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Cryptic Insect Diversity Is Better Represented as a Continuum of Evidential Support Than as a Binary Taxonomic Diagnosis

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ABSTRACT

Cryptic diversity is often discussed as though a lineage were either cryptic or not, and as though molecular discovery, species delimitation, diagnosis, and formal naming were interchangeable stages of a single decision. Recent insect systematics shows a more heterogeneous pattern. Molecular clusters may expose previously overlooked lineages, but cluster number can depend on analytical method; mitochondrial and nuclear signals may differ; morphology can contradict, corroborate, or become informative only after genomic discovery; and ecological or reproductive evidence can strengthen an interpretation without independently fixing taxonomic rank. This perspective develops a proposed qualitative continuum of evidential support that keeps four tasks analytically distinct: discovery, delimitation, diagnosis, and naming readiness. The continuum does not assign numerical scores or prescribe a universal evidential package. Instead, it treats support as a structured combination of concordance, discordance, contextual modifiers, diagnostic recoverability, and taxonomic comparability. In this framework, "cryptic" describes a state of detectability and evidential maturity rather than a binary taxonomic property. The approach is intended to make uncertainty visible, prevent analytical clusters from being promoted automatically to species, and clarify when additional genomic, morphological, geographic, ecological, life-stage, or nomenclatural evidence is needed. The framework remains a conceptual synthesis requiring prospective evaluation across taxonomically and geographically diverse insect systems.

Keywords: Cryptic species, Species delimitation, Integrative taxonomy, DNA barcoding, Phylogenomics, Insect systematics

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Introduction

The expansion of sequence-based biodiversity discovery has exposed an asymmetry in insect systematics: candidate lineages can now be generated much faster than they can be compared, diagnosed, and formally revised. In large dark-taxon samples of Phoridae, rapid barcode partitioning produced hundreds of preliminary species hypotheses that could then be subjected selectively to morphological validation, demonstrating the practical value of separating first-pass discovery from later evidential testing [1]. That separation matters because a molecular partition is not equivalent to a formal taxonomic diagnosis. Barcodes can organize specimens and reveal candidate diversity, yet barcode evidence alone does not necessarily supply the comparative and diagnostic information

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required for species description [2]. Equally, naming a candidate requires attention to already described taxa and potential synonyms; omission of relevant prior taxonomic comparisons can weaken the evidential basis for a new name even when molecular differentiation is clear [3].

A second asymmetry concerns species-delimitation models themselves. Coalescent boundaries can correspond closely to reproductive isolation in some datasets without being perfectly equivalent to it: comparative work in *Drosophila* documented substantial, but incomplete, concordance between coalescent delimitations and reproductive-isolation evidence [4]. Simulation studies further show that structured populations may receive strong species-level support under multispecies-coalescent analyses even where the biological interpretation remains population divergence rather than established speciation [5]. Geography also changes the meaning of genetic structure. Differentiation among allopatric populations can arise under spatially continuous or historically isolated population processes, whereas sympatric persistence of differentiated lineages provides a different inferential context; geographic configuration therefore modifies the interpretation of molecular discontinuity rather than serving as a species criterion by itself [6].

These observations expose the limitation of a binary formulation in which a taxon is either accepted as a cryptic species or dismissed as analytical noise. The binary formulation collapses at least four logically distinct questions: has hidden structure been discovered; is that structure consistent with separately evolving lineages under the methods used; can the candidate entities be diagnosed or reliably associated with specimens and life stages; and is the evidence sufficient for defensible nomenclatural action? This article argues that these questions should be represented as a proposed continuum of evidential support. The continuum is not a numerical confidence score, a replacement species concept, or a universal recipe for how many markers or character systems are required. It is an inference architecture for keeping evidence classes, their conflicts, and their limits visible while taxonomic interpretation advances.

