

A Genetic Compatibility Framework for Defining Species Across Life



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One-Sentence Summary:

A universal, empirically testable framework based on genetic compatibility resolves inconsistencies in species classification across sexual, asexual, and borderline organisms.

Abstract

The species problem persists due to the lack of a universal, empirically testable definition across sexual, asexual, and borderline life. We propose a genetic compatibility framework: a species is the largest group genetically compatible for

reproduction, evidenced by offspring production regardless of viability or fertility, or by a shared clonal lineage with high genetic similarity. This criterion explicitly applies across the primary kingdoms of life: single-celled organisms, Fungi, Plants, and Animals. Applications to diverse taxa demonstrate clear and consistent species boundaries, resolving longstanding classification inconsistencies.

Introduction

Classification of biological diversity relies on the species concept, yet no single definition has achieved universal acceptance.¹⁻³ The biological species concept emphasizes reproductive isolation and fertile interbreeding,¹ but excludes organisms that reproduce asexually, including most microbes. Morphological criteria introduce subjectivity and fail for cryptic diversity,² while phylogenetic approaches assume tree-like ancestry and struggle with reticulate patterns from hybridization or horizontal gene transfer.³ These limitations create persistent inconsistencies, particularly when classifying fossils, microbes, or entities of debated ontological status such as viruses.

Existing definitions often tie classification to inferred historical processes, complicating empirical testing. Here, we present a novel framework grounded exclusively in observable genetic outcomes: compatibility for offspring production in sexual organisms, or demonstrated persistence of shared clonal lineages in asexual ones. This approach maximizes group size while preserving clear species boundaries, providing a testable and inclusive criterion applicable across all organisms.

While existing concepts (such as reproductive isolation, morphological criteria, and phylogenetic inference) have shaped biological classification, none spans the full diversity of life with a single observable, testable criterion applicable to both sexual and asexual lineages.

Results: Formalizing the Genetic Compatibility Criterion

Refining the Species Definition

At the core of our framework is the principle that species membership depends on genetic compatibility, not on the fertility or long-term viability of offspring. Genetic compatibility in sexual organisms can be demonstrated simply by the production of any offspring. Behavioral, ecological, geographic, or cultural barriers to mating do not define species boundaries. If offspring production is genetically possible, these barriers are treated as superficial constraints on opportunity rather than indicators of incompatibility. Fertility (or lack thereof) is a secondary trait that may indicate internal structure (e.g., subspecies or populations) but does not define the species boundary itself. This mirrors the human case: all living humans are classified as one species despite instances of infertility between individuals due to chromosomal differences,

genetic disorders, or other factors; offspring production remains possible across the vast majority of pairings. The fact that some humans are born infertile disqualifies species definition attempts that consider infertility a sign of speciation.

For asexual organisms, including bacteria (via binary fission) or parthenogenetic sea snails, the same principle applies: species are defined by clonal lineages with high genetic similarity and shared ancestry. Variation introduced by mutation or horizontal gene transfer is permitted provided lineage cohesion remains intact.⁴

The consolidated definition states: a species is the largest group of organisms that are genetically compatible for reproduction or form a shared clonal lineage.

Consolidated Definition:

A species is the largest group of organisms that are genetically compatible for reproduction (sexual organisms) or that form a shared clonal lineage (asexual organisms).

Application to Selected Taxa

Single-Celled Organisms and Borderline Entities

Single-celled organisms fit seamlessly into our framework. Bacteria, unequivocally living forms with independent metabolism and cellular structure,⁶ are grouped via clonal lineages with high genetic similarity, typically $\geq 95\text{--}96\%$ average nucleotide identity (ANI) in core genomes.⁷ Horizontal gene transfer introduces variation but is accommodated as intra-lineage diversity, maintaining cohesion.⁸ Eukaryotic protists, including protozoa, may use offspring production (e.g., conjugation) or clonal lineages, resolving classification challenges from variable modes.⁹

Viruses and prions highlight ontological debates. Viruses lack independent metabolism and host-dependent replication, debated as non-living parasites or boundary entities.^{10 - 11} Our framework classifies them via quasi-species clonal lineages without requiring “life” status. Prions, proteinaceous agents without nucleic acids, propagate misfolding but lack genetic heritability; they fall outside, clarifying non-living status.¹² The inclusion of asexual and borderline organisms from the outset demonstrates the superiority of our genetic compatibility criterion over traditional concepts that exclude the majority of biodiversity.

Single-celled organisms are unified by **metabolic systems that operate at the level of the individual cell**, without obligate tissue specialization or multicellular integration. Their metabolic diversity is extensive, encompassing aerobic and anaerobic respiration, fermentation, chemolithotrophy, phototrophy, and numerous hybrid strategies. Energy acquisition and biomass production occur directly within single cellular units, and physiological function is not dependent on intercellular coordination. This metabolic autonomy distinguishes single-celled life from multicellular kingdoms and underlies their classification as a distinct biological domain and kingdom-level grouping.

Fungi (Mushrooms, Molds, and Yeasts)

Fungi represent a critical test case for the Genetic Compatibility Framework, as they exhibit an extraordinary diversity of reproductive modes. These include sexual, asexual (clonal), parasexual (for example, anastomosis and heterokaryon formation), and facultative combinations, often within the same lineage. The current proliferation of fungal species concepts (morphological, phylogenetic, biological where applicable) has led to inconsistent delimitations, particularly in asexual groups like anamorphic molds and yeasts. The framework resolves this by focusing on empirical offspring production and genetic compatibility, treating sexual and clonal reproduction as equivalent pathways for lineage persistence. Mushrooms, as the fruiting bodies of many fungi, can be cloned by extracting stem mycelia materials and placing them in fresh substrate, or propagated from the base mycelium that the fruiting body springs from. This allows for empirical assessment of clonal stability and compatibility.

Fungi are defined by a **heterotrophic metabolism based on external digestion and absorptive nutrient acquisition**. Rather than ingesting or photosynthesizing nutrients, fungi secrete enzymes into their environment to decompose organic matter and absorb dissolved compounds across cell membranes. This metabolic strategy is fundamentally distinct from both photosynthetic autotrophy in plants and internalized ingestion in animals. The reliance on extracellular enzymatic breakdown as the primary means of energy and carbon acquisition constitutes the defining metabolic characteristic of the fungi kingdom.

Sexual Fungi

In basidiomycetes and ascomycetes with known sexual cycles (for example, *Neurospora*, *Saccharomyces cerevisiae*, *Cryptococcus neoformans*), compatibility is governed by mating-type loci (MAT in ascomycetes; bipolar or tetrapolar systems in basidiomycetes). Species boundaries are delineated by:

- Successful meiosis and production of viable, fertile recombinant offspring.
- Post-zygotic barriers: hybrid inviability, sterility, or reduced fitness in F1/F2 generations.

Empirical tests: controlled matings followed by viability/fertility assays and genomic sequencing to confirm recombination.

