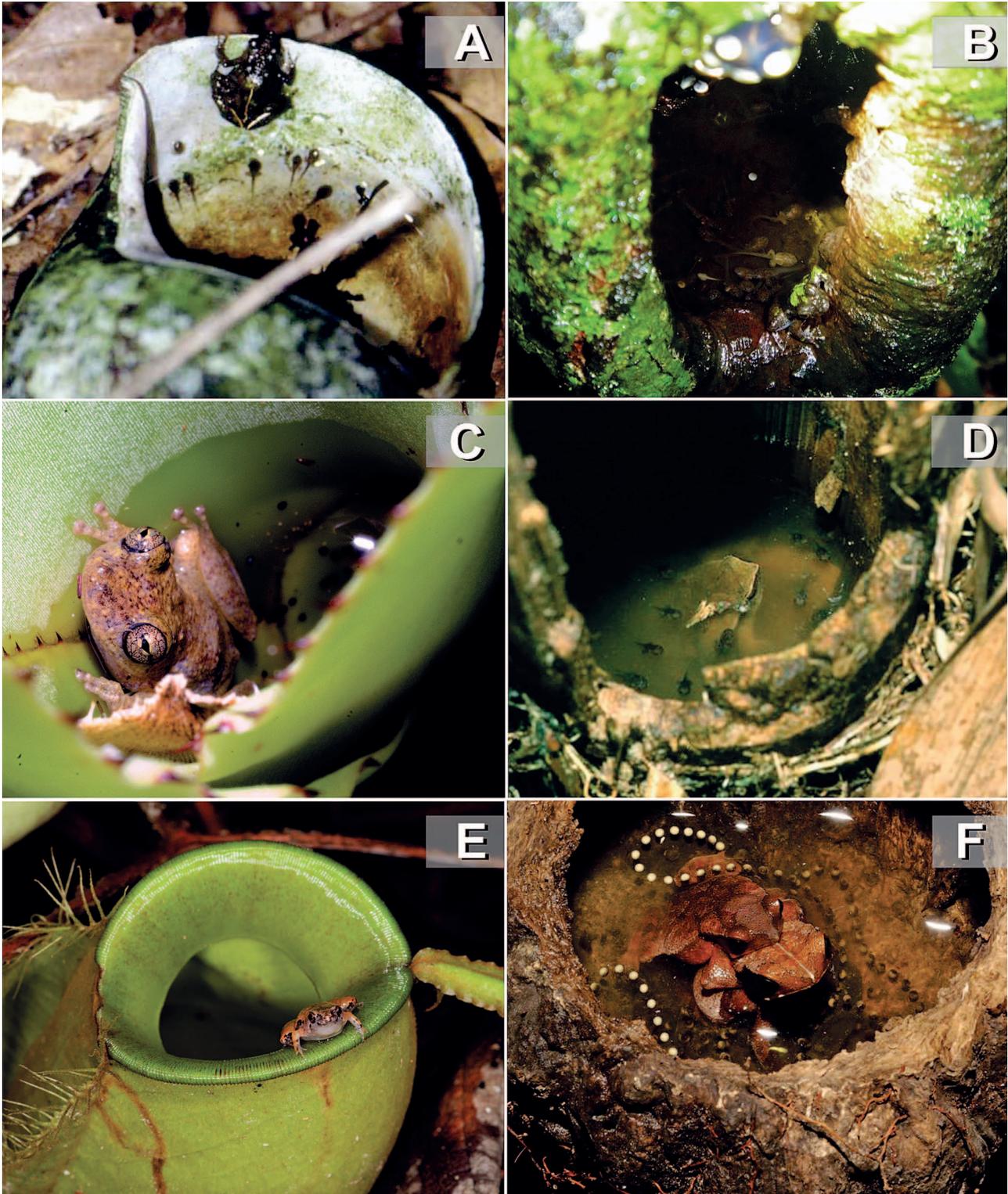


Figure 3. Anuran eggs laid on water-filled reservoirs: *Phrynobatrachus guineensis* tadpoles hatched from eggs laid inside the water accumulated in a snail shell (A), and eggs attached to a tree hole where tadpoles will develop (B), eggs of *Scinax alcatraz* in the water accumulated in a bromeliad (C), *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), amplexed pair of *Rhinella magnussoni* on a fruit capsule of the Brazil nut *Bertholletia excelsa*, where eggs are laid (F).

