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Original Article

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Towards systematics-based guidelines for stable taxonomy: lessons from sea slugs

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Abstract

Taxonomy is a cumulative science that translates evolutionary knowledge into a stable, communicable, and functional system of names. Yet its progress is often undermined not by new data, but by how evidence is interpreted and acted upon. We argue that taxonomic decisions should meet five foundational thresholds: (i) a classification reflecting the tree of life, ensuring replicated monophyly and rank symmetry; (ii) diagnosability, linking molecular and morphological traits to recognizable features; (iii) compatibility with topotypical material, minimizing misinterpretation and the need for further taxonomic remediation actions; (iv) collateral-impact assessment, preventing changes that induce downstream paraphyly and instability; and (v) transparent communication, fostering a civil, evidence-focused scientific debate. Together, these criteria frame taxonomy as a reproducible and accountable scientific enterprise, in which individual taxonomic decisions contribute coherently to an evolving classification. Using heterobranch sea slugs as a case study, we illustrate how departures from these standards generate instability without corresponding gains in explanatory power and demonstrate that the same evidence-based principles apply across the taxonomic hierarchy, from higher-level clades to families, genera, and species. Applying these principles supports retaining historically entrenched, monophyletic names, such as Nudibranchia *s.l.*, when redefining them offers no phylogenetic or practical advantage. We encourage shared, transparent standards across the taxonomic community.

Keywords diagnosability, Gastropoda, Heterobranchia, integrative taxonomy, Mollusca, monophyly, nomenclature, phylogenetic classification, systematics

Introduction

In a world under increasing strain, where human pressures are driving a biodiversity crisis, taxonomists play a crucial role in documenting and classifying the diversity of life (Wheeler *et al.* 2004). This role goes beyond naming: taxonomy provides the framework through which biodiversity is recognized, compared, and conserved. For this to work, classifications must be both rigorous and stable, ensuring names remain useful and reliable for the many communities that depend on them. During the past decade, heterobranch sea slug systematics, particularly within Nudibranchia, has undergone a rapid reconfiguration driven by expanded taxon sampling, phylogenomics, and integrative taxonomy (e.g. Karmeinski *et al.* 2021, Paz-Sedano *et al.* 2024, Galià-Camps *et al.* 2025, Henryco *et al.* 2025). This progress has resolved long-standing cases of hidden poly- and paraphyly. In the case of the traditional Flabellinidae, historically one of the most recognizable nudibranch groups, molecular data have revealed deep polyphyly, leading to its division into several genera, supported by clear diagnostic traits (Cella *et al.* 2016, Korshunova *et al.* 2017, Furfaro *et al.* 2018, Ekimova *et al.* 2019, 2026). However, not all taxonomic revisions have achieved a comparable balance between phylogenetic evidence, diagnosability, and long-term stability. These different approaches have also led to waves of rank reshuffling and a proliferation of names at multiple levels. This has resulted in an uneven taxonomic landscape in which some end-users, including ecologists, conservation planners, educators, biodiversity portals, and community scientists, struggle to keep up with ever-changing terminology and express confusion about the basis for these changes.

These challenges arise in two complementary contexts. At higher taxonomic levels, such as the delimitation of major clades, taxonomic decisions are matters of scientific judgement and are not regulated by the International Code of Zoological Nomenclature (ICZN 1999). By contrast, family-, genus-, and species-group names are governed by the Code, although decisions regarding whether taxonomic changes are warranted remain scientific hypotheses that depend on the strength, reproducibility, and broader consequences of the available evidence. Despite these differences in nomenclatural framework, the same scientific principles should guide taxonomic decision-making throughout the taxonomic hierarchy.

At the heart of this debate lie five guiding principles of evidence-calibrated taxonomy (Fig. 1): (i) ensuring a *tree-reflective structure* that captures evolutionary history in a phylogenetically coherent way, (ii) achieving *diagnosability* through clearly differentiated, independent, and recognizable characters, (iii) compatibility with *topotypical material*, minimizing misinterpretation and the need for further taxonomic remediation; (iv) maintaining *stability and usability* by preserving entrenched classifications, where appropriate, and minimizing unnecessary disruption, and (v) promoting *simplicity, accessibility, and communication* so that classifications serve the wider community rather than prioritizing disciplinary conventions or individual preferences.