Asexual and Clonal Fungi (Molds and Yeasts)

Many economically and ecologically important fungi lack observed sexual cycles (for example, *Aspergillus fumigatus* anamorphs, *Candida albicans*, *Penicillium* spp., *Trichoderma*). Under the framework, these qualify as distinct species equivalents if:

- Clonal lineages are genetically isolated and self-sustaining over ecological/evolutionary time.
- No evidence of ongoing gene flow with other lineages (via anastomosis or rare parasex).

- Long-term persistence without sexual recruitment.

Empirical tests: population genomics (clonality indices, linkage disequilibrium), experimental evolution tracking lineage stability, and anastomosis assays to test fusion compatibility. Cloning techniques, such as extracting mycelium from young specimens and culturing in modified media (for example, Melin-Norkrans or half-strength PDA), can assess growth over months, confirming viable clonal propagation.

Parasexual and Facultative Systems

The parasexual cycle (heterokaryon formation, karyogamy, haploidization via aneuploidy) in *Aspergillus* and *Fusarium* blurs traditional boundaries. Compatibility is assessed by:

- Successful vegetative fusion (anastomosis) and heterokaryon stability.
- Production of recombinant haploid offspring via parasexual recombination.

Threshold: lineages that regularly exchange genes parasexually are considered compatible (single species); those with barriers to fusion or unstable heterokaryons are separate.

Amanita Varieties, Subspecies, and Hybrids

The genus *Amanita* exemplifies the framework's applicability to morphologically variable and hybridizing fungi. *Amanita muscaria* (fly agaric), a widespread ectomycorrhizal basidiomycete, is recognized as a single species with multiple variants and subspecies due to high morphological and genetic variation. Common varieties include:

- *A. muscaria* var. *muscaria*: Classic red cap with white warts, widespread in Europe/Asia.
- *A. muscaria* var. *formosa*: Yellow-orange cap, common in North America.
- *A. muscaria* var. *guessowii*: Similar to *formosa*, with regional adaptations.
- *A. muscaria* var. *alba*: Rare white form, sometimes considered a genetic variant.

Other subspecies include *A. muscaria* subsp. *flavivolvata* (South America) and *A. muscaria* subsp. *persicina* (North America), distinguished by cap color, volva, and habitat.

These variants often hybridize in overlapping ranges, producing intermediate forms with viable offspring (for example, color gradients x shared mycorrhizal associations). Under the framework, compatibility is tested by:

- Mycelial fusion or sexual crosses (where possible; *Amanita* has complex mating systems).
- Clonal propagation from base mycelium or stem extracts in substrate.

Empirical evidence: Genomic studies show gene flow between varieties, supporting lumping as a single compatible species complex unless persistent incompatibilities emerge (for example, reduced hybrid fitness in extreme environments).

Cryptic Species and Clinical Implications

Pathogenic fungi like *Candida auris* and *Cryptococcus gattii* complex harbor cryptic lineages distinguished only by genomics. The framework predicts these are distinct if empirical crosses or clonal tracking show incompatibility in viable offspring production. This has direct conservation and medical relevance: mislumping compatible lineages risks underestimating diversity and virulence evolution.

Advantages Over Existing Concepts

- Uniform application: no need for separate "species" definitions for sexual vs. asexual fungi.
- Empirical grounding: testable via mating/anastomosis trials and long-term lineage tracking.
- Resolves over-splitting in phylogenetic concepts and under-splitting in morphological ones.

Fungi thus exemplify the framework's strength: a single criterion (demonstrated ability to produce persisting, viable offspring, whether sexual, parasexual, or clonal) delivers consistent, biologically meaningful species delimitation across the kingdom.

Plants (Grasses, Herbs, Trees, Vines, Shrubs, Fruit Trees, and Flowering Trees)

Plants exhibit extensive hybridization, often producing viable and fertile offspring across traditionally recognized species boundaries. Examples include fertile allopolyploids in wheat (*Triticum* species), rye, barley, and oats; fertile hybrids between maize and teosinte; complex hybrid swarms in mints (*Mentha*), sages (*Salvia*), and thymes; extensive viable and fertile offspring in oaks (*Quercus*) across sections; hybrid zones in willows (*Salix*), poplars (*Populus*), and birches (*Betula*); interspecific hybrids in grapes (*Vitis*) and ivy; highly interfertile citrus (oranges, lemons, limes, grapefruits) with most commercial varieties arising from ancient and modern hybrids; and freely hybridizing plums, cherries, peaches, and apricots (*Prunus*). Under our framework, many plant "species," especially in Poaceae, Rosaceae, and Salicaceae, represent variants within large compatible groups, with morphological and ecological differences reflecting intra-species adaptation rather than strict barriers.

Plants are distinguished by an **autotrophic metabolism centered on photosynthesis**, in which light energy is converted into chemical energy through the fixation of inorganic carbon. Using chloroplast-mediated pathways, plants synthesize organic compounds from carbon dioxide and water, forming the energetic base of most terrestrial ecosystems. This self-sustaining metabolic mode, coupled with the storage of energy in complex carbohydrates, differentiates plants from heterotrophic fungi and animals, as well as from metabolically autonomous single-celled organisms lacking multicellular photosynthetic integration.

Animals

Animals constitute a distinct biological kingdom defined by obligate multicellularity, extensive cellular differentiation, and coordinated physiological integration across tissues and organ systems. Members of this kingdom exhibit complex developmental programs, internal regulatory mechanisms, and active interaction with their environment. Animals are universally heterotrophic and depend on organic carbon sources produced by other organisms, placing them within interconnected ecological and energetic networks. These shared biological characteristics establish animals as a coherent kingdom-level grouping, within which species boundaries are evaluated according to genetic compatibility rather than morphological or ecological similarity.

Animals are characterized by a **heterotrophic, ingestive metabolism**, in which energy and nutrients are acquired through the consumption of organic material followed by internal digestion. Unlike fungi, digestion occurs within specialized internal compartments, and unlike plants, animals cannot synthesize biomass directly from inorganic carbon sources. This metabolic dependence on ingestion supports high energy throughput, complex tissue specialization, and coordinated multicellular activity. The ingestive metabolic strategy is the primary physiological criterion distinguishing animals from other multicellular kingdoms.

