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Forum

Chytridiomycosis, Amphibian Extinctions, and Lessons for the Prevention of Future Panzootics

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Abstract: The human-mediated transport of infected amphibians is the most plausible driver for the intercontinental spread of chytridiomycosis, a recently emerged infectious disease responsible for amphibian population declines and extinctions on multiple continents. Chytridiomycosis is now globally ubiquitous, and it cannot be eradicated from affected sites. Its rapid spread both within and between continents provides a valuable lesson on preventing future panzootics and subsequent erosion of biodiversity, not only of amphibians, but of a wide array of taxa: the continued inter-continental trade and transport of animals will inevitably lead to the spread of novel pathogens, followed by numerous extinctions. Herein, we define and discuss three levels of amphibian disease management: (1) post-exposure prophylactic measures that are curative in nature and applicable only in a small number of situations; (2) pre-exposure prophylactic measures that reduce disease threat in the short-term; and (3) preventive measures that remove the threat altogether. Preventive measures include a virtually complete ban on all unnecessary long-distance trade and transport of amphibians, and are the only method of protecting amphibians from disease-induced declines and extinctions over the long-term. Legislation to prevent the emergence of new diseases is urgently required to protect global amphibian biodiversity.

Keywords: chytrid, wildlife disease, amphibian declines, extinction, *Batrachochytrium dendrobatidis*, pet trade

The human-mediated transport of infected amphibians is the most plausible driver for the intercontinental spread of chytridiomycosis (Mazzoni et al., 2003; Weldon et al., 2004; Garner et al., 2006; Fisher and Garner, 2007; Skerratt et al., 2007), a recently emerged infectious disease responsible for amphibian population declines and extinctions on multiple continents (Berger et al., 1998; Bosch et al., 2001; Lips et al., 2006; Rachowicz et al., 2006). The chytrid fungus *Batrachochytrium dendrobatidis* (causative agent of chytridiomycosis) currently infects at least 287 amphibian species and occurs in at least 37 countries spanning six continents (Figure 1; Supporting Online Information Tables 1 and 2). It is widespread throughout Australia, Europe, Africa, and the Americas (Garner et al., 2005; Ouellet et al., 2005; Lips et al., 2006; Goldberg et al., 2007; Kriger et al., 2007; Pearl et al., 2007). *Batrachochytrium dendrobatidis* has been detected as far north as Alaska and as far south as Tasmania, as high as 5348 m a.s.l. (Seimon et al., 2007) and as low as nearly sea level (Kriger et al., 2007). The fungus was detected across the altitudinal gradient in all five studies that have examined its altitudinal distribution (Retallick et al., 2004; McDonald

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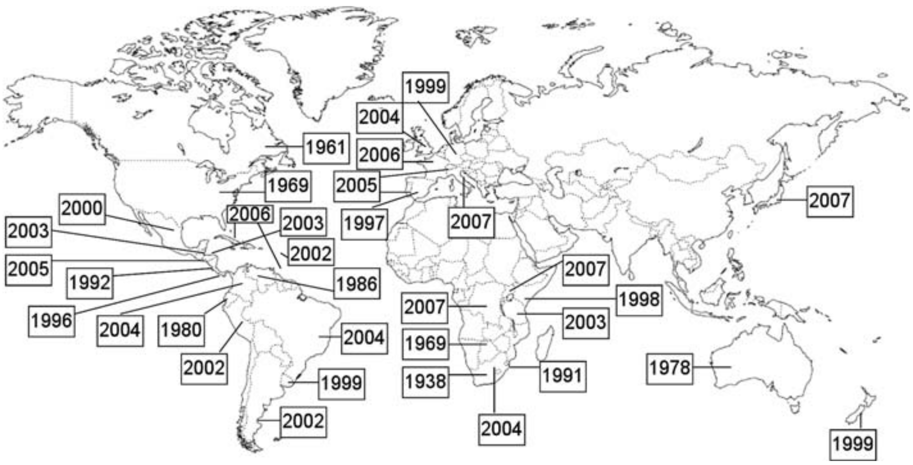

Figure 1. Global distribution of *B. dendrobatidis*. Years represent the dates of first known occurrence in the 37 infected countries.

et al., 2005; Woodhams and Alford, 2005; Puschendorf et al., 2006; Kriger and Hero, 2008), and bioclimatic modeling predicts it could occupy a significant portion of both the eastern and western hemispheres (Ron, 2005).

