An overview of the evolution and conservation of West Indian amphibians and reptiles

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Abstract. The total area of the West Indies is small, only 0.15% of Earth's land area, but the region supports 3.0% (180 species) of the world's amphibians and 6.3% (520 species) of the world's known reptiles. Nearly all species are endemic to a single island or island bank. Rates of discovery are high indicating that many more species remain to be found. Most or all of the groups arrived at different times during the Cenozoic Era (the last 65 million years) by dispersal over water, principally on flotsam from South America. This resulted in a filtered fauna that has relatively few higher-level groups. The vacant niches led to unusually large radiations (mega-radiations) of species, explaining the presence of extremes in ecology and morphology among the species. The conservation status of only the amphibians has been assessed comprehensively, and 84% of those species are considered threatened. The reptiles may be similarly threatened. Species are threatened mostly because they have small distributions and habitat destruction is continuing. Across the region only about 10% of primary forests remain, and some countries (e.g., Haiti) with high levels of faunal diversity have no original forests. Some species that have disappeared for decades are possibly extinct, while others face extinction soon from habitat destruction. Efforts to curb deforestation and to save targeted species through breeding programs are helping, but the continued survival of many West Indian amphibians and reptiles is tenuous. Measures having immediate impact, such as salaries and logistical support for park guards, are needed immediately. Greater facilitation of biotic surveys and inventories, through relaxing of permitting restrictions, also is needed to better understand the diversity that exists and to focus conservation efforts.

Key words: Antilles; biodiversity; Caribbean; deforestation; discovery; ecology; extinction; genetic resources; systematics; taxonomy.

Introduction

There are approximately 700 species of amphibians and reptiles that have been described from the West Indies (Hedges, 2006a), here defined as excluding Trinidad and Tobago which are adjacent to South America and have continental faunas. This includes approximately 180 amphibians (3.0% of all amphibian species) and 520 reptiles (6.3% of all reptile species). These proportions of the global faunas are high when it is realized that the West Indies comprises only 0.15% of the total land area of the Earth. At least another 20 new species are under study and additional species will surely be discovered. It is too soon to estimate the total number of species that exist, but it most likely exceeds 800 and could surpass 1000 if many of the taxa recognized today as subspecies are later found to be valid species, which is a current trend. Remarkably, nearly all native species are endemic to the region and rarely found on more than one island or island bank (Hedges, 2006b).

Only the amphibians have had a comprehensive assessment of their conservation status, as part of the Global Amphibian Assessment led by Conservation International and the International Union for the Conservation of Nature (Stuart et al., 2004; Young et al., 2004). That study concluded that a surprising 84% of the amphibian species are threatened, which is the highest proportion of any amphibian fauna in the world. The primary factors responsible for placing species in the high threat categories (vulnerable, endangered, and critically endangered) were small distributions and declining habitat, mainly through deforestation. These same factors are likely to affect the conservation status of West Indian reptiles when that group is assessed in the near future, and more generally explains why the West Indies is one of the hottest of biodiversity hot spots (Myers et al., 2000; Smith et al., 2005).

Currently, only a few species — mostly large reptiles — have been targeted for captive-breeding or population monitoring and other species-specific conservation measures (e.g., Bloxam and Tonge, 1995; Tolson, 1996; Vogel et al., 1996; Daltry et al., 2001; Goodman et al., 2005). These efforts are critical, especially when population numbers are perilously low as in these cases. But the vast majority of species are effectively invisible to such programs and to the conservation community in general. They are small, cryptic, and usually live in remote areas where their declines, from habitat destruction, are not being monitored. Many of these species have only been seen by their original discoverers, or perhaps a few times after that. For this majority of the West Indian herpetofauna, extinctions will occur before any captive breeding is done, and therefore attention must be focused on habitat conservation and stopping, or at least controlling, the loss of forests. At the same time, exploration and discovery efforts need to be encouraged so that the true diversity is as completely characterized as possible, both taxonomically and ecologically. The most effective conservation strategies are those based on the most accurate knowledge of a fauna.