Table 1. Amphibian reproductive modes (RMs) summarised: Total number of known species based on FROST (2021), 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.

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	8295	26%	80%	2171	74	4	74
Anura	7315	28%	80%	2012	71	4	56
Caudata	766	15%	100%	109	16	3	1
Gymnophiona	214	23%	60%	49	7	1	1

category applies only to indirectly developing amphibians, such as *Eupsophus emiliopugini* and *Allobates sumtuosus* (NUÑEZ & ÚBEDA 2009, SIMÕES & LIMA 2012). Exotrophic larvae may also absorb energy from vitellogenic yolk in the very beginning of their development, but endotrophic larvae do not benefit from subsequent parental feeding.

b. Exotrophic – Larvae or newborn amphibians obtain energy by oral consumption of food after hatching, after their vitellogenic yolk has run out (MCDIARMID & ALTIG 1999). We apply this category only to indirectly developing amphibians, such as *Rhinella proboscidea* and *Nymphargus lasgralarias* (MENIN et al. 2006, GUAYASAMIN et al. 2014) and directly developing amphibians that have specialized feeding strategies just after birth, such as in the caecilians *Microcaecilia dermatophaga* and *Siphonops annulatus* (WILKINSON et al. 2008). Exotrophic larvae and newborns may or may not benefit from parental feeding.

i. With parental feeding (W/PF) – Applied to when tadpoles feed on trophic eggs, as in *Leptodactylus labyrinthicus*, *Oophaga* spp., and *Pipa carvalhoi* (PRADO et al. 2005, GRANT et al. 2006, WELLS 2007), or newborns that feed on parents' skin, as in the caecilians *Microcaecilia dermatophaga* and *Siphonops annulatus* (WILKINSON et al. 2008).

ii. Without parental feeding (Wo/PF) – Larvae or newborns do not depend on their parents, or other adults, for feeding.

(11) Place of larval development

a. Lentic – Larvae develop in still water, such as lakes, ponds, or swamps, as has been reported for the many anurans, such as *Heterixalus madagascariensis* and *Vandijkophrynus amatolicus* (GLAW & VENCES 2007, WELLS 2007), including fossorial larvae that develop in the bottom sand, gravel or mud, as is the case in *Scaphiophryne gottlebei* and *Stauroides parvus* (MERCURIO & ANDREONE 2006, PREININGER et al. 2012). The water in WFRs is also lentic and may be the place of tadpole development of several other species, such as in *Fritziana ohausi* (HADDAD et al. 2013).

b. Lotic – Larvae develop in flowing waters, such as rivulets, streams or rivers, as has been reported for *Ansonia torrentis*, and including larvae that develop in the bottom sand, gravel or mud, such as in *Vitreorana eurygnatha*, *Micrixalus herrei*, and *Stauroides guttatus* (HEYER 1985, HAAS & DAS 2012, SENEVIRATHNE et al. 2016). Semi-terrestrial larvae, like those of the genera *Thoropa* and *Cycloramphus*

(WELLS 2007, NUNES-DE-ALMEIDA et al. 2016), were also included here, as these tadpoles live in the interface zone between lotic and terrestrial habitats.

c. Terrestrial – Larvae develop in a terrestrial environment, as is the case in *Allobates tapajos* and *Zachaenus parvulus* (LUTZ 1943, SIMÕES et al. 2013).

d. Internal, in or on animal – This applies to anurans whose eggs hatch and complete their development into froglets inside the male's hip pouch, as in *Assa darlingtoni* (WELLS 2007), those whose eggs are swallowed and hatch and complete the development into froglets in their mother's stomach, as in *Rheobatrachus silus* (MCDIARMID & ALTIG 1999), and those whose eggs hatch and develop inside the male's vocal sac, as in *Rhinoderma* spp. (MCDIARMID & ALTIG 1999). Also, marsupial frogs fit this category. A marsupium is a body pouch in which offspring develop (POUGH et al. 2009) and has been reported for hemiphractid anurans. 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). In species such as *Fritziana* spp., in spite of the eggs being kept in pouches, the tadpoles develop in lentic waters of WFRs. Therefore, they are not classified as belonging to this category. Finally, this strategy also applies to amphibians that give birth to tadpoles or juveniles, as is known from *Limnonectes larvaepartus* and *Nectophrynoides* spp. (LEE et al. 2006, ISKANDAR et al. 2014).