The apparent ubiquity of *B. dendrobatidis*, combined with the rapidity with which the fungus spreads within continents (Lips et al., 2006, 2008) and the high number of opportunities for its human-mediated transport between continents (Fisher and Garner, 2007), suggests that, barring drastic and immediate amphibian trade restrictions, *B. dendrobatidis* is likely to invade any currently unoccupied areas of its bioclimatic envelope. As approximately one-third of the world's 6350 amphibian species are already threatened with extinction (Stuart et al., 2004), preventing the further spread of chytridiomycosis and other infectious diseases represents one of the scientific community's most urgent challenges.

Herein, we define and discuss three levels of amphibian disease management: (1) post-exposure prophylactic measures, which include curing infected captive individuals, eradicating disease from infected wild populations, and facilitating evolved resistance; (2) pre-exposure prophylactic measures, such as routine diagnostic testing and quarantine of apparently healthy individuals destined for translocation, which are intended to reduce the likelihood of disease transfer; and (3) preventive measures that remove the threat of disease altogether, such as banning the translocation of amphibians.

Post-exposure Prophylactic Measures

Post-exposure disease prophylaxis is currently a viable option for only a very small proportion of the world's amphibians, namely those in captivity whose diseases can be cured by heat treatments or chemicals (Parker et al., 2002; Woodhams et al., 2003). There are no published accounts of studies that have successfully facilitated amphibians' evolved resistance to diseases, and it can be assumed that no such protocols will be imminently developed that can protect the world's amphibian populations in the short-term. This is due to: (1) the slow reproductive rate, and therefore evolutionary adaptivity of most amphibians; (2) our current lack of knowledge regarding amphibian husbandry (Lee et al., 2006); and (3) potential negative effects associated with the captive-breeding of amphibians over multiple generations (Kraaijeveld-Smit et al., 2006).

It is not currently feasible to eradicate *B. dendrobatidis* from infected sites (DEH, 2005), and it is unlikely that suitable methods will be developed prior to the fungus' initial epidemic wave wreaking havoc on any remaining naive and susceptible amphibian populations. Even if suitable eradication techniques were developed, the rapidity with which *B. dendrobatidis* causes population declines at sites in which it is newly introduced (Lips et al., 2006; Rachowicz et al., 2006) suggests that only a small proportion of the world's susceptible amphibians could be protected. The vast majority of the world's amphibians live in tropical countries (Duellman, 1999), where there are few herpetologists available to conduct regular disease monitoring, and even the best available disease detection techniques have a time-lag prior to *B. dendrobatidis* being detectable in infected amphibians (Hyatt et al., 2007). Thus, in most cases, the majority of the damage would be done before researchers would know to implement eradication protocols. In these tropical countries, most population declines due to chytridiomycosis are predicted to occur in moist areas (Ron, 2005; Kriger et al., 2007), where both amphibians and *B. dendrobatidis* are likely to persist away from water bodies, making eradication even more difficult. Further, eradication methods would likely provide only a short-term solution, as the fungus would inevitably recolonize any areas from which it had been temporarily extirpated.

The direct management of *B. dendrobatidis* in infected amphibian populations is thus futile in all but a few isolated cases, such as with endangered populations living on small islands that have only a few aquatic breeding sites (e.g., *Leiopelma hamiltoni* or *Alytes muletensis*). For such populations, the currently available management option would be to manually catch and then cure every infected individual, and repeat this process either indefinitely or until a suitable eradication method is developed. Thus, while continued research into eradication methods is important and may be necessary for protecting some critically endangered species, current (and quite possibly future) management options for the vast majority of the world's infected amphibian populations are restricted to the mitigation of all other threats to the populations (i.e., habitat destruction, invasive species, over-harvesting, loss of genetic variation, climate change, and pollutants).