Here I provide brief overview of the origin and evolution of the West Indian herpetofauna. This is followed by a discussion of two aspects vital to its conservation: stopping deforestation and facilitating systematic research. Certainly, other threats exist besides deforestation, such as climate change (e.g., Malcolm et al., 2006), disease (e.g., Burrowes et al., 2004), introduced predators (e.g., Iverson, 1978), introduced flora (Henderson and Powell, 2001), and human exploitation (e.g., Lescure, 1979; Powell et al., 2000). For some species, especially large reptiles, it has been claimed that introduced predators have had a greater negative impact than habitat alteration (Henderson, 2004). Although this probably is true in some instances, the point made here is that habitat destruction — in particular, deforestation — is the major and primary threat to the survival of most species.

Origin, Evolution, and Biogeography

Knowledge of the evolutionary history of West Indian amphibians and reptiles is helpful in understanding the conservation status of these animals and threats to their survival. The historical biogeography of the West Indies has been studied for more than a century and remains an active area of research. Knowledge of geologic history is crucial for any biogeographic scenario and therefore the history of the field can be neatly divided into work published before and after the general acceptance of continental drift (c.1960s). Most early workers assumed that there was no change in the position of the islands and their water gaps, thus leaving only over-water dispersal as the mechanism (Wallace, 1881; Matthew, 1915; Darlington, 1938; Simpson, 1956). An alternative viewpoint was that ancient land bridges existed between the continents and the Antilles, permitting dispersal over land (Barbour, 1916; Schuchert, 1935). However, continental drift showed that the foundations for both views were incorrect.

We now know that the Greater Antilles were once connected as a geologic unit with North and South America in the late Cretaceous (c. 60-70 million years ago), raising the possibility that the present fauna arose by "vicariance," which consisted of faunas drifting with their islands as they broke away from the continents (Rosen, 1975). Unfortunately, fossil and genetic research has been unable to identify more than a few West Indian groups that fit this model, including *Eleutherodactylus* frogs and the Cuban xantusiid lizard *Cricosaura typica* (Hedges et al., 1992; Hedges, 2006b). The great majority of groups probably arrived in the West Indies by flying, swimming, or floating on flotsam (mats of vegetation). The predominant flow of ocean currents moving east to west means that the source for almost all flotsam in the West Indies is South America, or more rarely, Africa, which agrees with the evolutionary relationships of most of the amphibians and reptiles (Hedges, 1996b).

The strongest support for over-water dispersal as the predominant mechanism has come from the taxonomic composition of the fauna, which is missing many higher-level groups such as salamanders, caecilians, most families and subfamilies of frogs, lizards, snakes, and turtles. This was noted in even the earliest accounts of West Indian biogeography (Wallace, 1881; Matthew, 1915) and has been reiterated over the years (Darlington, 1938; Simpson, 1956; Williams, 1989; Hedges, 1996a). The fossil record, although still sparse, shows this same "filtered" fauna of the Pleistocene and Recent extending back into the mid-Cenozoic. For example, there are multiple fossils of the extant genera *Anolis*, *Sphaerodactylus*, and *Eleutherodactylus* from Dominican amber (15-20 million years ago, Ma), but no indication of other groups that should have been there if there were dry land connections to the mainland in the past. Furthermore, the large radiations of species (mega-radiations) of those extant genera, obviously filling unoccupied niches, further suggests that this filtered fauna has existed for millions of years and did not just result from recent extinctions.

All of these same reasons argue against the existence of a dry land bridge (Aves Ridge) connecting South America with the Greater Antilles in the mid-Cenozoic (Holcombe and Edgar, 1990; Iturralde-Vinent and MacPhee, 1999). Such a faunal corridor would have brought a diversity of vertebrate groups to the Antilles which would have been evident at least in the fossil record (e.g., amber fossils) if not in the living fauna. Moreover, the times of divergence of the colonists from their mainland counterparts would be reflected in molecular estimates of divergence times, clustering around 35 Ma, but instead the lack of clustering supports over-water dispersal (Hedges et al., 1992; Hedges, 1996b). Also geologic evidence is silent on the existence (or not) of such as land bridge (Holcombe and Edgar, 1990; Hedges, 2001).