Birds (Aves)

Hybridization is widespread in birds, with approximately 16% of species known to produce hybrids, often fertile.^{1 3} Examples include viable and fertile offspring in mallards with numerous ducks; extensive hybrid zones with fertile backcrosses in gulls; frequent interbreeding in waterfowl, pheasants, and hummingbirds; crosses in landfowl (galliformes) such as common pheasants with grouse and turkeys, and quail with partridge within Phasianidae; hybrids between swans and geese (swoose); interspecific crosses in cuckoos, cranes, swallows, and warblers; documented cases in raptors (eagles, hawks, owls) in captivity or overlap zones; and occasional hybrids in storks, herons, pelicans, vultures, doves, ravens, and sparrows, typically within genera. Ostriches, as ratites, show no known intergeneric hybrids. Notably, peafowl (*Pavo cristatus* and *Pavo muticus*) produce fertile Spalding hybrids, demonstrating compatibility between recognized species. Under our framework, many traditionally separate bird “species,” particularly in waterfowl, gulls, and landfowl, form broad compatible groups via offspring production, with morphological and behavioral differences representing intra-species variation. Domestic chickens (**Gallus gallus domesticus**) hybridize extensively with wild junglefowl, pheasants, and (rarely) turkeys and guineafowl, often producing viable and fertile offspring. Pheasant species frequently interbreed, as do many galliformes in captivity and overlap zones. Under our framework, these taxa form broad compatible groups, with plumage and behavioral variation representing intra-species diversity.^{4 6 - 4 7} The Galápagos finches exhibit pervasive hybridization among forms, with viable and fertile hybrids

documented across multiple lineages. Genomic analyses reveal extremely low divergence, with most variation residing in regulatory regions associated with beak morphology rather than genome-wide isolation. Rapid adaptive shifts in beak size and shape arise through ecological selection acting within this compatible assemblage, not through intrinsic reproductive barriers. Under the genetic compatibility framework, Darwin's finches therefore constitute a single species, with the traditionally named taxa representing adaptive variants within one compatible reproductive group.^{13, 38}

Marine Animals

Cetaceans (Whales, Dolphins, and Porpoises)

Among cetaceans, documented hybrids include viable and sometimes fertile blue whale × fin whale crosses with evidence of backcrossing¹⁴ ; viable and fertile bottlenose dolphin × false killer whale (wholphins)¹⁵ ; narwhal × beluga (narlugas) viable and showing signs of fertility¹⁶ ; and numerous other delphinid crosses (e.g., common dolphin × striped dolphin, Risso's dolphin × bottlenose dolphin). Killer whale × bottlenose dolphin hybrids in captivity produce viable (though short-lived) offspring, indicating no absolute intrinsic barrier. Under our framework, many traditionally separate cetacean “species” form extensive compatible groups connected by demonstrated offspring production, with size, dietary, and habitat differences representing intra-species adaptation rather than reproductive boundaries.

Cetaceans display remarkable genetic compatibility across genera and families. Confirmed wild hybrids include blue whale × fin whale crosses with evidence of fertility and backcrossing; multiple documented bottlenose dolphin × false killer whale offspring (wholphins), some fertile; and increasing reports of narwhal × beluga hybrids (narlugas) in changing Arctic waters, viable and potentially fertile. Additional delphinid hybrids involve Risso's dolphins, striped dolphins, and common dolphins, often producing viable offspring despite behavioral and size differences. These patterns indicate broad compatible groups within Balaenopteridae and Delphinidae, unified by offspring production under our criterion.

Pinnipeds (Seals, Sea Lions, and Walruses)

Pinnipeds demonstrate considerable genetic compatibility across genera and families, often producing viable and fertile hybrids despite behavioral, morphological, and ecological differences. Documented examples include California sea lion × Steller sea lion; gray seal × harbor seal; harp seal × hooded seal; South American sea lion × fur seals; and various phocid-otariid crosses in overlap zones or captivity¹⁷ . Rare attempts involving walruses show no absolute barriers. Under our framework, the repeated production of viable and often fertile offspring unifies many pinniped taxa into broader compatible groups, with differences in body size, flipper structure, and breeding behavior reflecting intra-species variation rather than strict genetic boundaries.

Sirenians (Manatees and Dugongs)

Sirenians, comprising manatees (*Trichechus* spp.) and the dugong (*Dugong dugon*), are slow-moving, fully aquatic herbivorous mammals with disjunct tropical distributions. Direct intergeneric hybridization between manatees and dugongs has never been observed, reflecting deep phylogenetic divergence and allopatric ranges. Within manatees, the three recognized species—West Indian (*T. manatus*), Amazonian (*T. inunguis*), and West African (*T. senegalensis*)—show marked ecological separation, yet genetic studies reveal low divergence and evidence of historical gene flow in coastal populations. No controlled crosses have been attempted, but the absence of intrinsic post-zygotic barriers in related data suggests potential compatibility under overlap conditions. The dugong, more distantly related, exhibits greater genomic divergence. Under our framework, the *Trichechus* species form a single broad compatible group connected by potential offspring production, with habitat specialization indicating varieties of the same species; the dugong remains uncertain, due to the absence of demonstrated offspring production.

Cephalopods (Squids and Octopuses)

Cephalopods, including squids (Teuthida) and octopuses (Octopoda), are highly intelligent marine mollusks with complex nervous systems and behaviors. They reproduce exclusively sexually, with separate sexes, elaborate courtship displays, and internal fertilization via spermatophores transferred by a specialized male arm (hectocotylus). Most species are semelparous, spawning once before dying, though some exhibit multiple or intermittent spawning. No asexual reproduction or clonal lineages occur in cephalopods; parthenogenesis is unknown. Interspecific hybridization is extremely rare or undocumented, even between closely related species, due to behavioral barriers, precise mating mechanisms, and likely molecular incompatibilities in gamete recognition. Genomic studies reveal highly rearranged chromosomes and significant divergence even within orders. Under our framework, the absence of demonstrated offspring production delineates sharp boundaries between most traditionally recognized species, with cryptic genetic diversity often indicating distinct compatible groups rather than broad unification seen in vertebrates.

Cnidarians (Jellyfish and Corals)

Cnidarians, encompassing jellyfish (primarily Scyphozoa and Cubozoa) and corals (Scleractinia within Anthozoa), exhibit diverse life cycles with polyp and medusa stages in many species. Most reproduction is sexual via broadcast spawning, though asexual budding and fission are common in polyps, supporting clonal lineages. Observed instances of interspecific hybridization are rare in jellyfish, with mass spawnings potentially producing hybrids that settle as polyps, though survival and viability remain uncertain. In contrast, scleractinian corals, particularly in the genus *Acropora*, frequently hybridize naturally and experimentally, producing viable F1 offspring (e.g., *Acropora prolifera* as a hybrid of *A. palmata* and *A. cervicornis* in the Caribbean; similar patterns in Indo-Pacific *Acropora* species pairs)¹⁸. These hybrids often show intermediate morphologies and can be fertile, contributing to reticulate

evolution and increased genetic diversity. Under our framework, the prevalence of asexual clonal lineages in polyps supports broad cohesion within compatible groups; observed offspring production in corals unifies many traditionally separate *Acropora* taxa into larger compatible groups, while the rarity of confirmed jellyfish hybrids delineates sharper boundaries, with behavioral and temporal spawning differences acting as superficial barriers.

Sponges (Porifera)

Sponges, the simplest multicellular animals, predominantly reproduce asexually via fragmentation, budding, or gemmules, supporting extensive clonal lineages. Sexual reproduction involves broadcast spawning, with most species hermaphroditic but exhibiting temporal separation to favor cross-fertilization. Interspecific hybridization is extremely rare, with only isolated reports (e.g., potential hybrids in *Phakellia* species via genomic evidence of past gene flow, and occasional cryptic mixtures mistaken for single species)³¹. Under our framework, the dominance of clonal reproduction supports broad intra-specific cohesion; the near-absence of demonstrated interspecific offspring production delineates sharp boundaries between most traditionally recognized sponge species, with cryptic diversity reflecting distinct compatible groups.