Results

Based on our review that covered 2,170 species, representing 26% of the total known extant amphibian species in the world and including 80% of the families, we recognized 74 RMs for amphibians (Fig. 4, Supplementary Table S1, Supplementary document S2). Anurans (2,012 species sampled) exhibited 71 RMs (out of which 56 were exclusive), salamanders (109 species sampled) exhibited 16 RMs, with two exclusive RMs among amphibians (RM 9 and RM 35), and caecilians (50 species sampled) exhibited 7 RMs, with one exclusive to this order (Table 1). Some RMs were more commonly reported, like RMs 16 (represented in 569 anuran, 5 salamander and 1 caecilian species), 27 (represented in 384 anuran, 29 salamander and 11 caecilian species), and

Amphibian reproductive modes

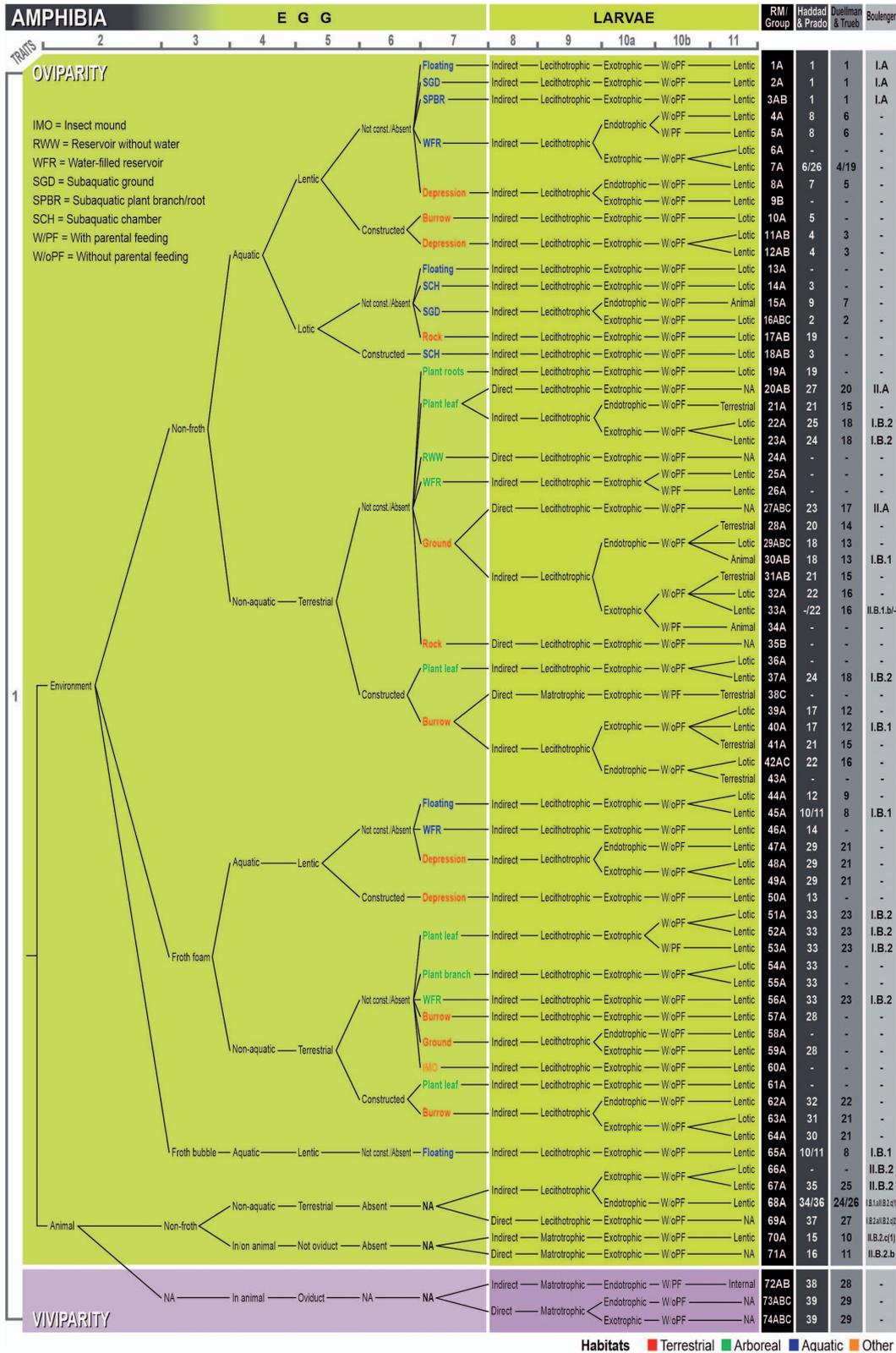


Figure 4. Dichotomous reproductive character and state key of Amphibia with 74 different reproductive modes. Letters indicate groups: Anura (A), Caudata (B), and Gymnophiona (C). Numbers in a top row and on lower left indicate the 11 trait categories. IMO = Insect mound, FLV = Floating vegetation, RWW = Reservoir without water, SGD = Subaquatic ground, SPBR = Subaquatic plant branch/root, SCH = Subaquatic chamber, WFR = Water-filled reservoir.

42 (represented in 122 anuran and 1 caecilian species). On the other hand, the more traditionally known RMs, RMs 1, 2 and 3, were reported for less than 50 amphibian species (Supplementary Table S1).

The treefrog *Rhacophorus viridis* exhibited four different RMs, representing the maximum number of modes known for one amphibian species. In the Caudata, four plethodontid species, *Desmognathus carolinensis*, *D. ocoee*, *D. orestes*, and *Hemidactylum scutatum*, exhibited three different RMs. Among the Gymnophiona, all species investigated shared only one RM (Tables 1, S1). In the RM tree for Amphibia (Fig. S4) it is also possible to compare the current 74 RMs with previous classifications (BOULENGER 1886, DUELLMAN & TRUEB 1986, HADDAD & PRADO 2005a).

Discussion