Niche-filling, Ecological Release, and Biological Extremes

This history of the fauna, dominated by over-water dispersal, explains why there are so few higher-level groups (families and genera) in the West Indies and an over-abundance of species. The frequent filling of vacant niches by resident groups is called "ecological release," and a side-effect is that some of the world's smallest and largest species occur in the West Indies. Among amphibians and reptiles, this includes the smallest frog *Eleutherodactylus iberia* (Estrada and Hedges, 1996), the smallest lizard *Sphaerodactylus ariasae* (Hedges and Thomas, 2001), and the smallest snake *Leptotyphlops bilineatus*. At the other end of the size spectrum, *Osteopilus crucialis* (Jamaica) and *O. vastus* are among the largest treefrogs in the New World (Trueb and Tyler, 1974), *Alsophis anomalus* is the largest xenodontine snake, and *Cyclura nubila* (Cuba) is the largest iguanid lizard. Other species nearly reach those extremes, indicating that mega-radiations and ecological release are major features of the West Indian herpetofauna.

Other unusual aspects of the ecology and behavior of individual species may be tied to ecological release as well, including live-bearing in the Puerto Rican frog *E. jasperi*, cave breeding and froglet transport in the Jamaican frog *E. cundalli* (Diesel et al., 1995), underground chamber construction in the Hispaniolan frogs *E. hypostenor*, *E. ruthae*, and *E. pelorius*, aquatic behavior in the lizards *Anolis eugenegrahami* and *A. vermiculatus*, among others. This distinctive quality of the herpetofauna, having extremes in morphology, ecology, and reproduction tied to its evolutionary history, is difficult to ignore from a conservation standpoint.

Deforestation

Most visitors to the West Indies are unaware that the current appearance of the islands bears little resemblance to what it was when Columbus arrived in 1492. Even small islands in the Bahamas were covered with thick forests, and giant, buttressed trees were abundant. Today, only a small fraction of that original forest remains, although the actual amount is unclear. The United Nations Food and Agriculture Organization (FAO) keeps track of global forest cover in individual countries (FAO, 2005; WRI, 2006). However, caution must be used in interpreting those data. Values for the percent of forest cover include introduced trees and forest plantations, the latter of which provide limited or no habitat for native amphibians and reptiles. Also, "forest" is defined as having $>10\%$ canopy, and means that as much as 90% of the trees in an area could be removed and it would still be classified as forest.

For some countries, data are available for more stringent levels of canopy extent, up to 75%, and in a few cases, for "natural forest" and "primary forest." The FAO defines natural forest as having native species of trees, but the 10% canopy cutoff value still applies (FAO, 2005). Primary forests are defined as having "no — or no visible — indications of past or present human activity," and it is this last category that is most relevant to assessing the natural habitat and conservation status of most West Indian amphibians and reptiles. Unfortunately, the FAO lists primary forest information for only three countries in our region, and for nearby Trinidad and Tobago. Comparing total forest area with primary forest area (respectively) in these four cases reveals some major differences: Dominica (61.3%, 36%), Grenada (11.8%, 2.9%), Guadeloupe (47.3%, 11.2%), and Trinidad and Tobago (44.4%, 2.7%). Dominica is considered to have one of the highest proportions of primary forest of any island in the region, in part due to its low human population density, and should be considered an exception. The other three are probably more representative, with two having less than 3% of their original primary forest remaining. Also, two of the four countries (Guadeloupe and Trinidad and Tobago) show striking differences between total and primary forest areas.

These comparisons indicate that it can be misleading to relate the extent of total forest cover to the preservation of native faunas and their habitats. The current primary forest area of the Greater Antilles is likely to be much less than the values listed for the total forest area in those countries, which are: Cuba (22.2%), Jamaica (31.4%), Haiti (4.0%), the Dominican Republic (28.4%), and Puerto Rico (45.9%) (FAO, 2005). Instead, an estimate of 10% "intact vegetation" for the region as a whole is a more realistic figure, with some countries (e.g., Haiti) having little or no remaining primary forest (Hedges and Woods, 1993; Smith et al., 2005).

After Columbus arrived, the lowland rainforest in the Greater Antilles was the first to go, and virtually none of it remains today aside from isolated trees in old plantations and a few small patches such as one near Cabezada, Guantánamo Province, Cuba (pers. obs.). These areas were quickly cleared for agriculture, and the wood was used for building materials to feed expansion of the New World colonies. Deforestation of the mountain slopes soon followed as European settlements continued to expand, and crops (e.g., coffee) were planted that required higher elevations for optimal growth. Some small regions of montane rainforest and cloud forest still exist on most of the larger islands, but the vast majority is gone.