As post-exposure prophylactic measures are unlikely to protect more than a small proportion of the world's amphibians, the optimal method of directly managing *B. dendrobatidis* is to prevent it from reaching new isolated locations where transport of proposed disease vectors is limited (e.g., Madagascar and Pacific Islands), and to prevent the transfer of new strains to currently affected sites, so as to facilitate amphibian populations' natural adaptation to the fungus (Berger et al., 2005; Kriger and Hero, 2006). Protecting remaining uninfected amphibian populations from *B. dendrobatidis* (and perhaps more importantly future diseases) will require drastic and immediate restrictions on the domestic and global trade and transport of amphibians, on a scale unlike any that have been implemented in the past. Appropriate restrictions would affect the pet, bait, food, zoo, and laboratory trades, all of which have been implicated as driving the global spread of chytridiomycosis (Aplin and Kirkpatrick, 1999; Pessier et al., 1999; Parker et al., 2002; Garner et al., 2006).

Pre-exposure Prophylactic Measures

The goal of a pre-exposure prophylactic measure is to reduce the likelihood of disease transfer in scenarios where infection is likely to be encountered. Such measures include quarantines and subsequent diagnostic tests to confirm infection-free status, batch-testing shipments, certifying farms as disease-free, and other similar bio-security precautions. These actions are necessary when translocations must occur, as is the case for zoos and laboratories, both of which can contribute to disease spread (Pessier et al., 1999; Parker et al., 2002), yet perform important conservation services such as captive-breeding and scientific research. As zoos and laboratories are part of the scientific community and are thus amenable to laws that benefit amphibian conservation, a reduction in trade and the enactment of appropriate quarantine and testing procedures by these sectors could likely be implemented with relative ease (Young et al., 2007). To further reduce the threat of disease transfer, captive-breeding should take place in the amphibian species' native geographical region whenever possible, and laboratories should conduct their research on either native species, or locally bred exotics.

The amphibian food trade is important in many developing countries where amphibians serve as a traditional source of protein. In these locations, amphibians tend to be harvested and consumed locally, and thus are unlikely to be significant sources of disease transfer. Such countries therefore have little reason to restrict domestic sales of amphibian species, assuming they are harvested in a sustainable manner. Conversely, most developed countries have no shortage of alternative food sources, and the amphibians they eat are seldom harvested locally. France, for instance, banned commercial frog farming in 1977 and now relies primarily on imports from southeast Asia. In such scenarios, countries should be required to either restrict their imports to dead amphibians, or to submit all imported amphibians to both quarantine periods and comprehensive disease testing and prophylactic treatment, the costs of which would be paid for by the importers and consumers. Similar restrictions should be placed on the domestic food trade if the species in question is being transported outside of its natural range.

We wish to make it clear, however, that it only takes one diseased individual to initiate an epizootic. Pre-exposure prophylactic measures are an important improvement over current laws, but are unlikely to protect biodiversity in the long-term. Diseased individuals would inevitably pass undetected, as existent diagnostic tests are seldom perfect, and many diseases have yet to be discovered. Thus, any unnecessary long-distance transfer of live amphibians, including those in a strictly regulated food trade, should eventually be phased out.

Preventive Measures

Preventing disease spread into naive amphibian populations can only be accomplished by removing the source of the problem: the translocation of infected amphibians. Unlike zoos and laboratories, whose conservation services render the translocation of amphibians an occasional necessity, the amphibian pet and bait trades are for the large part disposable, that is, they are unnecessary, serving little benefit to society. Their nearly complete dismantling would benefit amphibian populations, not only by eliminating a primary source of disease transfer, but also by simultaneously reducing the over-harvesting of wild amphibian populations, which is largely unregulated in many parts of the world (Li and Wilcove, 2005; Schlaepfer et al., 2005). At a minimum, these trades should be restricted to local sales of captive-bred individuals.

Though restricting the pet, bait, and food trades may have some initial negative economic impact, these actions may save perhaps hundreds of species from extinction, and thus will significantly reduce conservation and remediation costs (currently estimated at US$82 million per year; Gascon et al., 2007) in the long run. The free ecosystem services and benefits to human health that amphibians provide (Tyler et al., 2007) give further economic incentive that compensates for any initial economic losses. Australia successfully banned virtually all amphibian sales outside of zoo and research settings, yet remains one of the wealthiest countries in the world. There is little reason to believe that other nations would suffer undue losses were they to follow Australia's example.