Tunicates (Sea Squirts and Relatives)

Tunicates (Urochordata), close chordate relatives of vertebrates, exhibit diverse reproductive modes: solitary forms are typically sexual broadcasters, while colonial species combine sexual spawning with extensive asexual budding. Colonial tunicates like *Botryllus schlosseri* fuse only with genetically compatible individuals (sharing alleles at the Fu/HC locus), forming chimeras while rejecting non-kin. Interspecific hybridization is rare in nature but documented in laboratory crosses (e.g., viable but asymmetrically infertile hybrids between *Ciona robusta* and *Ciona intestinalis*)^{3 2}. Under our framework, asexual budding and fusion support broad clonal cohesion within compatible groups; limited interspecific offspring production delineates boundaries, with fusion compatibility providing a precise genetic recognition system analogous to offspring production in sexual forms.

Flatworms (Platyhelminthes)

Flatworms include free-living planarians (Tricladida) and parasitic flukes/tapeworms (Trematoda/Cestoda). Many species reproduce both sexually and asexually: planarians are famous for fission followed by regeneration, producing clonal lineages; parasitic forms typically have complex life cycles with sexual phases in definitive hosts and asexual multiplication in intermediate hosts. Interspecific hybridization is rare but documented in free-living forms (e.g., *Schmidtea mediterranea* × *Schmidtea polychroa* produce viable but often sterile hybrids in laboratory crosses; natural hybrid zones reported in *Dugesia*)^{3 3}. Parasitic flatworms show limited evidence of hybridization due to host specificity and life-cycle constraints. Under our framework, extensive asexual fission and regeneration support broad clonal cohesion in planarians; limited interspecific offspring production delineates sharper boundaries in most groups,

with documented hybrids unifying closely related *Schmidtea* and *Dugesia* forms into broader compatible groups while host barriers act as superficial constraints in parasites.

Gastropods (Slugs and Snails)

Gastropods, including terrestrial slugs, land snails, and numerous marine species (e.g., sea slugs/nudibranchs, cone snails, limpets, abalone), are mollusks with diverse reproductive strategies. Most are simultaneous or sequential hermaphrodites, capable of both self-fertilization and cross-fertilization. Asexual reproduction is rare, though some freshwater species exhibit parthenogenesis. Interspecific hybridization is documented in several groups: land snails (e.g., *Cepaea nemoralis* × *Cepaea hortensis* produce viable hybrids in contact zones^{3 4}); marine gastropods such as *Littorina littorea* × *Littorina obtusata* form hybrid zones with intermediate shell morphology³⁵; and nudibranchs show occasional hybridization in sympatric species pairs. Many terrestrial and freshwater gastropods form extensive hybrid swarms where ranges overlap. Under our framework, widespread hermaphroditism and documented interspecific offspring production unify many traditionally separate gastropod taxa into large compatible groups, with shell polymorphism and ecological differences reflecting intra-species adaptation rather than strict barriers.

Fish

Cartilaginous Fish (Chondrichthyes: Sharks, Rays, and Chimaeras)

Cartilaginous fish possess skeletons of cartilage rather than bone and reproduce via internal fertilization. Major groups include sharks (Selachimorpha), rays and skates (Batoidea), and chimaeras (Holocephali). Observed interspecific hybridization is rare but documented in several shark lineages: common blacktip shark (*Carcharhinus limbatus*) × Australian blacktip shark (*C. tilstoni*) produce viable and fertile hybrids in overlapping Australian waters¹⁹; similar viable hybrids occur between varieties of reef sharks (e.g., grey reef shark *C. amblyrhynchos* and Caribbean reef shark *C. perezi* in experimental settings, though natural occurrence is unconfirmed). Stingrays exhibit occasional hybrids (e.g., round stingray *Urolophus halleri* × yellow stingray *U. jamaicensis* in captivity). No hybrids are known between sharks and rays or with chimaeras, reflecting deep genetic barriers. Under our framework, demonstrated offspring production unifies closely related blacktip and some reef shark forms into broader compatible groups; the absence of hybrids across major orders delineates sharp boundaries, with most traditionally recognized shark and ray “species” representing distinct compatible groups.

Bony Fish (Osteichthyes: Ray-Finned and Lobe-Finned Fish)

Bony fish dominate marine and freshwater environments, with ray-finned fish (Actinopterygii) comprising the vast majority (e.g., tuna, salmon, cod, clownfish, groupers, parrotfish, jacks/trevallies (Carangidae, including giant trevally, bluefin

trevally, crevalle jack), and marine angelfish (Pomacanthidae)). Hybridization is widespread, particularly in freshwater and reef-associated families. Documented examples include viable and often fertile hybrids between Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*); numerous cichlid hybrids in African Great Lakes with fertile backcrosses; extensive hybridization in cyprinids (carp, minnows); sunfish (*Lepomis*) species producing fertile hybrids; grouper (*Epinephelus*) species forming hybrid swarms on reefs; parrotfish hybrids showing intermediate coloration and viability; jacks such as bluefin trevally \times giant trevally and bluefin trevally \times bigeye trevally; and marine angelfish exhibiting exceptionally high hybridization rates (nearly half of all species documented to hybridize, often with intermediate coloration), including crosses in *Pomacanthus* (e.g., emperor \times bluering), *Holacanthus* (e.g., queen \times blue), and *Centropyge* genera.²⁰ Marine pelagic species like tuna show rare but confirmed hybrids (e.g., bluefin \times yellowfin in captivity). Under our framework, the frequent production of viable and often fertile offspring unifies many traditionally separate bony fish taxa—especially in Salmonidae, Cichlidae, Serranidae, Scaridae, Carangidae (jacks/trevallies with multiple varieties unified by hybrids), and Pomacanthidae (angelfish with prolific hybridization across genera)—into large compatible groups, with ecological and morphological variation reflecting intra-species adaptation rather than absolute genetic barriers.

Echinodermata (Starfish, Brittle Stars, Sea Urchins, Sea Cucumbers, Sand Dollars, and Crinoids)

Echinoderms predominantly reproduce sexually via broadcast spawning, with external fertilization in open water; many species also exhibit asexual modes such as fission (body division followed by regeneration) or larval cloning. Starfish (Asterozoa), including cushion stars, sugar stars, and multi-armed forms, frequently regenerate lost arms and, in some species, undergo fission to produce clones. Brittle stars and basket stars (Ophiurozoa) possess distinct arms separate from the central disk; they are prolific regenerators and include many fissiparous species. Sea urchins (Echinozoa), encompassing heart urchins, egg urchins, and pencil urchins, are herbivores that graze on kelp; laboratory crosses sometimes yield viable hybrids between closely related forms, though natural interspecific offspring production is rare due to molecular gametic incompatibilities (species-specific sperm-egg recognition proteins such as bindin and its corresponding egg receptors). Sea cucumbers (Holothurozoa) are worm-like, burrowing filter-feeders capable of transverse fission and autotomy. Sand dollars are flattened, burrowing irregular urchins. Crinoids (sea lilies and feather stars) are often stalk-attached filter-feeders with limited mobility. Under our framework, the prevalence of clonal lineages and regeneration in asterozoans, ophiurozoans, and holothurozoans supports broad intra-class cohesion via asexual criteria; sexual groups are delineated by genomic similarity thresholds, with cryptic diversity in forms like sea urchins reflecting substructure rather than absolute boundaries.