Materials and Methods

The continuum was constructed as a qualitative synthesis of recent methodological and empirical insect-systematics literature, with emphasis on studies that explicitly reveal how species hypotheses change when evidence classes or analytical assumptions change. Three methodological properties were treated as modifiers of delimitation evidence rather than as detachable technical details: violation of species-tree assumptions, evolutionary scenario dependence, and gene flow. Simulation and model-development studies show that inferred boundaries can change when multispecies-coalescent assumptions are violated, when divergence depth, population size, or migration differ among scenarios, and when gene flow is modeled rather than implicitly excluded [7–9]. These sources do not establish that coalescent methods are intrinsically unreliable. They establish that model support has to be interpreted relative to the demographic and analytical conditions under which it was obtained.

A second construction rule was to preserve evidence classes as analytically separable even when they are combined. Integrative work on Nearctic ambush bugs, for example, combines molecular evidence, geometric morphometrics, and ecological associations while retaining the possibility that the data classes will not resolve species boundaries identically [10]. Accordingly, the proposed continuum does not use majority voting across marker systems. Concordance can increase support, but discordance is retained as information because it may reflect incomplete lineage sorting, introgression, population structure, insufficient marker resolution, phenotypic overlap, sampling gaps, or genuinely competing taxonomic hypotheses.

The framework therefore organizes literature-supported observations into four functions: discovery evidence, delimitation evidence, diagnostic evidence, and naming readiness. These functions are ordered analytically but are not assumed to form an irreversible pipeline. A lineage may be strongly delimited but weakly diagnosed; a historically named species may be morphologically diagnosable while its genomic boundaries remain uncertain; or newly generated molecular candidates may later collapse after geographic or genomic reconciliation. The staged hypothesis-validation logic used for large-scale integrative taxonomy provides a practical precedent for separating preliminary partitions from validation [1], but the continuum introduced here is a proposed synthesis rather than an empirically validated scale. No numerical weights, universal thresholds, or predicted probabilities are assigned.

Results and Discussion

Recent insect studies use "cryptic" for biologically different situations. In the long-horn moth *Nemophora degeerella* complex, morphology and COI indicated hidden diversity, but genome-wide ddRAD data provided stronger lineage resolution than genital characters and a smaller nuclear-marker set [11]. Crypticity in this case therefore did not mean absence of phenotypic information; it described a condition in which conventional characters and limited loci did not express the same evidential resolution as denser genomic data. The evidential problem was not simply "morphology versus molecules," but unequal information content among character systems.

Other systems show that crypticity can diminish after targeted revision. An integrative revision of the *Encarsia pergandiella* parasitoid complex combined morphology, morphometrics, mitochondrial and nuclear data, and biological information to resolve diversity that had previously been hidden within a broader taxonomic concept [12]. Thus, "cryptic" should not be treated as synonymous with permanently undiagnosable. Some lineages are cryptic at discovery because relevant characters have not yet been identified, quantified, associated with the correct sex or life stage, or interpreted in a sufficiently resolved phylogenetic context.

Conversely, discovery of strong genetic structure need not complete the taxonomic task. In native North American *Solenopsis* fire ants, multilocus population-genetic analyses supported recognized taxa while also exposing divergent populations beyond existing species assignments [13]. Those populations constitute evidence of unresolved diversity, but genetic divergence alone does not specify whether every population should be described as a species. Across these examples, "cryptic diversity" is better understood as an evidentially heterogeneous condition: hidden lineage structure may be weakly supported, method-sensitive, strongly delimited but poorly diagnosed, or sufficiently corroborated for formal revision. The term therefore identifies a problem of detectability and inference maturity, not a single biological state.

Discovery evidence

Discovery evidence answers the narrowest question in the continuum: is there a reproducible signal suggesting that currently recognized taxonomy fails to capture all lineage structure? Genome-scale data can make that signal visible where gross morphology does not. In the *Temnothorax salvini* ant group, phylogenomic evidence revealed substantially more diversity than was apparent from the starting taxonomy, after which detailed morphological work helped diagnose the recovered entities [14]. The important sequence is evidential rather than procedural: genomics exposed candidate structure, but candidate structure was not treated as self-authenticating species status.