Conclusions

In terms of its impact on biodiversity, chytridiomycosis may be the worst disease in recorded history (Skerratt et al., 2007). That the disease cannot be managed at affected sites should serve as a valuable lesson for the prevention of future panzootics: the continued inter-continental trade and transport of animals (be they amphibians or other taxa) will inevitably lead to the spread of novel pathogens, followed by numerous extinctions. To protect global amphibian biodiversity, we must now focus on preventing future panzootics. The immediate implementation and enforcement of appropriate biosecurity measures, including a virtually complete ban on all unnecessary long-distance trade and transport of live amphibians, should be the highest priority for the scientific and legislative communities.

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Table 1 (Supporting Online Information). The 287 amphibian species and 25 families reported infected with *Batrachochytrium dendrobatidis*.

Family/*Species*	Reference
Ambystomatidae	
Ambystoma altamirani	(Frias-Alvarez et al. 2008)
Ambystoma granulosum	(Frias-Alvarez et al. 2008)
Ambystoma californiense	(Padgett-Flohr and Longcore 2005)
Ambystoma macrodactylum	(USGS 2003)
Ambystoma maculatum	(Ouellet et al. 2005)
Ambystoma mexicanum	(Berger et al. 1999)
Ambystoma rivulare	(Frias-Alvarez et al. 2008)
Ambystoma tigrinum	(Davidson et al. 2003)
Ambystoma velasci	(Frias-Alvarez et al. 2008)
Amphignathodontidae	
Gastrotheca cornuta	(Lips et al. 2006)
Gastrotheca pseustes	(Berger et al. 1999)
Amphiumidae	
Amphiuma tridactylum	(Speare and Berger 2004)
Aromobatidae	(Lampo et al. 2006)

Mannophryne cordilleriana	
Mannophryne olmonae	(Alemu et al. 2008)
Arthroleptidae	
Leptopelis christyi	(Goldberg et al. 2007)
Leptopelis kivuensis	(Goldberg et al. 2007)
Bombinatoridae	
Bombina pachypus	(Stagni et al. 2004)
Bufonidae	
Atelopus bomolochos	(Ron et al. 2003)
Atelopus carbonerensis	(La Marca et al. 2005)
Atelopus chiriquiensis	(Berger et al. 1998)
Atelopus cruciger	(Bonaccorso et al. 2003)
Atelopus mittermeieri	(Ruiz and Rueda-Almonacid 2008)
Atelopus mucubajiensis	(La Marca et al. 2005)
Atelopus pulcher	(La Marca et al. 2005)
Atelopus sorianoi	(La Marca et al. 2005)
Atelopus spumarius spumarius	(La Marca et al. 2005)
Atelopus varius	(Berger et al. 1998)
Atelopus zeteki spp. 11	(La Marca et al. 2005)
Atelopus zeteki spp. 13	(La Marca et al. 2005)

Atelopus zeteki spp. 9	(La Marca et al. 2005)
Bufo americanus	(Ouellet et al. 2005)
Bufo baxteri	(Green et al. 2002)
Bufo boreas	(Green et al. 2002)
Bufo calamita	(Bosch and Martinez-Solano 2006)
Bufo canorus	(Green and Kagarise Sherman 2001)
Bufo funereus	(Goldberg et al. 2007)
Bufo guttatus	(Diaz et al. 2007)
Bufo haematiticus	(Berger et al. 1998)
Bufo longinasus dunni	(Diaz et al. 2007)
Bufo marinus	(Berger et al. 2004)
Bufo microscaphus californicus	(Nichols 2003)
Bufo robinsoni	(Speare and Berger 2005)
Bufo viridis	(Nichols et al. 1998)
Nectophrynoides asperginis	(Weldon and du Preez 2004)

Centrolenidae

Centrolene ilex	(Lips et al. 2006)
Centrolene prosoblepon	(Lips et al. 2006)
Cochranella albomaculata	(Lips et al. 2006)
Cochranella euknemos	(Lips et al. 2006)
Cochranella prosoblepon	(Berger et al. 1998)
Hyalinobatrachium colymbiphyllum	(Lips et al. 2006)