These principles frequently come into tension. Taxonomic decisions may hinge on whether monophyly alone suffices, or whether morphological divergence and diagnosability should temper that decision. Not every well-supported clade necessarily warrants a formal name; naming should depend on whether the group can be consistently recognized and applied by users and whether doing so improves communication or understanding of evolutionary relationships. The balance between sister-group equivalence (Hennig 1966, De Queiroz and Gauthier 1992) and long-term stability remains a central dilemma, as does determining how much intraspecific variation a species should encompass. At times, restraint itself

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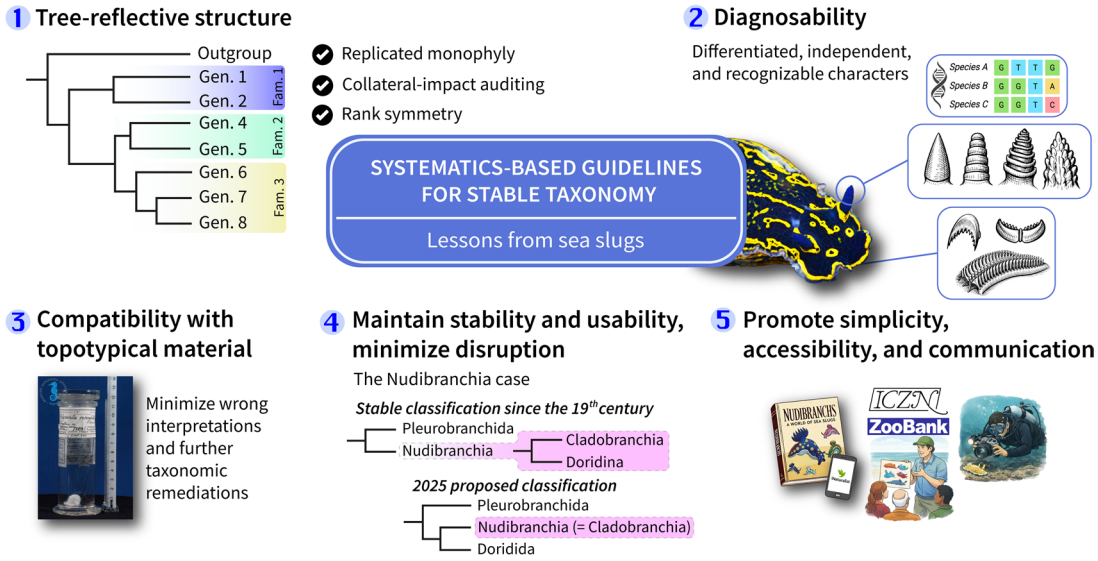

Figure 1 Conceptual workflow for evidence-calibrated taxonomic decisions.

is the sounder option, as incomplete sampling can generate artificial paraphyly when naming proceeds in advance of adequate and representative taxon sampling (Wiens 2003).

Here, we use the gastropod subclass Heterobranchia as a case study to illustrate how evidence-calibrated taxonomy can be applied across the taxonomic hierarchy, from higher-level clades to families, genera, and species. We outline a small set of core principles and demonstrate their application using selected case studies from Heterobranchia. When backbone phylogenies remain fragile or higher-level relationships remain uncertain, phylogenetic structure should be communicated through informal clade labels or subgeneric concepts rather than by erecting premature formal ranks. For instance, the recognition of Pneumopulmonata without a formal Linnaean rank provides a useful precedent for this approach (Krug *et al.* 2022). The operational framework proposed here is summarized in Table 1 and is intended as a practical guide for authors, reviewers, editors, and database curators. Together, these core principles aim to reduce nomenclatural instability while aligning classification with evolutionary understanding and usability across the taxonomic community.