Discovery can also be unstable in magnitude. In Xenidae, alternative molecular delimitation procedures generated materially different numbers of putative species, demonstrating that the existence of substantial hidden diversity and the exact number of candidate entities are separable claims [15]. A high candidate count can therefore justify targeted taxonomic attention without licensing adoption of the largest analytical partition as the species total. Phylogenomic work on morphologically cryptic *Nylanderia* likewise shows how genome-scale evidence can clarify closely similar species complexes that would be difficult to resolve from superficial morphology alone [16]. Yet a well-supported genomic clade still requires interpretation at the relevant taxonomic level.

The opposite pattern is equally important: molecular discovery does not invariably increase species richness. In *Gnaptorina* darkling beetles, molecular species-delimitation results were largely congruent with morphology while also informing specific revisions [17]. Discovery evidence can therefore reveal overlooked candidates, corroborate established morphospecies, or expose disagreement among existing classifications. The proposed continuum treats these outcomes symmetrically. What matters at the discovery stage is whether a candidate signal is reproducible and interpretable under the sampling and method used, not whether it increases the number of named species.

Delimitation evidence

Delimitation evidence asks a stronger question than discovery: does the available evidence support treating candidate entities as separately evolving lineages under defensible analytical assumptions? It remains distinct from formal diagnosis because a model may strongly delimit lineages that are difficult to recognize phenotypically, and distinct from naming because delimitation does not by itself address every relevant synonym, type, or comparative taxon.

The *Phoebis* butterfly study illustrates why analytical output and taxonomic interpretation should remain separate. One delimitation outcome yielded more candidate entities than the final evidence-reconciled interpretation, showing that model-supported partitions can be revised when morphology, barcode patterns, and multilocus

evidence are considered together [18]. This is not evidence for a general rule that integrative taxonomy should always reduce species numbers. It is evidence that the number returned by a delimitation procedure can remain provisional.

Marker systems may also partition diversity at different granularities. In *Stenocorse* parasitoid wasps, nuclear 3RAD and mitochondrial data recovered broadly related but nonidentical genetic structure, with the main nuclear clusters not mapping mechanically onto every finer mitochondrial division [19]. Such discordance should not be erased by selecting the preferred marker after the fact. Mitochondrial subdivision can reflect lineage history, sex-biased processes, introgression, or population structure, while nuclear genomic evidence may integrate a different inheritance history. The appropriate taxonomic response is therefore to retain the discordance as part of the delimitation state.

Evidence for restricted contemporary gene flow can strengthen delimitation when it is interpreted together with divergence. In the *Bombus bifarius* complex, substantial genomic differentiation and lack of recent gene flow supported recognition of cryptic species despite overlapping colour variation [20]. The inference is bounded: failure to detect recent gene flow is not proof of permanent reproductive isolation, and the evidential significance depends on geographic sampling and analytical sensitivity. Conversely, greater genomic resolution can overturn apparent conflict. In the *Melanoplus scudderi* grasshopper complex, genome-wide data resolved a rapid radiation and supported morphologically recognized species that had appeared paraphyletic under earlier molecular evidence [21]. Apparent morphology–molecule disagreement can therefore result from insufficient marker resolution rather than from erroneous morphology.

For taxonomic practice, these cases are more informative when organized as delimitation states rather than as a list of techniques. The following ledger distinguishes recurrent evidence configurations and the response each configuration warrants without converting them into a score.