Dendrobatidae	(Lips et al. 2006)
Colostethus nubicola	(Lips et al. 2006)
Colostethus olfersioides	(Carnaval et al. 2006)
Colostethus pratti	(Lips et al. 2006)
Colostethus talamancae	(Lips et al. 2006)
Colosthethus panamensis	(Lips et al. 2006)
Dendrobates auratus	(Pessier et al. 1999)
Dendrobates azureus	(Pessier et al. 1999)
Dendrobates galactonotus	(Speare and Berger 2004)
Dendrobates granulosus	(Speare and Berger 2004)
Dendrobates pumilo	(Mutschmann et al. 2000)
Dendrobates terribilis	(Speare and Berger 2004)
Dendrobates tinctorius	(Mutschmann et al. 2000)
Phyllobates bicolor	(Mutschmann et al. 2000)
Phyllobates lugubris	(Mutschmann et al. 2000)
Phyllobates vittatus	(Mutschmann et al. 2000)
Discoglossidae	
Alytes muletensis	(Fisher and Garner 2007)
Alytes obstetricans	(Bosch et al. 2001)
Heleophrynidae	

Heleophryne purcelli	(Weldon 2005)
Heleophryne regis	(Weldon 2005)

Hylidae

Acris crepitans	(Pessier et al. 1999)
Agalychnis callidryas	(Lips et al. 2006)
Agalychnis moreletii	(Felger et al. 2007)
Aplastodiscus callipygius	(Toledo et al. 2006a)
Aplastodiscus cf. leucopygius	(Toledo et al. 2006a)
Bokermannohyla circumdata	(Toledo et al. 2006a)
Bokermannohyla gouveai	(Carnaval et al. 2006)
Bokermannohyla hylax	(Toledo et al. 2006a)
Cyclorana platycephala	(Berger et al. 2004)
Exerodonta melanomma	(Frias-Alvarez et al. 2008)
Hyla arenicolor	(Bradley et al. 2002)
Hyla euphorbiacea	(Frias-Alvarez et al. 2008)
Hyla microcephala	(Lips et al. 2006)
Hyla psarolaima	(Ron et al. 2003)
Hyla punctata	(Speare and Berger 2004)
Hyla vasta	(Ron 2005)
Hyla versicolor	(Ouellet et al. 2005)
Hylomantis lemur	(Lips et al. 2006)
Hyloscirtus bogotensis	(Ruiz and Rueda-Almonacid 2008)

Hyloscirtus colymba	(Lips et al. 2006)
Hyloscirtus palmeri	(Lips et al. 2006)
Hypsiboas albopunctatus	(Toledo et al. 2006a)
Hypsiboas freicanecae	(Carnaval et al. 2006)
Hypsiboas semilineatus	(Toledo et al. 2006a)
Litoria adelaidensis	(Berger et al. 1999)
Litoria aurea	(Berger et al. 2004)
Litoria barringtonensis	(Mahony 2000)
Litoria caerulea	(Pessier et al. 1999)
Litoria chloris	(Kriger et al. 2006a)
Litoria citropa	(Berger et al. 2004)
Litoria dorsalis	(Aplin and Kirkpatrick 1999)
Litoria ewingii	(Berger et al. 2004)
Litoria fallax	(Kriger and Hero 2007)
Litoria genimaculata	(Berger et al. 2004)
Litoria gracilenta	(Berger et al. 2004)
Litoria infrafrenata	(Berger et al. 2004)
Litoria latopalmata	(Kriger and Hero 2007)
Litoria lesueuri	(Berger et al. 1999)
Litoria moorei	(Berger et al. 1999)
Litoria nannotis	(Berger et al. 2004)
Litoria nasuta	(DEH 2005)
Litoria pearsoniana	(Kriger et al. 2006a)