Examples from Heterobranchia

The Nudibranchia case study: higher-level nomenclatural stability

The recurrent attempt to redefine Nudibranchia provides a useful case study illustrating the tension between phylogenetic refinement and the social contract of taxonomic stability (see Box 1 and Fig. 2). In the recent reinterpretation by Korshunova *et al.* (2025), Nudibranchia is restricted to Cladobranchia, resurrecting Blainville's (1814) original, morphologically-based concept of Polybranchia, while excluding Doridina as a separate order (i.e. Doridida). Yet both Cladobranchia and Doridina are well-supported, monophyletic lineages sharing a common evolutionary origin (e.g. Wägele and Willan 2000, Vonnemann *et al.* 2005, Zapata *et al.* 2014, Brenzinger *et al.* 2021, Moles and Giribet 2021, Krug *et al.* 2022). The dispute thus concerns not phylogenetic instability but primarily the semantics of rank and scope, providing an opportunity to examine how the principles outlined above apply when evaluating changes to long-established higher-level classifications. This differs fundamentally from the dismantling of demonstrably paraphyletic groups such as Opisthobranchia or Pulmonata (Dayrat and Tillier 2002, Klussmann-Kolb *et al.* 2008, Jörger *et al.* 2010, Schrödl *et al.* 2011, Kocot *et al.* 2013, Schrödl 2014, Wägele *et al.* 2014).

Throughout the history of malacology, analogous situations have arisen where traditional group names were reinterpreted to accommodate new evidence without erasing their accumulated meaning: Bivalvia, Scaphopoda, and Cephalopoda have each undergone shifting delimitations since the nineteenth century (Ponder *et al.* 2019), and Euthyneura heterobranchs have been repeatedly redefined to integrate new molecular and anatomical insights while retaining nomenclatural continuity (Klussmann-Kolb *et al.* 2008, Haszprunar 1985, Schrödl and Neusser 2010, Kano *et al.* 2016, Brenzinger *et al.* 2021). In such cases, consensus emerged through gradual calibration and community discussion, rather than through unilateral redefinition. By contrast, limiting Nudibranchia to cladobranchs would abruptly separate dorids, including many of the best-known and most frequently encountered sea slugs, from a name entrenched across two centuries of scientific, educational, and outreach usage, illustrating how taxonomic changes can incur substantial downstream costs without a commensurate gain in explanatory power while higher-level relationships remain only partially resolved. Rather than reflecting new phylogenetic or biological insights, the proposal to redefine Nudibranchia primarily concerns how categorical ranks are interpreted (see Giribet *et al.* 2016). As a result, it risks creating substantial nomenclatural and communicative disruption while providing little additional explanatory value. Comparable considerations have also shaped the treatment of other higher-level clade names. For example,

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Table 1 Operational summary of principles for evidence-calibrated taxonomy.

Step	Guideline	Key outcome
Replicate	Base taxonomic changes on independent datasets (e.g. molecular and morphological) that recover the same clade with strong, congruent support.	Reduces artefactual splits and increases the durability of taxonomic acts.
Diagnose	Provide concise, comparative diagnoses based on one or more reproducible diagnostic characters, which may include molecular diagnostic characters (MDCs), internal anatomy, ecology, distribution, behaviour, and externally recognizable traits; explicitly link all diagnostics to images, sequences, and voucher material. Species-level comparisons and taxonomic changes should be anchored to the *locus typicus* (ICZN, Art. 76) and based on direct comparison with topotypical material, or demonstrably equivalent reference material, whenever feasible.	Ensures identifiability and reproducibility across both morphologically distinct and genuinely cryptic taxa.
Respect rank equivalence	Treat sister lineages of comparable divergence at equivalent rank; defer asymmetrical elevation until additional evidence accumulates.	Maintains logical hierarchy and rank comparability.
Audit collateral effects	Confirm that proposed changes do not create unnecessary downstream instability (e.g. para- or polyphyletic neighbouring taxa); document pre- and post-change topology.	Prevents cascading instability across classifications.
Prepare metadata	Include ZooBank LSIDs, type repositories, and diagnoses at publication; for print works, document public distribution (Art. 8.1.2); for electronic works, meet Art. 8.5 requirements.	Enables immediate interoperability and unambiguous Code compliance.
Differentiate availability vs. acceptance	Verify ICZN availability before adoption; defer use of names that are formally unavailable regardless of evidentiary merit.	Upholds nomenclatural integrity and database consistency.
Be transparent and civil	Publish vouchers, data, methods, and imagery openly; frame debate around evidence and methodology rather than authorship or intent.	Builds trust, reproducibility, and collective credibility.