Table 1. Delimitation states that change the interpretation of cryptic insect lineage hypotheses

Cryptic-lineage signal		**Delimitation permission**	
Evidence conflict	**Lineage/marker context**	**Consequence for delimitation**	**Resolution test and binary-diagnosis boundary**
Model-output excess	Candidate entities outnumber the final integrative interpretation. A delimitation procedure resolves finer partitions than the combined taxonomic assessment retains	Treat the extra partitions as hypotheses requiring reconciliation, not as an automatic species total. Evidence-supported pattern; response is proposed.	Outcome may depend on model assumptions, sampling, and which independent evidence is available. Re-examine geography, morphology, genomic concordance, and existing taxonomy before formal action
Marker-granularity discordance	Nuclear and mitochondrial datasets divide the same complex differently. Major lineage structure is shared, but finer subdivisions are not equivalent across marker systems	Preserve competing partitions instead of selecting one marker system as intrinsically authoritative. Evidence-supported pattern; response is proposed.	Introgression, lineage sorting, sex-biased history, population structure, and unequal marker resolution can remain unresolved. Add genomic, geographic, or contact-zone evidence targeted to the discordant boundaries
Divergence with restricted recent gene flow	Genomic differentiation is accompanied by little detected contemporary exchange. Multiple genomic signals support differentiated lineages despite overlapping external phenotype	Species-boundary support is strengthened relative to divergence evidence alone. Evidence-supported pattern; response is proposed.	Non-detection of gene flow is conditional on sampling, analytical power, geography, and time scale. Test additional contact zones and independent diagnostic characters where feasible
Resolution-dependent reconciliation	Dense genomic evidence resolves a conflict produced by earlier limited markers. Earlier molecular paraphyly or ambiguity gives way to genome-wide lineage resolution consistent with other evidence	Reinterpret the earlier conflict as potentially data-limited rather than automatically taxonomic. Evidence-supported pattern; response is proposed.	Greater locus number does not remove sampling or model assumptions and is not universally decisive. Determine whether added loci resolve the same boundary across populations and analytical models

Diagnostic evidence

Diagnostic evidence addresses whether the entities under consideration can be recognized, associated, or distinguished in practice. This function is different from delimitation. A lineage can be strongly supported phylogenomically yet remain difficult to distinguish from a close relative in routine material; conversely, a useful diagnostic character does not independently demonstrate the evolutionary history that produced the difference.

Quantitative morphology can recover diagnostic information that is not obvious from traditional inspection. Wing geometric morphometrics has been used to assign historical bumblebee type specimens among cryptic species, illustrating that "cryptic" does not preclude measurable phenotypic discrimination [22]. Such performance remains dependent on the taxa, reference material, specimen condition, and character system examined. It should therefore be treated as diagnostic evidence for the tested complex rather than as a general expectation that morphometrics will resolve all cryptic insects.

Diagnosis also has a life-stage dimension. High-throughput NGS barcodes can match larval and adult insects that would otherwise be difficult to associate morphologically, thereby extending taxonomic information across ontogeny [23]. Stage matching, however, does not itself delimit species: identical or near-identical barcode assignments connect specimens to an existing lineage hypothesis but do not establish that the lineage represents an independently evolving species. In the proposed continuum, life-stage association therefore increases diagnostic completeness without automatically increasing delimitation support.

Automated image recognition introduces a further distinction between diagnostic capability and transferability. In Miridae, machine-learning identification of very similar species performed more strongly under controlled collection-image conditions than under less standardized image domains, demonstrating that diagnostic performance is conditional on acquisition setting [24]. Experimental work on computer vision in insect systematics likewise shows that image-based classification can supplement expert recognition when the training and test conditions are appropriate [25]. Neither result turns an algorithmic classification into a taxonomic diagnosis in the nomenclatural sense. Automated phenotypic evidence is useful only within a validated domain and should remain subordinate to the broader evidential question of what entity is being diagnosed.

Taken together, diagnostic evidence can arise from subtle morphology, quantitative morphometrics, molecular association across life stages, or validated image-based recognition. These tools answer different operational questions and should not be collapsed into a single "diagnosable/not diagnosable" variable. A cryptic candidate may be diagnosable only in one sex, one life stage, one geographic region, one imaging domain, or one genomic assay. Diagnostic support is therefore multidimensional and conditional, which is precisely why it must remain analytically separate from discovery and delimitation in any evidential continuum.