Our review roughly doubles the number of RMs previously reported for amphibians. With the newly proposed classification and redefinition of RMs, we will be able to better describe RM diversity for amphibians and effect more standardized comparisons of RMs across amphibians. One aspect that we have highlight here is that the current RMs 1, 2 and 3, previously considered RM 1 (DUELLMAN & TRUEB 1986, HADDAD & PRADO 2005a), are not the most common RMs. The assumption that these modes were ancestral relative to the others was probably based on its supposed higher frequency in nature (DUELLMAN & TRUEB 1986, HADDAD & PRADO 2005a), however they may in fact not be the most common RMs among anurans on a global scale. An expansion of our dataset would be interesting and would possibly provide information to this assumption, and maybe the evolution of amphibian RMs was different from what we thought it to be so far.

On top of our classification for amphibians, we propose further that a single classification system covering all tetrapods be applied to an even broader range of taxa for comparisons, and to characterize assemblages and investigate whether and how the community diversity of RMs is correlated with other traits such as size-fecundity and developmental relationships (CRUMP 1974). As amphibians are both terrestrial and aquatic, which increases the possibilities for oviposition and larval development sites, it is possible that they are the vertebrate class with the greatest RM richness. Therefore, it would be interesting to compare amphibian RMs with those represented in fishes, which is a group with exceptional species richness and is regarded as a group with an outstanding number of RMs (BALON 1975, 1981), which could about match the number of amphibian RMs (GOMEZ-MESTRE et al. 2012), but a standardized RM classification system has never been applied to compare these two groups. On the other hand, amniotes must avoid aquatic sites for reproduction. This basic eco-physiological difference between amniotes and amphibians would limit their possible number of RMs. Therefore, it is likely that amniotes have a much-reduced number of RMs if the classification system we are proposing here were applied to those taxa.