The original forests that remain today in the West Indies occur mostly in remote areas that are difficult to access and thus are rarely seen except on foot. Of course, it is this difficulty of access that has delayed their demise. Among these are the major limestone forests in the Greater Antilles, such as the Cockpit Country of Jamaica, the Viñales region of Cuba, the Haitises of the Dominican Republic, and the karst region of northwest Puerto Rico, and forests on some of the highest and inaccessible mountain tops. But even in these areas, access roads and trails have permitted local squatters to enter the forest illegally, clear forested valleys between mogotes, and plant crops. These cleared patches can be seen on satellite photos and make up large portions of regions designated as protected areas, including the Haitises National Park and the Cockpit Country Forest Reserve. Comparison with earlier satellite and aerial photos shows that these last remaining forests are disappearing, even in so-called protected areas (e.g., Tole, 2002). In Haiti, clearing of forest and charcoaling has left a denuded landscape (fig. 1).

Much of the lush, green roadside vegetation seen along major roadways in the West Indies is introduced vegetation from the Old World such as mango, breadfruit, papaya, banana, bamboo, and various ornamentals, weeds, and shrubs. To a casual observer, this may give the false impression that the islands are heavily forested, but this introduced vegetation is usually sparse and associated with low species diversity of the herpetofauna (Henderson and Powell, 2001). Also, forest recovery in deforested areas of the West Indies can be slow, and the regenerated forest may not resemble the original forest in terms of dominant tree species and overall species diversity (Aide et al., 1995; Rivera and Aide, 1998; Rivera et al., 2000). Even secondary impacts of deforestation are now becoming known. For example, the clearing of lowland rainforest, which has already occurred throughout the West Indies, is known to alter the climate in nearby upland forests (Lawton et al., 2001).

Habitat Protection

The most important conservation measure for saving West Indian amphibians and reptiles applies to essentially the entire West Indian terrestrial biota: Stop deforestation. Although it can be stated this simply, putting a halt to deforestation is a complicated and difficult problem, not even considering the large numbers of governments, cultures, and languages involved in the region. Almost every country has made attempts to address this problem and many have help from non-governmental organizations, which in some cases even take charge of national parks. But parks and other protected areas in the West Indies afford varying degrees of habitat protection. For example, the national parks of Haiti are essentially “paper parks,” because logging and clearing of forests continues unabated within park boundaries. For this reason, *the existence of protected areas should effectively be ignored in assessing the conservation status of native species, unless there is unambiguous evidence that such a designated area is truly affording protection.* Even on islands with good enforcement of tree-cutting (e.g., Puerto Rico), native