Naming readiness

Naming readiness is the point at which evidence supporting a lineage hypothesis is evaluated against the separate obligations of formal taxonomy. A barcode partition may aid discovery, but description requires evidence distinguishing the proposed entity from relevant alternatives [2]. A candidate is also inadequately assessed when previously described species that could encompass or synonymize it are omitted [3]. Naming readiness therefore concerns whether evidence addresses the taxonomic act contemplated.

Phylogenomic resolution can precede nomenclatural completion. In *Nylanderia*, genome-scale data clarified relationships and biogeographic history while leaving substantial species-level work to subsequent revision [26]. Phylogenetic confidence and nomenclatural readiness therefore occupy different dimensions. A supported lineage may still lack an accessible diagnosis, type linkage, geographic coverage, comparison with historical names, or evidence that discontinuous populations warrant species rank.

When several dimensions converge, formal action can become defensible. Integrative revision of *Agraulis* and *Dryas* combined multilocus delimitation, morphology and morphometrics to clarify species limits and support taxonomic changes [27]. This supports a proposed naming-readiness criterion based on task completion rather than a fixed evidence quota: lineage support, practical diagnosability and comparison with existing taxonomy should each be sufficiently addressed. Unresolved discordance should remain visible rather than becoming an artificial certainty grade.

Because these dimensions can mature at different rates, naming readiness is better visualized as repeated integration across taxonomic assessment episodes than as the final box in a linear pipeline. **Figure 1** compresses that distinction by keeping lineage, diagnosis and nomenclatural-comparison signals separate while allowing targeted re-examination to alter later interpretation.

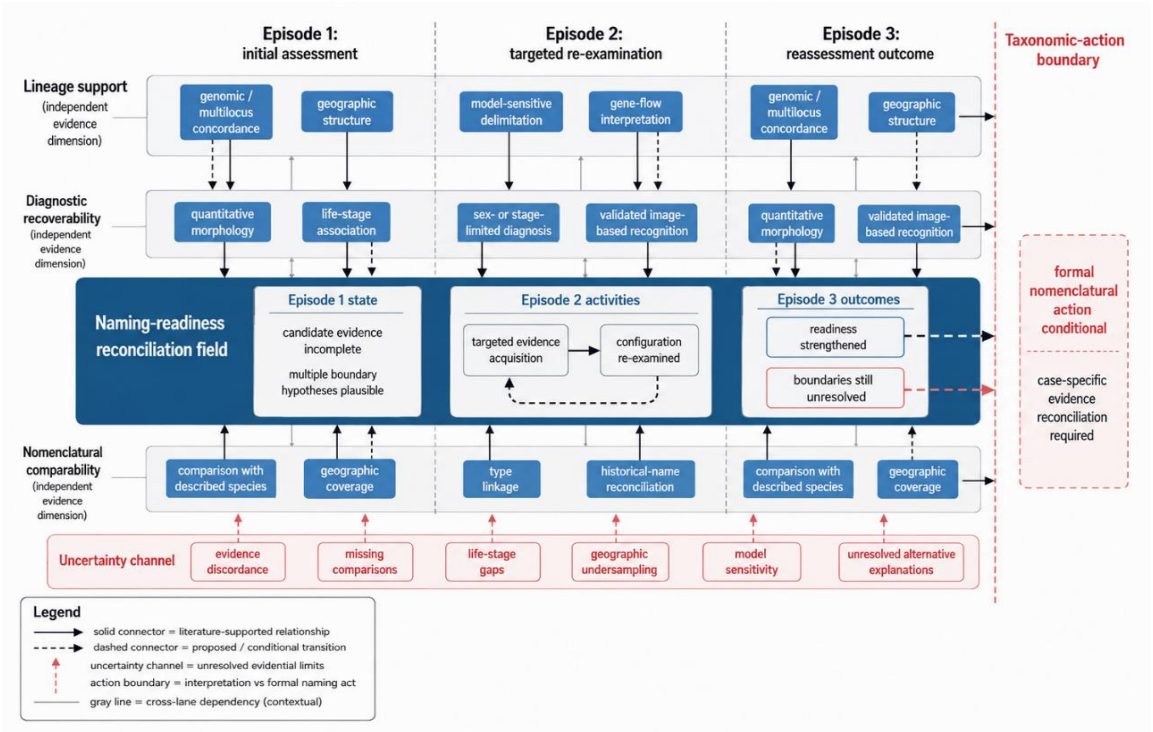


Figure 1. Naming readiness as repeated reconciliation of lineage support, diagnosability and nomenclatural comparability