Future experimental and modelling studies may help to elucidate causes and consequences of RM diversification, and our proposed system will facilitate this task. For example, the previous amphibian RM 1 (eggs deposited in lentic waters) is now divided into three different RMs, depending on whether the eggs incubate floating (RM 1), subaquatic on the ground (RM 2), or subaquatic attached to plant structures (RM 3). This differentiation might prove useful for future studies, as the proposed new classification system allows for specific comparisons between amphibians and aquatic animals such as fishes or even invertebrates. For example, fish RMs differ if they deposit their eggs on subaquatic plants (RM 3) or if the eggs are left floating (RM 1). This differentiation was not included in the previous RM 1, but has now been resolved. On the other hand, this subdivision also revealed that we lack sufficient information for many amphibian species, hindering their classification, in part as a consequence of the simpler classification methods applied in the past. For example, for some species that have been classified as making use of RM 1, we were unable to assign a current RM as authors did not specify their oviposition microhabitats. Therefore, based on our proposed method we also expect greater resolution in the description of RMs in future studies.

Anurans, especially those that produce froth nests, exhibit RM plasticity; specifically, these species vary in their choices of 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 deposits its eggs in froth nests, uses shallow pools, water accumulated in the axils of bromeliads, or even uses wet soil (HADDAD & POMBAL 1998, HADDAD & PRADO 2005). Other species (of the same family – i.e., Leptodactylidae) also whip up their froth nests on the ground or in terrestrial bromeliads, displaying similar behavioural plasticity (TOLEDO et al. 2012). Additionally, amphibians may even exhibit facultative exotrophy, such as that observed in *Fritziana goeldii* (WEYGOLDT & CARVALHO-E-SILVA 1991). Such plasticity may be adaptive, providing advantages in cases of rapid environmental changes. For example, if one species is able to deposit its eggs both in bromeliads and directly in ponds (e.g., TOLEDO et al. 2012), and bromeliads are locally extinct, but ponds are still present, the population will be able to resort to that site. Therefore, we advocate that RM plasticity is adaptive in, and of immense value to, amphibians, especially in the current scenario of accelerated global climatic changes (LOARIE et al. 2009).

While several expressions of variation are observed within the same clade and strong ecological constraints act in the evolution of RMs, other groups appear to be quite conservative. For example, almost all species within the Brachycephaloidea (> 1,100 anuran species) have the same RM (RM 27: eggs on ground, larvae 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 deposited in burrows (*Eleutherodactylus aporostegus*; SCHWARTZ 1965, HEDGES et al. 2008), and viviparity (*Eleutherodactylus jasperi*; WAKE 1978). This is only one example of the clear influence of phylogeny on RMs. On the other hand, other factors (besides evolutionary history) may influence RM diversity in other groups, leading to the evolution of convergent RMs. For example, froth nests evolved independently and multiple times within amphibian families. Therefore, those interested in testing homology and convergence within amphibians (or other animals) will have to delimit the characters or states differently – not as we presented here. Despite that, our study can serve as a baseline from which deeper evolutionary forays can be developed (e.g., GOMEZ-MESTRE et al. 2012). For example, researchers could collect data from all species with froth nests and then refine the traits and states they want to test for their target species.

Based on our proposed classification system, we noted that some possibly alternative RMs have apparently not yet been described. 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 deposited in aquatic environments indicates that it is an adaptation to terrestrial environments; it probably indicates an apomorphic condition to indirect development. On the other hand, other as yet undescribed RMs seem plausible; for example, a froth nest on a rock wall, or eggs with direct development without a constructed nest in an insect mound. A range of other options could be promptly envisaged. Therefore, we expect that future natural history observations will increase the number of classifiable reproductive modes.

Conclusions

Our review updates the current amphibian reproductive mode classification system and can support further advances in both amphibian and vertebrate breeding biology. We do not propose this system to be static or applied solely as is. Analyses of different taxa may benefit by the inclusion or exclusion of additional traits or character states. For example, for mammals, if the inclusion of the diapause trait is necessary, the system could be adapted, or, if dividing RMs based on oviposition sites proves inappropriate, that trait could be ignored. Hence, we hope this system will be well used, tested, modified, amplified and, most importantly, evolves and promotes the increase of information on animal breeding biology.