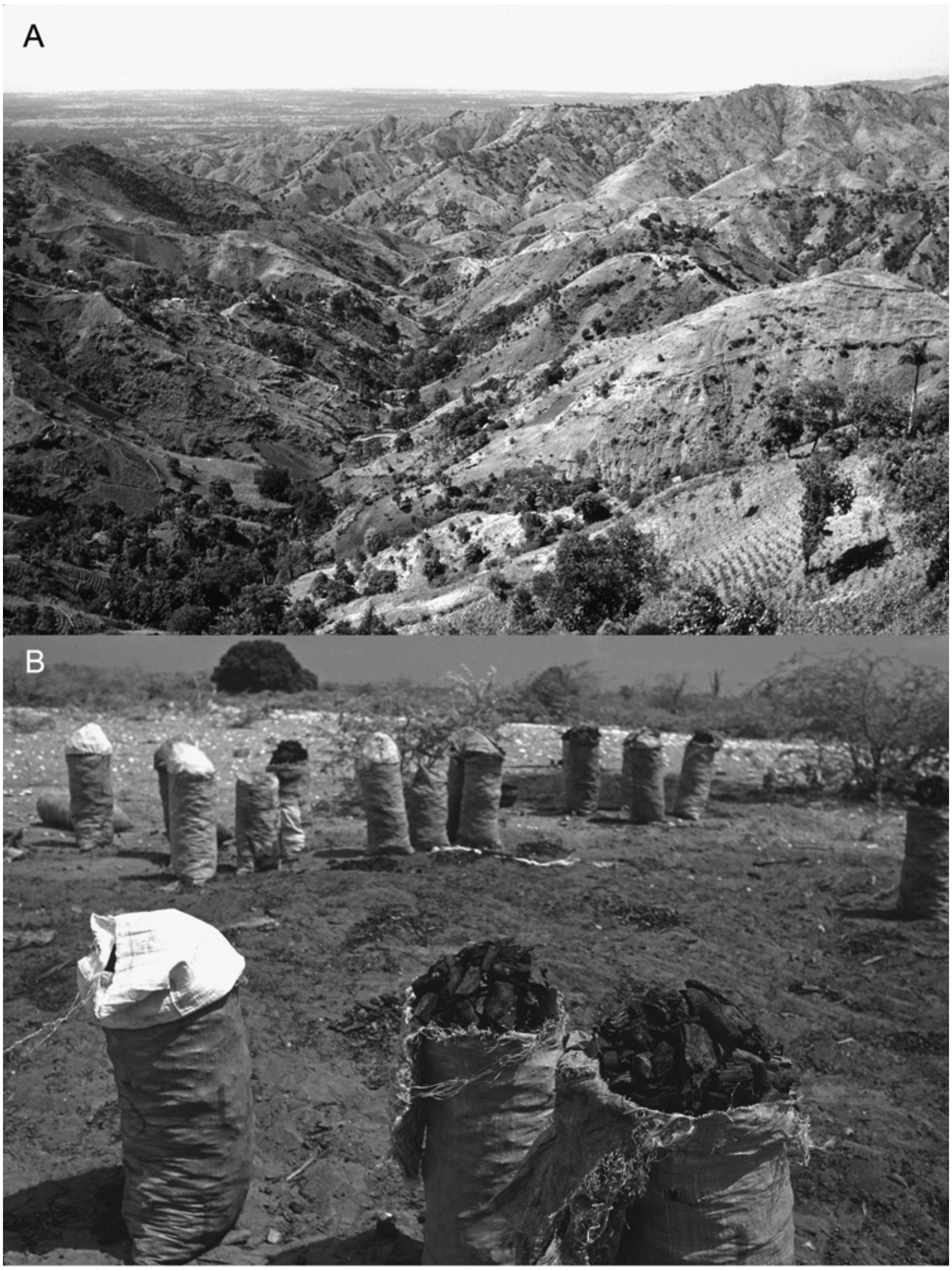

Figure 1. (A) Deforested hills north of Jacmel on the Haitian Tiburon peninsula. (B) Charcoal being removed from a pit in the northwest peninsula of Haiti and placed in bags for transport. The clearing of forests for charcoal production (cooking fuel) is a major cause of deforestation in the West Indies. Both photographs taken in July, 1991 by S.B. Hedges.

species of amphibians and reptiles are still threatened within protected areas by abundant introduced predators (e.g., black rats). Thus, there are no "pristine" forests in the West Indies.

Plans have been proposed for protecting the natural areas of the most species-rich islands (e.g., Woods et al., 1992; Hedges and Woods, 1993; Sergile and Woods, 2001) and most focus on habitat protection. However, habitat alteration and destruction continues in the West Indies despite the hard work of many local and international conservationists and funding agencies. Because extinctions are eminent in some areas, efforts should focus now on achieving immediate benefits by, for example, funding of park guards and their associated logistical needs (e.g., supplies and vehicles).

Exploration, Discovery, and Systematics

Discovery curves are graphs that show the cumulative number of described species at different points in time. For West Indian amphibians and reptiles, these curves show steeply rising slopes indicating that many more species remain to be discovered (fig. 2). However, relatively few systematists are now conducting herpetological survey work in the region. In part it is related to the small total number of taxonomists globally and their continuing decline in numbers as an outcome of cultural shifts in scientific research and funding (Raven, 2004; Wilson, 2004). Modern systematics usually involves DNA sequencing, phylogenetic analyses, morphological descriptive analyses, and biostatistics, all of which require training and most of which is expensive. This is especially a problem for local scientists in the West Indies where funding opportunities are limited. It is important that conservation agencies and funding programs recognize that such survey and inventory work is