Continuum states of cryptic diversity

The preceding sections imply that cryptic diversity cannot be represented adequately by a single threshold separating "species" from "not species." The proposed continuum instead describes qualitative states that can strengthen, weaken or change direction as evidence is added; they differ by the structure of support and uncertainty, not numerical scores.

A first boundary-sensitive condition is differentiation with residual contact. In *Junonia* butterflies of the American southwest and Mexico, mitochondrial, nuclear and morphological variation revealed cryptic diversity together with hybrid zones [28]. Hybridization need not erase lineage differentiation, but differentiated markers do not demonstrate complete reproductive isolation. Such cases occupy a proposed discordance-retaining state in which the meaning of gene exchange remains context dependent.

Ecological differentiation provides another modifier rather than an independent endpoint. In Japanese *Octotemnus* beetles, host use differed among cryptic taxa that were also supported by molecular and morphological evidence and subsequently described [29]. Host association can strengthen a lineage interpretation when independent evidence concurs, but it cannot prove an adaptive mechanism or species boundary. The continuum records ecology as corroborative or conflicting context.

Taxonomic level also constrains what a given signal can establish. Molecular evidence in *Choristoneura* informed genus delimitation, biogeography and diversification, demonstrating that strong phylogenetic evidence can have consequences above the species level [30]. Yet support for a genus-level relationship cannot be transferred unchanged into a species diagnosis. The proposed continuum is therefore inference-level specific: evidence is evaluated against the taxonomic question it actually tests.

These distinctions yield a small set of proposed states defined by relationships among discovery, delimitation, diagnosis and naming readiness rather than by an assumed linear ascent. **Table 2** makes the boundaries explicit and identifies what further test would be informative in each state.

Table 2. Proposed continuum states linking cryptic-diversity evidence to unresolved taxonomic boundaries

Evidential maturity			Naming readiness	
Continuum position	**Focal distinction**	**Evidence configuration**	**Taxonomic consequence**	**Boundary and next test**

Signal-only candidate	Discovery exceeds delimitation	Reproducible molecular or population structure without adequately reconciled species-level evidence	Retain as a candidate lineage; do not equate the partition with a species	Population structure, geography, marker choice or incomplete sampling may generate the signal. Test independent loci, geography and alternative delimiters
Delimited but discordant candidate	Strong lineage support coexists with conflicting evidence classes	Nuclear, mitochondrial, morphological or gene-flow evidence differs in granularity	Preserve the supported lineage hypothesis together with the discordance	Introgression, incomplete lineage sorting, phenotype overlap or model sensitivity remains plausible. Target the particular discordant boundary with genomic, contact-zone or phenotypic data
Delimited–diagnosable, nomenclaturally incomplete	Lineage and diagnostic support exceed naming readiness	Candidate entities can be distinguished, but type linkage, historical names or comparative coverage remain incomplete	Taxonomic action remains premature despite strong biological evidence	Existing synonyms, unsampled ranges or inadequate name-bearing material may alter the formal conclusion. Resolve nomenclatural comparisons and type association
Boundary-sensitive differentiated lineage	Differentiation persists with hybridization, ecological overlap or geographic complexity	Multiple evidence classes support structure, but exchange or context complicates discreteness	Avoid both automatic lumping and automatic splitting	Gene flow, ecological association or spatial structure has ambiguous taxonomic meaning. Expand temporal, geographic and reproductive-context sampling
Convergent high-support case	Discovery, delimitation, diagnosis and nomenclatural comparison are mutually compatible	Independent evidence supports the same taxonomic interpretation and relevant alternatives have been addressed	Formal revision may be defensible, but action remains case-specific	No universal number of evidence classes or numerical cutoff exists. Document remaining limitations and apply nomenclatural rules explicitly