Acknowledgements

We thank ANAT BELASEN for reviewing the manuscript, and MIN ZHU, CHRISTOPHER ROSE, KELLY R. ZAMUDIO, CYNTHIA P. A. PRADO, EMYGDIO LEITE DE ARAUJO MONTEIRO-FILHO, WESLEY RODRIGUES SILVA, and SELMA MARIA DE ALMEIDA-SANTOS for

providing valuable comments on earlier versions of the same. We thank EDÉLCIO MUSCAT (Fig. 1A), SUSAN CHRISTMAN (Fig. 1C), DIEGO SANTANA (Fig. 1D), ISAIAS SANTOS (Fig. 1E), DANIEL LOEBMANN (Figs 2B, D), KAROLINE CERON (Fig. 2C), MARK-OLIVER RÖDEL (Fig. 3A), LEGRAND (Fig. 3B), VÍCTOR FÁVARO AUGUSTO (Fig. 3C), JEET SUKUMARAN (Fig. 3D), BJØRN OLESEN (Fig. 3E), LUIS FERNANDO STORTI (Fig. 3F) for permission to use their photos. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brazil (CAPES) – Finance Code 001, CHLNA. The São Paulo Research Foundation (FAPESP) provided grants to LFT (processes #2008/50325-5, #2011/51694-7, #2014/23388-7, #2019/18335-5) and to CFBH (processes #2013/50741-7 and 2014/50342-8). The National Council of Technological and Scientific Development (CNPq) provided research fellowships to LFT (#302589/2013-9 and #302834/2020-6) and CFBH (#302518/2013-4).

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Supplementary data

The following data are available online:

Supplementary Table S1. Amphibian species classified with the new reproductive modes.

Supplementary document S1. Definitions of applied character or its states.

Supplementary document S2. Description of reproductive modes of amphibians.

Supplementary document S3. References for Supplementary Table S1.

Supplementary document S1 – Definitions of applied character or its states

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 with parental feeding 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.

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 the amphibian, 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 individuals. 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, after the 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.

Froth – Related to nest type. There are three types of froth nests: Froth foam and froth bubble. Froth nests are a specialized feature for amphibians that could be considered constructed nests, but according Simon and Pacheco (2005), they are not. See below “Nest construction”.

Froth bubble – 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 jelly of eggs and the air bubbles become trapped in the jelly.

Froth foam – Foam nests are produced by amphibians. The 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.

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 oviduct of amphibians. In amphibians, the eggs may also be incubated in the dorsum and legs of adults.

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 made by termites or ants.

Internal – Applied to offspring development. This is only applied to indirect or with parental feeding 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.

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

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 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.

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

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.

Nest – Adapted from Simon and Pacheco (2005), nest is any delimited 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.

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 or bubbles.

Not constructed nest – Delimited nest not constructed by amphibians.

Not oviduct – This term is related to eggs surrounding medium. Eggs are embedded in dorsum or dorsal pouches of amphibians.

Offspring development – For amphibians the terms direct and indirect development are recognizable discrete categories, referring to the absence or presence of larval stage, respectively.

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.

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.

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.

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.

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. It can also be related to offspring development. Offspring develop on terrestrial environment.

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).

Wall – Term applied to the microhabitat where eggs were laid. In this case, eggs are laid on rocky cliffs and ravines.

Water-filled reservoir (WFR) – Term applied to the microhabitat where eggs were laid. WFR are phytotelmata, holes in branches, trunks and logs, including bamboo internodes, and also includes empty snail shells (Gastropoda) containing water.

Without parental feeding (W/oPF) – In this case, the young do not depend on its parents or other adults for feeding.

With parental feeding (W/PF) – Applied to those species in which the young relies on their parents for feeding.

Supplementary document S2 – Description of reproductive modes of amphibians

1) Oviparity

1.1.) Anamniotic egg

1.1.1) Eggs in environment

Mode 1 – Nest absent, non-froth floating eggs laid in lentic water. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 2 – Nest absent, non-froth subaquatic eggs laid on bed of lentic water. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 3 – Nest absent, non-froth subaquatic eggs laid on plants, branches, or roots in lentic water. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known for anurans and salamanders.

Mode 4 – Non-froth eggs laid in water-filled container. Offspring with indirect development, lecithotrophic nutrition, endotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 5 – Non-froth eggs laid in water-filled container. Offspring with indirect development, lecithotrophic nutrition, endotrophic, with non-milk parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 6 – Non-froth eggs laid in water-filled container. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lotic water. Known only for anurans.

Mode 7 – Non-froth eggs laid in water-filled container. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 8 – Non-froth eggs laid in depression. Offspring with indirect development, lecithotrophic nutrition, endotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 9 – Non-froth eggs laid in depression. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 10 – Non-froth eggs laid in constructed burrow. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lotic water. Known only for anurans.