Box 1 Nudibranchia—a name too well established to redefine.

[Restricting Nudibranchia to Cladobranchia, as proposed by Korshunova *et al.* (2025), would exclude Doridina from a name that has been used continuously and unambiguously for more than two centuries following its early nineteenth-century consolidation by Cuvier (1817) and Gray (1821). Both Cladobranchia and Doridina are robustly supported, reciprocally monophyletic lineages that together form a well-corroborated natural group, as demonstrated by multiple independent molecular and morphological analyses (Wägele and Willan 2000, Vonnemann *et al.* 2005, Zapata *et al.* 2014, Brenzinger *et al.* 2021, Moles and Giribet 2021, Krug *et al.* 2022). The disagreement, therefore, concerns the assignment of rank and nomenclatural scope rather than phylogenetic accuracy: redefining Nudibranchia would not resolve paraphyly, which is not at issue, but would instead disrupt long-standing terminological and conceptual continuity. Within the framework proposed here, this case exemplifies a situation in which taxonomic change provides little additional explanatory value while imposing substantial costs to nomenclatural and communicative stability. Retaining Nudibranchia in its inclusive sense (*s.l.*) preserves nomenclatural and communicative stability while fully accommodating current understanding of evolutionary relationships.

Applied significance: This case illustrates the importance of proportionality between the strength of the evidence and the broader consequences of taxonomic change, historical usage, and community consensus when considering changes to names at high taxonomic rank, particularly where long-established terms function as shared scientific infrastructure across research, education, and public engagement.]

the stability of Mammalia has been achieved by defining the name through common ancestry rather than diagnostic characters, ensuring that it retains the same evolutionary meaning even as new fossil discoveries and revised diagnoses alter our understanding of the clade (Rowe and Gauthier 1992). As in Nudibranchia, this illustrates how preserving historically entrenched, monophyletic names can provide continuity without compromising phylogenetic accuracy.

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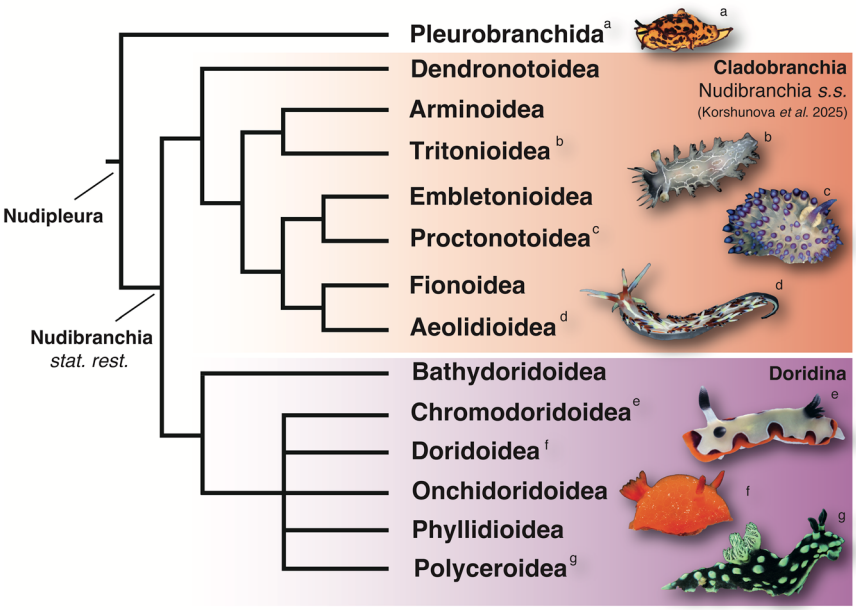

Figure 2 Consensus phylogenetic framework of Nudibranchia, summarizing the relationships among Cladobranchia (Nudibranchia *s.s.* according to Korshunova *et al.* 2025) and Doridina, based on Karmeinski *et al.* (2021) and Paz-Sedano *et al.* (2026). The superfamily Doridoxoidea was excluded due to conflicting results regarding its phylogenetic placement (see Mahguib and Valdés 2015, Moles *et al.* 2024). Depicted species: (a) *Tomoberthella martensi*; (b) *Tritonia festiva*; (c) *Janolus savinkini*; (d) *Caloria indica*; (e) *Goniobranchus fidelis*; (f) *Gargamella rosi*; (g) *Nembrotha cristata*. Image credits: (a, d, e) Juan Moles and Tauana J. Cunha; (b) Alex Bairstow; (c) Colin Marshall; (f) Marinko Babić; (g) Steve Childs.