Litoria peronii	(Kriger and Hero 2007)
Litoria phyllochroa	(Mahony 2000)
Litoria raniformis	(Berger et al. 2004)
Litoria rheocola	(Berger et al. 2004)
Litoria spenceri	(Berger et al. 2004)
Litoria tasmaniensis	(Speare and Berger 2005)
Litoria tyleri	(Kriger and Hero 2007)
Litoria verreauxii	(Berger et al. 2004)
Litoria wilcoxii	(Kriger et al. 2006a)
Nyctimystes dayi	(Berger et al. 2004)
Pachymedusa dacnicolor	(Frias-Alvarez et al. 2008)
Phrynomedusa cf. marginata	(Toledo et al. 2006a)
Phyllomedusa bicolor	(Speare and Berger 2004)
Pseudacris maculata	(Green and Muths 2005)
Pseudacris regilla	(Fisher and Garner 2007)
Pseudacris triseriata	(Ouellet et al. 2005)
Ptychohyla erythromma	(Lips et al. 2004)
Ptychohyla hypomykter	(Mendelson et al. 2004)
Ptychohyla leonhardschultzei	(Lips et al. 2004)
Scinax albicans	(Toledo et al. 2006a)
Smilisca phaeota	(Lips et al. 2006)

Hyperoliidae

Hyperolius kivuensis	(Goldberg et al. 2007)
Hyperolius kuligae	(Greenbaum et al. 2008)
Kassina senegalensis	(Weldon 2005)

Leiopelmatidae

Leiopelma archeyi	(Bell et al. 2004)

Leptodactylidae

Atelognathus patagonicus	(Fox et al. 2006)
Ceratophrys ornate	(Nichols 2003)
Craugastor bufoniformis	(Lips et al. 2006)
Craugastor cerasinus	(Lips et al. 2006)
Craugastor cf. azueroensis	(Lips et al. 2006)
Craugastor cf. bransfordii	(Lips et al. 2006)
Craugastor cf. podiciferus	(Lips et al. 2006)
Craugastor crassidigitus	(Lips et al. 2006)
Craugastor gollmeri	(Lips et al. 2006)
Craugastor megacephalus	(Lips et al. 2006)
Craugastor noblei	(Lips et al. 2006)
Craugastor punctariolus	(Lips et al. 2006)
Craugastor tabasarae	(Lips et al. 2006)
Craugastor talamancae	(Lips et al. 2006)
Crossodactylus caramaschii	(Carnaval et al. 2006)

Eleutherodactylus aurilegulus	(Puschendorf et al. 2006)
Eleutherodactylus cf. caryophyllceus	(Lips et al. 2006)
Eleutherodactylus cf. diastema	(Lips et al. 2006)
Eleutherodactylus coqui	(Burrowes et al. 2004)
Eleutherodactylus cruentus	(Berger et al. 1998)
Eleutherodactylus elegans	(Ruiz and Rueda-Almonacid 2008)
Eleutherodactylus emcelae	(Berger et al. 1998)
Eleutherodactylus karlschmidti	(Burrowes et al. 2004)
Eleutherodactylus melanostictus	(Lips et al. 2003)
Eleutherodactylus museosus	(Lips et al. 2006)
Eleutherodactylus patriciae	(Ron 2005)
Eleutherodactylus pituinus	(Ron 2005)
Eleutherodactylus ridens	(Lips et al. 2006)
Eleutherodactylus saltator	(Lips et al. 2004)
Eleutherodactylus vocator	(Lips et al. 2006)
Hylodes dactylocinus	(Toledo et al. 2006a)
Hylodes magalhaesi	(Toledo et al. 2006b)
Hylodes meridionalis	(Toledo et al. 2006a)
Hylodes perplicatus	(Toledo et al. 2006a)
Hylodes phyllodes	(Toledo et al. 2006a)
Hylodes sp. (aff. sazimai)	(Toledo et al. 2006a)
Leptodactylus fallax	(Malhotra et al. 2007)
Leptodactylus ocellatus	(Herrera et al. 2005)

Leptodactylus pentadactylus	(Lips et al. 2006)
Megaelosia cf. boticariana	(Toledo et al. 2006a)
Megaelosia massarti	(Toledo et al. 2006a)
Pleurodema marmorata	(Seimon et al. 2007)
Telmatobius atacamensis	(Barrionuevo and Mangione 2006)
Telmatobius marmoratus	(Seimon et al. 2005)
Telmatobius niger	(Ron et al. 2003)
Telmatobius pisanoi	(Barrionuevo and Mangione 2006)
Thoropa miliaris	(Carnaval et al. 2006)
Thoropa taophora	(Toledo et al. 2006a)
Mantellidae	
Mantella cowanii	(Nichols et al. 1998)
Microhylidae	
Cophixalus ornatus	(Kriger and Hero 2006)
Dyscophus antongilii	(von Oevermann et al. 2005)
Dyscophus guineti	(Annis et al. 2004)
Nelsonophryne aterrima	(Lips et al. 2006)
Myobatrachidae	
Adelotus brevis	(Kriger et al. 2006a)
Assa darlingtoni	(Kriger and Hero 2007)