Mode 11 – Non-froth eggs laid in constructed depression. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lotic water. Known only for anurans and salamanders.

Mode 12 – Non-froth eggs laid in constructed depression. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known for anurans and salamanders.

Mode 13 – Nest absent, non-froth floating eggs laid in lotic water. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lotic water. Known only for anurans.

Mode 14 – Non-froth eggs laid in subaquatic chamber in lotic water. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lotic water. Known only for anurans.

Mode 15 – Nest absent, non-froth subaquatic eggs laid on bed of lotic water. Offspring with indirect development, lecithotrophic nutrition, endotrophic, without parental feeding, and larvae develop in/on parents. Known only for anurans.

Mode 16 – Nest absent, non-froth subaquatic eggs laid on bed of lotic water. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lotic water. Known only for amphibians.

Mode 17 – Non-froth eggs laid on rock nest in lotic water. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lotic water. Known for anurans and salamanders.

Mode 18 – Non-froth eggs laid in constructed subaquatic chamber nest in lotic water. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lotic water. Known for anurans and salamanders.

Mode 19 – Terrestrial non-froth eggs laid in plant root. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lotic water. Known only for anurans.

Mode 20 – Terrestrial non-froth eggs laid on plant leaf. Offspring with direct development, lecithotrophic nutrition, exotrophic, and without parental feeding. Known for anurans and salamanders.

Mode 21 – Terrestrial non-froth eggs laid on plant leaf. Offspring with indirect development, lecithotrophic nutrition, endotrophic, without parental feeding, and larvae with terrestrial development. Known only for anurans.

Mode 22 – Terrestrial non-froth eggs laid on plant leaf. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lotic water. Known only for anurans.

Mode 23 – Terrestrial non-froth eggs laid on plant leaf. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 24 – Terrestrial non-froth eggs laid in bamboo. Offspring with direct development, lecithotrophic nutrition, exotrophic, and without parental feeding. Known only for anurans.

Mode 25 – Terrestrial non-froth eggs laid in water-filled container. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding and larvae develop in lentic water. Known only for anurans.

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

Mode 27 – Nest absent, terrestrial non-froth eggs laid on ground. Offspring with direct development, lecithotrophic nutrition, exotrophic and without parental feeding. Known only for amphibians.

Mode 28 – Nest absent, terrestrial non-froth eggs laid on ground. Offspring with indirect development, lecithotrophic nutrition, endotrophic, without parental feeding, and terrestrial development. Known only for anurans.

Mode 29 – Nest absent, terrestrial non-froth eggs laid on ground. Offspring with indirect development, lecithotrophic nutrition, endotrophic, without parental feeding, and larvae develop in lotic water. Known only for amphibians.

Mode 30 – Nest absent, terrestrial non-froth eggs laid on ground. Offspring with indirect development, lecithotrophic nutrition, endotrophic, without parental feeding, and larvae develop in/on parents. Known for anurans and salamanders.

Mode 31 – Nest absent, terrestrial non-froth eggs laid on ground. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and terrestrial development larvae. Known for anurans and salamanders.

Mode 32 – Nest absent, terrestrial non-froth eggs laid on ground. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lotic water. Known only for anurans.

Mode 33 – Nest absent, terrestrial non-froth eggs laid on ground. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 34 – Nest absent, terrestrial non-froth eggs laid on ground. Offspring with indirect development, lecithotrophic nutrition, exotrophic, with non-milk parental feeding, and larvae develop in/on parents. Known only for anurans.

Mode 35 – Terrestrial non-froth eggs laid on rock. Offspring with direct development, lecithotrophic nutrition, exotrophic, and without parental feeding. Known only for salamanders.

Mode 36 – Terrestrial non-froth eggs laid in constructed plant leaf. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding and larvae develop in lotic water. Known only for anurans.

Mode 37 – Terrestrial non-froth eggs laid in constructed plant leaf. Offspring with indirect development, matrotrophic nutrition, exotrophic, with parental feeding and larvae develop in lentic water. Known only for anurans.

Mode 38 – Terrestrial non-froth eggs laid in constructed burrow. Offspring with direct development, lecithotrophic nutrition, exotrophic, with parental feeding and terrestrial development larvae. Known only for caecilians.