Terrestrial Land Animals

Reptiles

Snakes

Snakes (Serpentes) rarely hybridize in nature but produce viable offspring in captivity (e.g., corn snake × kingsnake, gopher snake × bullsnake, puff adder × gaboon viper). Under our framework, the presence of viable offspring in captivity unifies some closely related snake forms into broader compatible groups, with behavioral barriers often acting as superficial constraints.

Lizards

Lizards exhibit frequent hybridization: whiptail lizards (*Aspidoscelis*) include parthenogenetic hybrid-derived species; fence lizards (*Sceloporus*) form hybrid zones; *Liolaemus* species show common interspecific hybrids. Under our framework, widespread offspring production unifies many lizard taxa, such as in *Aspidoscelis* and *Sceloporus*, into large compatible groups.

Crocodiles

Crocodiles show documented hybrids mostly in captivity (e.g., Cuban × American crocodile, Siamese × saltwater crocodile, American × Nile crocodile), with viable offspring but rare fertility. Under our framework, the production of viable hybrids unifies some *Crocodylus* taxa into compatible groups, though natural occurrence is limited.

Turtles

Turtles produce occasional viable hybrids (e.g., red-eared slider × yellow-bellied slider, hawksbill × green sea turtle, loggerhead × hawksbill). Under our framework, demonstrated offspring production unifies many turtle taxa, especially in *Trachemys* (sliders) and *Cheloniidae* (sea turtles), into broader compatible groups.

Amphibians

Frogs and Toads

Frogs and toads (*Anura*) produce viable and sometimes fertile hybrids (e.g., gray treefrog complex with diploid and tetraploid forms; European water frog hybrids forming klepton species; common × spined toads; American toad × Fowler's toad). Under our framework, widespread offspring production unifies many anuran taxa into large compatible groups, with polyploidy reflecting internal complexity.

Salamanders

Salamanders (Urodela) show frequent hybridization with unisexual hybrid lineages (e.g., *Ambystoma jeffersonianum* complex; blue-spotted × Jefferson salamanders; spotted salamander hybrids)^{2 6} . Under our framework, documented offspring production unifies many salamander taxa, such as in *Ambystoma*, into compatible groups, with hybrid origin often leading to parthenogenetic lineages.

Terrestrial Invertebrates

Insects

Insects show variable hybridization: butterflies (*Heliconius*) form hybrid zones^{2 7} ; *Drosophila* species produce hybrids with varying viability; longhorn beetle hybrids (e.g., Asian longhorn beetle crosses). Under our framework, documented sexual hybrids unify some insect taxa, while clonal reproduction in groups like aphids supports broad cohesion.

Spiders

Spiders rarely hybridize, but documented cases include *Habronattus* jumping spider hybrids (e.g., *H. americanus* × *H. ustulatus*) and *Tegenaria* house spider hybrids. Under our framework, the presence of viable hybrids unifies some arachnid taxa, with genital morphology often acting as a barrier.

Worms (Annelids)

Earthworms exhibit occasional interspecific crosses (e.g., *Eisenia andrei* × *E. fetida* producing fertile hybrids). Under our framework, demonstrated offspring production unifies some annelid taxa, with clonal lineages supporting cohesion in parthenogenetic forms.

Mammals

Felids (Cats)

Domestic cats (*Felis catus*) and European wildcats (*Felis silvestris*) produce fully fertile hybrids. Among larger felids, lions (*Panthera leo*) and tigers (*Panthera tigris*) generate viable ligers and tigons²¹; some ligers are fertile (particularly females, which can backcross with lions or tigers). Similar patterns appear in leopard-jaguar crosses. The *Panthera* lineage thus constitutes one species under offspring-production criteria, with fertility reduction indicating internal structure rather than separation. No hybrids form between small and large felids due to deeper genetic barriers.

Canids (Dogs)

Domestic dogs (*Canis familiaris*), grey wolves (*Canis lupus*), coyotes (*Canis latrans*), and eastern wolves produce viable and typically fertile offspring readily, forming extensive hybrid swarms (coywolves) in eastern North America with varying admixture (typically 60 – 84% coyote, 8 – 25% wolf, 8 – 11% dog)²². Identical chromosome number (78) and absence of intrinsic barriers support classification as a single species despite pronounced morphological variation from domestication.

Bears

Documented hybrids include viable and frequently fertile grizzly × polar bear crosses (grolar/pizzly bears), with at least eight confirmed wild cases descending from one female polar bear and multiple grizzly males, including second-generation backcrosses²³; viable and fertile American black bear × brown bear crosses; historical captive hybrids between various *Ursus* species, such as brown × Asiatic black bear²⁴ and sloth bear × Asiatic black bear; and genomic evidence of ancient hybridization between polar and brown bears²⁵. Under the genetic compatibility framework, nearly all *Ursus* individuals belong to a single species. Giant pandas (*Ailuropoda melanoleuca*), belonging to a separate genus, produce no offspring with *Ursus* and are therefore excluded.

Ungulates

Under our framework, the production of viable and often fertile offspring unifies many ungulate taxa, such as in Equidae (horse-donkey-zebra), Bovidae (cattle-bison), and Caprinae (sheep-goat), into large compatible groups.

Deer

Deer (Cervidae) produce viable and often fertile hybrids (e.g., red deer × sika deer, mule deer × white-tailed deer, Père David's deer × red deer, sambar deer × red deer)²⁶. Under our framework, demonstrated offspring production unifies many Cervidae taxa into broader compatible groups, with ecological differences reflecting intra-species variation.

Equidae (Horse, Zebra, Donkey, Mule)

Horses show broad compatibility: horses (*Equus caballus*) × donkeys produce viable mules (jack × mare) and hinnies (stallion × jenny), with mules more common and often used for work despite sterility²⁷; horses × zebras produce viable zorses or zebroids (usually stallion zebra × mare horse), though typically sterile²⁸.

Bovidae (Cattle)

All species within the genus *Bos* (domestic cattle *Bos taurus/indicus*, yak *Bos grunniens*, gaur *Bos gaurus*, banteng *Bos javanicus*) readily hybridize, producing viable offspring, with female hybrids often fertile. Domestic cattle also cross with American bison (*Bison bison*) to produce fertile beefalo, and with yak. These patterns unify a large compatible group across traditionally separate species and genera, with morphological and ecological differences reflecting adaptation rather than intrinsic barriers.^{4 3- 4 5} Domestic cattle (*Bos taurus*) × American bison (*Bison bison*) yield fertile beefalo²⁹; yak × cattle produce viable hybrids.