Crinia georgiana	(Aplin and Kirkpatrick 1999)
Crinia glauerti	(Aplin and Kirkpatrick 1999)
Crinia insignifera	(Aplin and Kirkpatrick 1999)
Crinia pseudinsignifera	(Berger et al. 1999)
Crinia signifera	(Boyle et al. 2004)
Crinia tasmaniensis	(Obendorf 2005)
Geocrinia rosea	(Aplin and Kirkpatrick 1999)
Geocrinia vitellina	(Aplin and Kirkpatrick 1999)
Heleioporus australiacus	(Berger et al. 2004)
Heleioporus eyrei	(Berger et al. 1999)
Heleioporus natalensis	(Smith et al. 2007)
Lechriodus fletcheri	(Berger et al. 2004)
Limnodynastes dorsalis	(Berger et al. 1999)
Limnodynastes dumerilii	(Berger et al. 2004)
Limnodynastes peronii	(Kriger and Hero 2007)
Limnodynastes tasmaniensis	(Berger et al. 2004)
Limnodynastes terraereginae	(Berger et al. 2004)
Mixophyes fasciolatus	(Berger et al. 2004)
Mixophyes fleayi	(Berger et al. 2004)
Mixophyes iteratus	(Kriger et al. 2006b)
Mixophyes shevilli	(Woodhams and Alford 2005)
Neobatrachus kunapalari	(Berger et al. 2004)
Neobatrachus pelobatoides	(DEH 2005)

Pseudophryne corroboree	(DEH 2005)
Pseudophryne pengilleyi	(Berger et al. 2004)
Taudactylus acutirostris	(Berger et al. 2004)
Taudactylus eungellensis	(Kriger et al. 2006a)
Uperoleia fusca	(Kriger and Hero 2007)
Uperoleia laevigata	(Berger et al. 2004)
Petropedetidae	
Arthroleptides yakusini	(Weldon and du Preez 2004)
Pipidae	
Hymenochirus boettgeri	(Raverty and Reynolds 2001)
Xenopus gilli	(Weldon et al. 2004)
Xenopus laevis	(Weldon et al. 2004)
Xenopus meulleri	(Weldon et al. 2004)
Xenopus petersii	(Weldon 2005)
Xenopus tropicalis	(Parker et al. 2002)
Xenopus wittei	(Goldberg et al. 2007)
Plethodontidae	
Bolitoglossa colonnea	(Lips et al. 2006)
Bolitoglossa dofleini	(Pasmans et al. 2004)
Bolitoglossa schizodactyla	(Lips et al. 2006)

Oedipina cf. parvipes	(Lips et al. 2006)
Oedipina collaris	(Lips et al. 2006)
Oedipina grandis	(Lips et al. 2003)
Plethodon neomexicanus	(Cummer et al. 2005)

Proteidae

Necturus maculosus	(Speare and Berger 2004)

Ranidae

Afrana angolensis	(Weldon 2005)
Afrana dracomontana	(Weldon 2005)
Afrana fuscigula	(Hopkins and Channing 2003)
Amietia vertebralis	(Smith et al. 2007)
Ceratobrachus guentheri	(Nichols et al. 1998)
Cacosternum boettgeri	(Weldon 2005)
Ptychadena anchietae	(Speare and Berger 2004)
Ptychadena mascareniensis	(Goldberg et al. 2007)
Rana arvalis	(Speare and Berger 2004)
Rana aurora	(Nieto et al. 2007)
Rana berlandieri	(Sredl and Caldwell 2000)
Rana blairi	(Parris 2004)
Rana boylii	(Ouellet et al. 2005)
Rana catesbeiana	(Hanselmann et al. 2004)