Mode 39 – Terrestrial non-froth eggs laid in constructed burrow. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding and larvae develop in lotic water. Known only for anurans.

Mode 40 – Terrestrial non-froth eggs laid in constructed burrow. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding and larvae develop in lentic water. Known only for anurans.

Mode 41 – Terrestrial non-froth eggs laid in constructed burrow. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding and terrestrial development larvae. Known only for anurans.

Mode 42 – Terrestrial non-froth eggs laid in constructed burrow. Offspring with indirect development, lecithotrophic nutrition, endotrophic, without parental feeding and larvae develop in lotic water. Known only for anurans and caecilians.

Mode 43 – Terrestrial non-froth eggs laid in constructed burrow. Offspring with indirect development, lecithotrophic nutrition, endotrophic, without parental feeding and terrestrial development larvae. Known only for anurans.

Mode 44 – Nest absent, froth floating eggs laid in lentic water. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lotic water. Known only for anurans.

Mode 45 – Nest absent, froth floating eggs laid in lentic water. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 46 – Froth eggs laid in water-filled container. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 47 – Froth eggs laid in depression. Offspring with indirect development, lecithotrophic nutrition, endotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 48 – Froth eggs laid in depression. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lotic water. Known only for anurans.

Mode 49 – Froth eggs laid in depression. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 50 – Froth eggs laid in constructed depression. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 51 – Terrestrial froth eggs laid on plant leaf. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lotic water. Known only for anurans.

Mode 52 – Terrestrial froth eggs laid on plant leaf. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 53 – Terrestrial froth eggs laid on plant leaf. Offspring with indirect development, lecithotrophic nutrition, exotrophic, with non-milk parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 54 – Terrestrial froth eggs laid on plant branch. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lotic water. Known only for anurans.

Mode 55 – Terrestrial froth eggs laid on plant branch. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 56 – Terrestrial froth eggs laid in water-filled container. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 57 – Terrestrial froth eggs laid in burrow. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 58 – Nest absent, terrestrial froth eggs laid on ground. Offspring with indirect development, lecithotrophic nutrition, endotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 59 – Nest absent, terrestrial froth eggs laid on ground. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 60 – Terrestrial froth eggs laid in insect mound. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 61 – Terrestrial froth eggs laid in constructed plant leaf. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 62 – Terrestrial froth eggs laid in constructed burrow. Offspring with indirect development, lecithotrophic nutrition, endotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 63 – Terrestrial froth eggs laid in constructed burrow. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lotic water. Known only for anurans.

Mode 64 – Terrestrial froth eggs laid in constructed burrow. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 65 – Nest absent, froth bubble floating eggs laid in lentic water. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

1) Oviparity

1.1.) Anamniotic egg (Amphibia)

1.1.2) Eggs kept in/on animal

Mode 66 – Terrestrial non-froth eggs, nest absent. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lotic water. Known only for anurans.

Mode 67 – Terrestrial non-froth eggs, nest absent. Offspring with indirect development, lecithotrophic nutrition, exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 68 – Terrestrial non-froth eggs, nest absent. Offspring with indirect development, lecithotrophic nutrition, endotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 69 – Terrestrial non-froth eggs, nest absent. Offspring with direct development, lecithotrophic nutrition, exotrophic, and without parental feeding. Known only for anurans.

Mode 70 – Non-froth eggs kept in/on the animal, nest absent. Offspring with indirect development, matrotrophic nutrition (besides lecithotrophic), exotrophic, without parental feeding, and larvae develop in lentic water. Known only for anurans.

Mode 71 – Non-froth eggs kept in/on the animal, nest absent. Offspring with direct development, matrotrophic nutrition (besides lecithotrophic, may include oophagy and adelphophagy), exotrophic, and without parental feeding. Known only for anurans.

2) Viviparity

Mode 72 – Offspring with indirect development, matrotrophic nutrition, endotrophic, with parental feeding, and internal development. Known for anurans and caudatans.

Mode 73 – Offspring with direct development, matrotrophic nutrition, endotrophic, and without parental feeding. Known for caudatans and caecilians.

Mode 74 – Offspring with direct development, matrotrophic nutrition, exotrophic, and without parental feeding. Known for caudatans and caecilians.

Supplementary document S3 - References for Table S1

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