Caprinae (Sheep and Goats)

Sheep (*Ovis aries*) and goats (*Capra hircus*) belong to different genera yet produce rare viable hybrids ("geeps" or sheep-goat chimeras) when crossed artificially, with documented live births showing intermediate traits.^{3 0} Although most such offspring are sterile and survival is low, occasional female fertility has been reported in stabilized lines. Under our framework, the production of any viable offspring demonstrates genetic compatibility sufficient to unify sheep and goats within a broader compatible group, with deep chromosomal and behavioral differences accounting for rarity and reduced fertility; treated as intra-species variation rather than absolute barriers.

Elephants (Proboscidea)

Elephants represent an informative test of the genetic compatibility framework due to long-standing taxonomic debates. Within Africa, the forest elephant (*Loxodonta cyclotis*) and savanna elephant (*L. africana*) show genomic introgression and hybrid zones, especially across ecotones in central and eastern Africa.^{39 - 4 0} Genetic surveys have identified individuals of mixed ancestry where forest and savanna populations meet, including first-generation (F1) and multi-generation hybrids, with evidence that some hybrids are fertile and contribute to subsequent gene flow.^{39 - 4 0} These data demonstrate bidirectional hybridization between the African elephant lineages, indicating reproductive compatibility despite deep divergence and morphological differences.^{39 - 4 0}

In contrast, intergeneric hybrids between the African and Asian elephant (*Elephas maximus*) have been documented only once in the zoological record. In 1978 at Chester Zoo (UK), an Asian female and African male produced a male calf named "Motty," confirming that cross-genus mating can yield viable hybrid offspring under captive conditions.^{4 1- 4 2} Motty exhibited morphological traits intermediate between the two parent species, and although he died in infancy due to complications, his existence confirms genetic compatibility for offspring production between *Loxodonta* and *Elephas* when geographic and ecological barriers are removed.^{4 1- 4 2} Under the

genetic compatibility framework, these observations place African forest and savanna elephants within a broader compatible continuum, and demonstrate that even deeper phylogenetic divisions (e.g., between *Loxodonta* and *Elephas*) can produce viable offspring under appropriate conditions, challenging strict species boundaries defined by reproductive isolation alone.

Rodents

Rodents exhibit frequent hybridization in genera such as *Mus* (house mouse hybrids, e.g., *Mus musculus* × *Mus spretus*) and *Peromyscus* (deer mouse hybrids, e.g., *Peromyscus maniculatus* × *Peromyscus polionotus*), often with viable and fertile offspring. Under our framework, demonstrated offspring production unifies many rodent taxa into broader compatible groups, with cryptic diversity reflecting internal structure.

Monkeys, Apes, and Humankind

Monkeys show limited but documented cases of hybridization (e.g., baboon hybrids such as olive × yellow baboons, macaque hybrids such as rhesus × long-tailed macaques, and hybrid origins inferred in several colobine lineages). Under the genetic compatibility framework, observed offspring production unifies some primate taxa (e.g., *Papio*, *Macaca*) into compatible groups, while deeper genetic barriers maintain separation in others.

Bonobos (*Pan paniscus*) and Chimpanzees (*Pan troglodytes*)

Complete genome analyses of bonobos and common chimpanzees reveal extensive shared variation, incomplete lineage sorting, and clear evidence of historical gene flow between the two lineages, indicating that their separation has not been absolute at the genomic level.⁵,³⁶ In addition to genomic evidence, viable bonobo–chimpanzee hybrid offspring have been reported in captive settings, documented in zoological and primatological literature. These hybrids exhibited intermediate morphological and behavioral traits consistent with mixed ancestry.³⁷,⁴⁸ The demonstrated production of viable offspring satisfies the empirical criterion of genetic compatibility under this framework, irrespective of ecological or behavioral barriers that prevent such pairings in the wild. No confirmed wild hybrids are known, primarily due to strong allopatric separation imposed by the Congo River and divergent social systems. These barriers, however, represent constraints on opportunity rather than intrinsic genetic incompatibility. Under the genetic compatibility criterion, bonobos and chimpanzees therefore constitute a single compatible reproductive group, best interpreted as varieties or subspecies within a broader *Pan* species.

In contrast, no offspring have ever resulted from human – ape pairing attempts, including with chimpanzees. Barriers include chromosomal differences (46 chromosomes versus 48 in *Pan*), and extensive structural divergence revealed by

telomere-to-telomere genome assemblies.⁵ Across complete ape and human genome comparisons, 12.5 – 27.3% of each genome fails to align one-to-one, with gap divergence greatly exceeding single-nucleotide variation.⁵ These differences restrict successful gamete pairing and embryogenesis, establishing an unambiguous species boundary between *Homo sapiens* and *Pan*.

Resolution of the Species Problem

The proposed framework overcomes key limitations of prior concepts in four principal ways.

First, it achieves universality by incorporating asexual reproduction through clonal lineage criteria, thereby encompassing much of Earth's biodiversity — particularly microbes and protists, which are excluded under traditional reproductive-isolation definitions.

Second, it rests on empirical, testable evidence: offspring production or measurable genomic similarity, rather than subjective morphological traits or inferred historical isolation.

Third, it naturally accommodates hybridization and continua. Groups exhibiting any gene flow via offspring remain unified, while complete absence of offspring sharply delineates boundaries. This eliminates ambiguity in cases historically problematic, such as ring species or partial hybrid sterility.

Fourth, it extends coherently to entities of uncertain status, accommodating debated organisms through clonal criteria.

By focusing exclusively on genetic outcomes, the framework provides a consistent operational criterion that resolves the longstanding species problem.

The Principle of Genetic Compatibility:

An Empirical Fact Elevated to a Principle of Biology

The consistent application of the genetic compatibility criterion across all domains of life: from bacteria and viruses to plants, invertebrates, fish, amphibians, reptiles, birds, and mammals; reveals a deeper empirical regularity in biology.

The Principle of Genetic Compatibility:

“If organisms can produce offspring, they are genetically compatible.”

Organisms that can produce offspring or maintain a shared clonal lineage are by definition the same species.

The Principle of Genetic Compatibility

All replicating organisms on Earth belong to the largest group within which genetic material can be successfully transmitted to offspring:

- Sexual Organisms: *evidence of successful transmission is the production of any offspring, regardless of viability or fertility.*
- Asexual Organisms: *evidence of successful transmission is maintenance of a shared clonal lineage.*

This principle unifies the diversity of life under a single, testable principle and provides the long-sought resolution to the species problem. It may be regarded as a general biological law.

Methods/Proposed Empirical Tests of the Genetic Compatibility Framework

The Genetic Compatibility Framework is designed to be empirically testable across sexual, asexual, and mixed-reproduction taxa. Species boundaries are delineated by demonstrated incompatibility in producing viable, persisting offspring — either sexually (fertile hybrids) or asexually (stable clonal lineages). Below are practical testing protocols:

1. Sexual Taxa (e.g., hybridizing vertebrates, plants, invertebrates)

Perform controlled crosses between putative species or populations. Measure:

- F1 hybrid viability and fertility.
- F2 and backcross success rates.
- Long-term fitness (survival, reproduction in natural or semi-natural conditions).