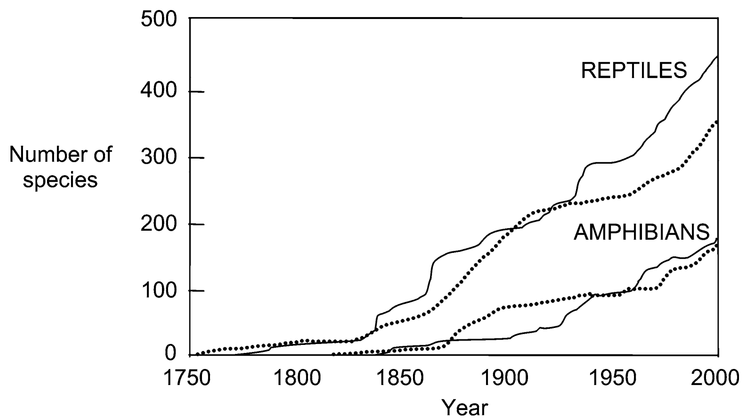

Figure 2. Discovery curves for West Indian amphibians and reptiles (continuous lines) compared with those for Malagasy amphibians and reptiles (dashed lines). The lines show cumulative numbers of described native species at each time period.

vital to conservation efforts, and that they make concerted efforts, through targeted grant funding, to facilitate such research.

A separate problem that impedes the work of systematists who conduct survey-and-inventory research in the West Indies involves restrictions imposed by countries on areas that can be visited, species and numbers of individuals that can be collected, and tissue samples that can be taken for molecular systematic research. These restrictions affect both local and foreign scientists, but can be particularly discouraging for the latter. When faced with the high costs of an expedition and the likelihood that the research will be greatly curtailed by restrictions to collecting, especially the taking of tissues for molecular systematics, many foreign scientists simply do not bother making the trip or choose to do work elsewhere, in a country that is less restrictive to scientific research. Thus, one can be certain that the small number of systematists conducting surveys and inventories in the West Indies is in part due to inhibition of research caused by these restrictions.

Biotic survey work in Cuba has been greatly curtailed during the last decade by severe restrictions on travel around the country imposed by the Cuban military. This has affected research by both Cuban and foreign scientists. If the Cuban government believes that systematists represent a security threat, a possible solution might be to assign a military escort to the expedition, funded by the expedition sponsor. Many would consider that additional expense to be a better alternative than canceling the work altogether.

It is understandable that the number of individuals to be collected should be regulated by governments, and almost all countries impose limitations. Nonetheless, consideration should be given to the fact that small animals often exist in high population densities and that scientists need to sample as broadly as possible to detect geographic variants and assess population variation. For example, densities as high as 23,600 ha^{-1} for *Anolis* (Reagan, 1992) and 52,800 ha^{-1} for *Sphaerodactylus* (Rodda et al., 2001), the two most species-rich genera of West Indian lizards, have been recorded. Scientific collecting is unlikely to affect the health of such populations, or even those with densities that are orders of magnitude smaller. The benefits of routine geographic sampling of populations are seen frequently in studies that have revealed cryptic species, such as the discovery of 16 new species of salamanders in the eastern U.S. (Highton et al., 1989). For conservation, this information is priceless.

Yet scientists are often told not to collect more than a small number of individuals (e.g., 1-5) of these abundant vertebrates, reducing the potential value of the research. This is unfortunate, because in all realistic cases that can be envisioned, *the scientist is not the threat*. The number of individuals of most species killed by clearing a single hectare of forest habitat, by the building a single house or garden, by vehicles on highways, or by a storm that blows over some trees, will far exceed the sampling effect of systematists (Hedges and Thomas, 1991).

Finally, another major problem is occurring throughout the world which is impeding conservation efforts. It is the restriction on collection of "genetic resources."

To conservation biologists, tissues samples for DNA sequencing provide invaluable data on a spectrum of ecological and evolutionary questions that can facilitate conservation efforts. For example, DNA sequences can tell us how many species exist in an area, especially with cryptic organisms, as already noted. Also, they can provide critical data about the population structure, related to population size and dispersal. The problem is actually a misunderstanding that conservation biologists will profit from these samples by finding new drugs worth millions or billions of dollars, through a procedure called "bioprospecting." Such fears are unwarranted. But to alleviate these concerns, a possible solution might be to stipulate on collecting and export permits that the samples are not to be used for drug discovery, rather than to restrict collection of the samples themselves.

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