Family and generic levels

The same principles apply to taxonomic decisions at regulated ranks, where phylogenetic evidence must also be balanced against nomenclatural stability, diagnosability, and community impact. For instance, molecular and genomic evidence supported the resurrection of *Neomonachus* Slater & Helgen, 2014 for Western Hemisphere monk seals, distinct from *Monachus* Fleming, 1822 *s.s.* (Scheel *et al.* 2014, Espregueira Themudo *et al.* 2024), a change that was phylogenetically justified but carried non-trivial downstream implications for conservation legislation, management plans, and public communication. Among delphinids, phylogenomic studies demonstrated that *Lagenorhynchus* Gray, 1846 is paraphyletic with respect to *Cephalorhynchus* Gray, 1846 and *Delphinus* Linnaeus, 1758, prompting proposals for generic reassignment while explicitly cautioning that rapid genus-level inflation could generate confusion in ecological monitoring and regulatory contexts (LeDuc *et al.* 1999, Vollmer *et al.* 2019, Galatius *et al.* 2025).

Within Heterobranchia, recent phylogenomic studies have similarly revealed deep lineage structure within long-established genera, thereby sharpening long-standing questions about when such structure warrants formal taxonomic subdivision. For example, Cella *et al.* (2016) proposed uniting several families and genera within a single family, Fionidae, comprising nine genera. Shortly after, Furfaro *et al.* (2018), following the same 'lumping' approach, redefined the genus *Flabellina* McMurtrie, 1831, demonstrating, through an integrative taxonomic study, that several diagnostic characters traditionally used at the generic level had been misinterpreted. Based on multilocus molecular analyses and morphological investigations, the genus *Calmella* Eliot, 1906 was synonymized with *Flabellina*. Contrarily, Korshunova *et al.* (2017) adopted a more subdivided classification, interpreting the Fionidae clade *sensu* Cella *et al.* (2016) as comprising eight families with numerous genera, including several narrowly circumscribed or monospecific genera. In several cases, generic rank was assigned primarily based on lineage-level monophyly, without clear expansion of comparative sampling or consistently diagnostic character sets. For example, the genus *Paraflabellina* Korshunova, Martynov, Bakken, Evertsen, Fletcher, Mudianta, H. Saito, Lundin, Schrödl & Picton, 2017 has *Paraflabellina ischitana* (Y. Hirano & T. E. Thompson, 1990) as the type species, although Furfaro *et al.* (2018) recovered the same species as a complex of two species. Therefore, the use of *P. ischitana* as the type species of *Paraflabellina* is complicated by uncertainty surrounding its species delimitation. Kim *et al.* (2024) subsequently highlighted practical difficulties associated with this splitting approach and proposed a more conservative classification recognizing only well-defined genera. Nevertheless, Martynov and Korshunova (2025) adopted a classification in which the same clade is divided into nine families comprising 41 genera. Such progressive rank subdivision substantially increases nomenclatural complexity, particularly in the absence of phylogenetic conflict among the major lineages. Under this framework, five additional lineages recovered by Kim *et al.* (2024) would also require recognition as new genera, despite at least 70 further species in the group remaining undescribed and lacking phylogenetic assessment. Moreover,

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Box 2 *Dendrodoris*—stability over premature splitting.