Threshold: Persistent incompatibility (e.g., <5% fertile offspring over generations) supports separate species status. Examples: Darwin's finches (*Geospiza* spp.), polar/grizzly bears, coral hybrid zones.

2. Asexual/Clonal Taxa (e.g., bdelloid rotifers, parthenogenetic lizards, reef corals, many plants and microbes)

Assess clonal lineage stability and independence:

- Genetic divergence (whole-genome sequencing or markers) between lineages.
- Long-term persistence without sexual recruitment (monitor field populations over years).

- Absence of viable sexual recombination (if occasional sex occurs).

Threshold: Genetically isolated, self-sustaining clonal lineages with no ongoing gene flow qualify as distinct species equivalents.

3. Mixed or Facultative Systems (e.g., brooding corals, aphids, certain brittle stars)

Compare sexual vs. asexual offspring production under varying conditions (stress, density). Test whether clonal propagation maintains independent lineages despite potential sexual gene flow.

4. Fossil and Historical Application

Compatibility can be inferred from descendant lineages or from morphological and genetic proxies in extant relatives. These assessments are feasible using existing tools, including controlled breeding trials, genomic analyses, and field observations, and can be applied uniformly across taxa, addressing the current fragmentation of species concepts. The framework is falsifiable. If a lineage were discovered in which reproductive mode changes occur without corresponding genetic divergence, this would challenge its validity.

Discussion

The genetic compatibility framework prioritizes direct observation of gene flow potential over interpretive narratives. It reveals broad compatibility within many traditionally subdivided groups while identifying absolute barriers where they exist, as between humans and apes. By decoupling fertility from the primary species criterion, just as infertility among some humans does not split *Homo sapiens*, the definition avoids arbitrary thresholds and aligns with observable genetic reality. Integration of complete genomic data continues to refine divergence estimates and compatibility thresholds. Future extensions may establish quantitative similarity cut offs for clonal lineages and systematic application across microbial diversity, enabling testable predictions of species boundaries across all domains of life.

The framework establishes a clear hierarchical structure in biological classification. Species are defined as the largest empirically verifiable group capable of genetic transmission, via any offspring production in sexual organisms or shared clonal lineages in asexual ones. Absolute boundaries arise only where transmission fails entirely, as in human and great ape pairings blocked by extensive structural genomic divergences.

Within each maximal compatible species, morphological, ecological, behavioral, and adaptive differences appear as varieties or subspecies; intra-specific variations driven by local adaptation or historical factors, not intrinsic barriers. Examples include lions and tigers as varieties within a single *Panthera* species; polar bears as an Arctic variety

within broader *Ursus*; bonobos and chimpanzees as subspecies within unified *Pan*; Darwin's finches as adaptive varieties within one hybridizing Galápagos assemblage; and dogs, wolves, and coyotes as morphological varieties within a single canid species. Similarly, forest and savanna elephants are ecological varieties in *Loxodonta*, with the Asian elephant potentially a deeper variety given rare but documented cross generic offspring (Motty, 1978).

This framework is not proposed as a replacement for existing taxonomic practice, but as an operational criterion by which species boundaries can be evaluated consistently across biological systems. Current classifications may be retained, revised, or left unchanged depending on empirical outcomes under this criterion. The intent is not to collapse biological diversity, but to provide a testable, non-arbitrary definition of species membership applicable across sexual, asexual, and clonal lineages.

By focusing on empirical outcomes rather than inferred processes, the framework unifies taxa previously divided by morphological, ecological, or behavioral differences. Many traditionally separate “species,” such as plants, waterfowl, carnivores, and ungulates, are now understood as variations within larger compatible wholes. Sharp discontinuities remain only where gene transmission is impossible; providing a natural, testable boundary.

Empirical Hierarchy of Life Under the Genetic Compatibility Framework

Under the genetic compatibility framework, species represent the largest group of organisms capable of producing offspring, with varieties or subspecies reflecting intra-specific adaptation. Above species, reproduction is no longer possible; membership in higher ranks is therefore defined empirically by systemic and reproductive divergence. Families unite organisms with homologous reproductive systems and developmental patterns; classes group families with broader morphological and developmental similarities but completely incompatible reproductive mechanisms. At the kingdom level, fundamental differences in metabolism, cellular organization, and reproductive systems create absolute barriers to hybridization; empirically separating bacteria, plants, animals, fungi, and other kingdoms.

The resulting hierarchy:

Kingdom → Class → Family → Species → Varieties

grounds taxonomy in observable, testable biological realities. Genetic compatibility dictates species boundaries; systemic divergence defines all higher levels, providing a consistent, empirically driven scaffold for classifying the diversity of life.

Practical and Conservation Implications

The genetic compatibility framework offers a unified, empirical criterion for species delimitation but does not require or advocate revisions to current taxonomic nomenclature, conservation statuses, or management strategies.

Species names serve practical roles beyond scientific delimitation: they enable clear communication, support legal protections, and guide targeted conservation. Many traditionally recognized species represent ecologically distinct units with unique vulnerabilities, even when genetic compatibility permits offspring production.

A clear example is polar bears (traditionally **Ursus maritimus**) and grizzly/brown bears (**Ursus arctos**). Despite viable and sometimes fertile hybrids and evidence of gene flow, these bears occupy fundamentally different niches and face divergent threats; sea-ice loss imperils polar bears while many grizzly populations remain stable or expanding. Maintaining separate recognition preserves focused conservation efforts on their distinct needs. Under this framework they constitute ecological varieties (or subspecies) of the same species, given demonstrated offspring production.

Similar reasoning applies to other compatible yet ecologically specialized groups, such as African forest and savanna elephants, certain cetaceans, and Darwin's finches. The framework thus complements, rather than replaces, ecological and pragmatic considerations in applied conservation. Any taxonomic changes should follow established processes through relevant authorities, balancing empirical compatibility with real-world management requirements.

Scope and Limitations

The genetic compatibility framework is intentionally operational in scope. It does not seek to explain the evolutionary mechanisms by which compatibility arises or is lost; nor does it attempt to reconstruct phylogenetic histories or rates of divergence. Its sole criterion concerns the empirical fact of genetic transmission: whether genetic material can be passed across generations through offspring production in sexual organisms or maintained through shared clonal lineages in asexual ones.

Because the framework prioritizes observable outcomes, it does not assign species boundaries on the basis of morphology, ecology, behavior, or inferred evolutionary processes alone. Such features remain biologically informative, but are treated as descriptive attributes within species or as indicators of higher level systemic divergence rather than as primary criteria for species delimitation.

The framework is not intended to resolve all borderline or rare cases immediately. In instances where genetic compatibility has not been directly tested, species boundaries

remain provisional and subject to revision as empirical data become available. The approach therefore accommodates uncertainty without redefining boundaries on speculative grounds.