Decision consequences for taxonomy

The practical consequence of a continuum is not indecision; it is better matching of taxonomic action to the inference actually supported. Resolving cryptic diversity can alter ecological interpretation. In *Sycophila* parasitoid wasps associated with oak galls, phylogenomic delimitation exposed previously hidden diversity and corresponding differences in host associations [31]. Treating unresolved lineages as a single species could therefore obscure ecological specialization, while treating host association alone as proof of species status would reverse the same inferential error.

Taxonomic decisions must also remain level specific. In *Diestramima* cave crickets, several molecular delimitation approaches supported the sampled species-level entities, whereas parts of the higher classification were not similarly supported [32]. Agreement at one level cannot validate another. Likewise, the *Phoebis* example shows that an analytical candidate count can be reconciled after additional evidence rather than translated mechanically into names [18]. The proposed decision rule is therefore conditional: maintain unresolved candidates when evidence remains discovery-level, intensify targeted testing where delimitation is discordant, undertake diagnostic and nomenclatural reconciliation where lineage support is strong, and consider formal revision only when the evidence relevant to that act has been addressed.

The proposed continuum is not a new species concept and does not solve the philosophical problem of what species are. Its narrower purpose is to prevent statistical support, phenotypic distinction, ecological association and nomenclatural readiness from being treated as interchangeable. Structured populations can receive species-like support under some coalescent conditions [5]. Model violations can alter inferred boundaries [7], and delimiter performance changes across speciation scenarios [8]. These limitations make a context-free evidential hierarchy difficult to defend.

Nor should integrative taxonomy become a rigid requirement that every study measure every possible evidence class. Ambush-bug research demonstrates the value of combining molecular, morphometric and ecological

information when those dimensions address the boundary under study [10]. In *Bombus*, genomic divergence and restricted recent gene flow carried particular inferential weight despite overlapping colour variation [20]. In other bumblebee problems, wing morphometrics can be especially useful for assigning type material [22]. Evidence value is therefore task dependent. A missing data class is important when it leaves a plausible alternative unresolved, not merely because a universal checklist says it should be present.

The framework also changes how uncertainty is reported. Method disagreement, hybridization, geographic gaps, undiagnosed life stages and unresolved historical names identify which inferential transition remains weak. Large-scale integrative taxonomy shows the practical value of separating rapid hypothesis generation from targeted validation [1], while critiques of barcode-only description emphasize that accelerated discovery should not erase taxonomic comparison [2]. Downstream ecological work further shows why the distinction matters: delimiting cryptic parasitoid lineages can change the host associations attributed to a nominal species [31].

Prospective validation is required. Independent insect revisions should test whether separating discovery, delimitation, diagnosis and naming readiness improves agreement, exposes disagreement earlier, or merely redescribes existing expert practice. Such evaluation should include morphologically conservative and conspicuous taxa, sexual and asexual systems, sympatric and allopatric populations, hybrid zones, larval–adult associations, museum material, and geographically uneven sampling. Until such tests exist, the continuum should be used as a transparent reasoning aid rather than a validated decision instrument.

Conclusion

Cryptic insect diversity is not a single taxonomic condition. It can denote an initial molecular signal, a method-sensitive candidate partition, a strongly delimited but poorly diagnosed lineage, a boundary complicated by gene flow or geography, or a case sufficiently reconciled for formal revision. Treating these conditions as a continuum of evidential support preserves distinctions that binary diagnosis obscures.

The proposed continuum separates discovery, delimitation, diagnosis and naming readiness while allowing evidence to move in either direction as discordance changes. It prescribes neither universal data combinations nor numerical thresholds. Its value is analytical: it makes explicit what is supported, what remains uncertain and what evidence is relevant next. The framework therefore offers a disciplined vocabulary for handling cryptic insect diversity without converting analytical convenience into unwarranted taxonomic certainty.

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