Rana chiricahuensis	(Bradley et al. 2002)
Rana clamitans	(Ouellet et al. 2005)
Rana draytonii	(Morgan et al. 2007)
Rana esculenta	(Fisher and Garner 2007)
Rana lessonae	(Simoncelli et al. 2005)
Rana luteiventris	(Pearl et al. 2007)
Rana maculata	(Felger et al. 2007)
Rana megapoda	(Frias-Alvarez et al. 2008)
Rana montezumae	(Frias-Alvarez et al. 2008)
Rana muscosa	(Green et al. 2002)
Rana neovolcanica	(Frias-Alvarez et al. 2008)
Rana palustris	(Ouellet et al. 2005)
Rana perezi	(Bosch et al. 2007)
Rana pipiens	(Green et al. 2002)
Rana pipiens sp. E	(Lips et al. 2006)
Rana pretiosa	(Pearl et al. 2007)
Rana ridibunda	(Fisher and Garner 2007)
Rana septentrionalis	(Ouellet et al. 2005)
Rana sevosa	(Drake et al. 2007)
Rana sierrae	(Vredenburg et al. 2007)
Rana spectabilis	(Frias-Alvarez et al. 2008)
Rana sphenocephala	(Green et al. 2002)
Rana sylvatica	(Ouellet et al. 2005)

Rana warszewitschii	(Lips et al. 2006)
Rana yavapiensis	(Bradley et al. 2002)
Strongylopus fasciatus	(Weldon 2005)
Strongylopus grayii	(Hopkins and Channing 2003)
Strongylopus hymenopus	(Smith et al. 2007)
Tomopterna cryptotis	(Weldon 2005)
Tomopterna natalensis	(Weldon 2005)
Salamandridae	
Mesotriton alpestris	(Fisher and Garner 2007)
Notophthalmus viridescens	(Ouellet et al. 2005)
Salamandra salamandra	(Bosch and Martinez-Solano 2006)
Taricha granulosa	(Fisher and Garner 2007)
Taricha torosa	(Padgett-Flohr and Longcore 2007)
Sirenidae	
Siren lacertina	(Speare and Berger 2004)

Table 2 (Supporting Online Information). The global distribution of *Batrachochytrium dendrobatidis*, and the earliest date the fungus is known to have infected wild or captive amphibians in each country.

Country	Year of first record	Reference
South Africa	1938	(Weldon et al. 2004)
Canada	1961	(Ouellet et al. 2005)
USA[1]	1969	(Ouellet et al. 2005)
Botswana	1969	(Weldon 2005)
Australia	1978	(Berger et al. 1999)
Ecuador	1980	(Ron and Merino 2000)
Venezuela	1986	(Bonaccorso et al. 2003)
Swaziland	1991	(Weldon 2005)
Costa Rica	1992	(Puschendorf 2003)
Panama	1996	(Lips 1999)
Spain[2]	1997	(Bosch et al. 2001)
Kenya	1998	(Speare and Berger 2004)
Uruguay	1999	(Mazzoni et al. 2003)
New Zealand	1999	(Waldman 2001)
Germany	1999	(Mutschmann et al. 2000)
Mexico	2000	(Lips et al. 2004)
Argentina	2002	(Herrera et al. 2005)
Dominica	2002	(Malhotra et al. 2007)

Peru	2002	(Seimon et al. 2005)
Guatemala	2003	(Mendelson et al. 2004)
Honduras	2003	(Puschendorf et al. 2006)
Tanzania	2003	(Weldon and du Preez 2004)
Colombia	2004	(Ruiz and Rueda-Almonacid 2008)
Brazil	2004	(Carnaval et al. 2005)
United Kingdom	2004	(Cunningham et al. 2005)
Italy	2004	(Stagni et al. 2004)
Lesotho	2004	(Weldon 2005)
El Salvador	2005	(Felger et al. 2007)
Portugal	2005	(Garner et al. 2005)
Switzerland	2005	(Garner et al. 2005)
Cuba	2006	(Diaz et al. 2007)
France	2006	(Garner et al. 2006)
Trinidad and Tobago	2006	(Alemu et al. 2008)
Uganda	2006	(Goldberg et al. 2007)
Democratic Republic of Congo	2007	(Greenbaum et al. 2008)
Japan	2007	Y. Une, Unpub. data

[1]Including Guam, Hawaii, Alaska and Puerto Rico

[2]Including Mallorca

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