Application of the framework across all domains of life necessarily abstracts from taxon specific complexities. While the same criterion is applied universally, its empirical evaluation differs in practice between sexual, asexual, and clonal organisms. This variability reflects biological reality rather than inconsistency in the framework itself.

Finally, the taxonomic consequences of the framework are descriptive rather than prescriptive. The reclassification of traditionally named species follows from observed compatibility or incompatibility; it does not mandate changes to nomenclature, conservation policy, or regulatory practice. Such applications require separate normative and administrative considerations beyond the scope of the present work.

Data Availability and Original Contributions

This manuscript introduces a unified, empirically testable framework for species delimitation based on genetic compatibility, defined through observable offspring production in sexual organisms and shared clonal lineage continuity in asexual organisms. No new experimental organisms were generated for the purposes of this study. Instead, the framework data is established through the synthesis and integration of previously published observational, experimental, and genomic data drawn from peer-reviewed literature across evolutionary biology, systematics, genomics, and taxonomy.

All empirical observations referenced, including documented cases of hybridization, offspring viability and fertility, clonal lineage continuity, and genomic alignment statistics, are derived from publicly available sources cited within the manuscript. Comparative genomic figures, such as large-scale regions that do not align and single-nucleotide variant divergence between taxa, rely on published telomere-to-telomere assemblies and established genomic databases. No proprietary datasets were used.

The original contribution of this work lies not in the generation of new raw data, but in the formal synthesis, reorganization, and empirical unification of existing biological evidence into a single, falsifiable criterion for species definition that applies consistently across sexual organisms, asexual organisms, and biologically borderline entities. The manuscript explicitly reframes species boundaries as outcomes of demonstrable genetic transmission capacity, rather than inferred historical processes, morphological distinctions, or assumed reproductive isolation mechanisms.

By consolidating disparate observations under a single empirical rule, this work provides a predictive framework that can be directly tested using future observational, experimental, and genomic studies. All data necessary to evaluate the claims presented are accessible through the cited literature, and the framework is explicitly designed to be refined, constrained, or rejected as new evidence becomes available.

Experiments, Observations, and Sequences to Test and Prove the Law

The proposed genetic compatibility law is explicitly falsifiable, predictive, and testable, distinguishing it from prior species concepts that rely on retrospective inference. Its validity can be evaluated through multiple independent empirical approaches, several of which are already partially satisfied by existing data.

1. Observation-Based Tests: Natural and Ongoing Hybridization

Natural hybrid zones provide immediate, non-invasive tests of genetic compatibility. As geographic ranges shift due to environmental change, novel overlap zones emerge; these create opportunities for offspring production that were previously impossible.

Expanding overlap between grizzly bears (*Ursus arctos*) and polar bears (*Ursus maritimus*) predicts increasing frequencies of viable and fertile offspring; continued gene flow across generations confirms inclusion within a single species under the law. Highly hybridizing clades such as Darwin's finches, coral genera (*Acropora*), and many waterfowl species predict persistent offspring production and introgression across named taxa, supporting their classification as single, maximally compatible species.

Long-term population monitoring in such systems allows direct testing: continued genetic transmission confirms species unity; absolute failure confirms separation.

2. Experimental Tests: Captive or Controlled Crosses

In taxa where natural overlap is absent or rare, controlled breeding experiments provide direct tests of compatibility, subject to ethical, logistical, and conservation constraints.

Crosses among uncertain or disputed taxa, including within *Trichechus* manatees or among closely related felids and canids, predict viable offspring if genomic compatibility exists. Rare or controversial crosses, such as sheep–goat pairings, can be evaluated statistically across larger sample sizes; consistent offspring production, even with reduced fertility, supports inclusion within a broader compatible group.

Failure to produce offspring under controlled conditions, despite repeated attempts and appropriate pairing, predicts a true species boundary. Fertility and long-term viability are treated as secondary outcomes; offspring production itself constitutes the decisive empirical test.

3. Genomic Sequencing and Alignment Tests

High-resolution genomic data provide a quantitative means to predict compatibility prior to, or in lieu of, direct breeding experiments.

Telomere-to-telomere genome assemblies enable precise measurement of non-alignable genomic regions and structural incompatibilities. The law predicts that taxa unable to produce offspring will exhibit substantial alignment failure, as observed in human–ape comparisons, with approximately 12.5–27.3% non-alignable regions plus additional single-nucleotide divergence.

In borderline cases, including dugong–manatee comparisons and deep felid or cetacean splits, genomic alignment metrics predict whether offspring production is theoretically possible. In microbes, refinement of average nucleotide identity thresholds using newly sequenced strains predicts clonal species boundaries, with ≥ 95 –96% identity corresponding to cohesive, transmissible lineages.

4. Logical Structure of Empirical Proof

The law is confirmed when maximal biological groups permit genetic transmission and is falsified when absolute transmission failure occurs despite opportunity. Each test is direct, empirical, and independent of prior taxonomic assumptions. No circular reasoning is involved.

Existing observations already satisfy many of these conditions, demonstrating that the framework is supported by current evidence. Future experiments and genomic analyses do not rescue the law from uncertainty; rather, they serve to strengthen, refine, or delimit its predictive scope.

Novel Contributions

1. Unified Empirical Species Criterion Across All Life

This work presents the first explicit unification of species delimitation for sexual organisms, asexual organisms, and mixed reproductive systems under a single empirical criterion based on genetic compatibility: offspring production in sexual organisms and clonal lineage continuity in asexual organisms.

2. Formal Reclassification of Fertility as a Secondary Trait

The framework demonstrates that fertility and long-term viability cannot define species boundaries, as infertility occurs within universally accepted single species. Offspring production alone is identified as the decisive empirical indicator of compatibility.

3. Definition of Species as Maximal Compatible Groups

Species are formally defined as the largest biologically compatible groups capable of genetic transmission. Subdivisions below this level are treated as population structure, ecotypes, or variants rather than distinct species.

4. Explicit Separation of Genetic Incompatibility from Opportunity Barriers

Behavioral, ecological, geographic, and cultural barriers are formally distinguished from genetic incompatibility and are classified as constraints on mating opportunity rather than indicators of species boundaries.

5. Integration of Genome-Scale Alignment Failure into Species Delimitation

Large-scale genomic non-alignment and structural divergence are introduced as predictive indicators of absolute reproductive incompatibility, providing a direct genomic test of species boundaries.

6. Empirical Classification of Borderline Biological Entities

The framework provides a consistent, non-philosophical classification of bacteria, viruses, and prions based on genetic transmission capacity, resolving long-standing ambiguities without redefining life.

7. Demonstration of Empirical Inconsistencies in Legacy Species Concepts

The synthesis shows that widely accepted hybridization data directly contradict reproductive isolation-based species definitions, revealing systematic empirical failures in legacy frameworks.

8. Transformation of Species Delimitation into a Predictive Science

Species classification is converted from retrospective inference into a forward-predictive framework that generates testable expectations for hybridization, genomic compatibility, and future observational outcomes.

Competing interests

The authors declare no competing interests.

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