[Recent phylogenomic analyses based on whole mitochondrial genomes and BUSCO nuclear protein-coding genes revealed that the radula-less nudibranch genus *Dendrodoris* comprises three deeply divergent lineages, associated with accelerated mitochondrial evolutionary rates and correlated with external morphological traits (tuberculated, slender, and smooth morphotypes; Galià-Camps *et al.* 2024). Such mitochondrial structural differences could be interpreted as supporting generic-level separation. However, mitochondrial and nuclear signals may conflict, as shown for *Dendrodoris* in a larger independent dataset: mitochondrial markers (cytochrome *c* oxidase subunit I and 16S rRNA) rendered the genus paraphyletic, whereas nuclear 18S rRNA data supported monophyly (Maniei and Wägele 2024), highlighting the risk of over-interpreting mitochondrial signal alone. Moreover, taxon sampling in the initial phylogenomic analysis was limited, with few representatives per lineage. Rather than resurrecting *Doridopsis* Alder & Hancock, 1864 for tuberculated species, creating an additional genus for slender-bodied species, and restricting *Dendrodoris* to smooth-bodied species, Galià-Camps *et al.* (2024) adopted a conservative approach by retaining a single, inclusive genus while acknowledging lineage-specific traits. This decision prioritizes nomenclatural stability and communicative clarity while allowing hypotheses of lineage divergence to remain testable. Subsequent analyses incorporating expanded taxon sampling demonstrated that some putative diagnostic characters were unstable: specimens of the tuberculated species *Dendrodoris warta* Ev. Marcus & Gallagher, 1976 were recovered within the smooth-bodied lineage, undermining dorsum tuberculation as a reliable generic criterion (Galià-Camps *et al.* 2025). This outcome illustrates how premature rank escalation based on incomplete evidence can necessitate rapid revision as datasets mature.

Applied significance: This case exemplifies how evidence-calibrated taxonomic decisions can prevent recursive taxonomic splitting, showing that informal lineage recognition or subgeneric classification may provide flexible alternatives that preserve evolutionary information without destabilizing a long-established, diagnosable genus.]

prioritizing additional rank subdivision before adequately documenting the existing diversity risks diverting taxonomic effort from describing the substantial backlog of undescribed species within these groups.

Similarly, in the dorid nudibranch genus *Dendrodoris* Ehrenberg, 1831, phylogenomic analyses identified several deeply divergent lineages; nevertheless, authors have explicitly adopted a conservative approach, retaining a single, inclusive genus pending broader taxon sampling and confirmation of stable diagnostic characters (Box 2). Comparable dynamics are widespread across malacology: in several iconic and intensively studied marine genera, deep phylogenetic structure has been documented and explicitly acknowledged, without prompting immediate or wholesale genus-level fragmentation. For example, species in *Littorina* A. Férussac, 1822 (periwinkles) exhibit pronounced internal phylogenetic structuring while remaining a coherent operational genus (Reid *et al.* 2012), and long-used names such as *Octopus* Cuvier, 1797 (octopuses) and *Haliotis* Linnaeus, 1758 (abalones) have accommodated extensive molecular and phylogenomic refinement during multiple decades without losing conceptual coherence or functional stability (Guzik *et al.* 2005, Streit *et al.* 2006). In these cases, the internal structure has been explored and communicated through phylogenies, species-level revisions, or informal clade recognition, thereby decoupling phylogenetic resolution from mandatory rank inflation, while maintaining genus-level continuity. Collectively, these examples illustrate that entrenched names function as shared scientific infrastructure and that taxonomic restraint can be justified as a proportionate response when premature splitting would generate disproportionate disruption relative to evidentiary gain. This principle applies equally to family- and genus-level classifications, where preserving diagnosable taxa may better serve scientific communication than premature subdivision based solely on phylogenetic structure.

Classification should reflect the Tree of Life

Taxonomy's primary function is to provide a classification that mirrors evolutionary history, and we consider monophyly a necessary foundation of taxonomic classification across all ranks. Accordingly, any proposed change must be supported by replicated phylogenetic evidence (i.e. derived from independent datasets or analytical frameworks) and accompanied by a coherent diagnosis that researchers beyond the original describing group can apply. The re-evaluation of the traditional Flabellinidae by Korshunova *et al.* (2017) illustrates both the strengths and challenges of contemporary revisionary practice. By integrating multilocus phylogenies with detailed anatomical comparisons, that study convincingly demonstrated that Flabellinidae, as then circumscribed, was deeply polyphyletic, a conclusion later corroborated by independent analyses (Ekimova *et al.* 2019). However, the subsequent taxonomic response involved extensive subdivision before this interpretation had been independently corroborated. This approach substantially increased nomenclatural complexity relative to alternative contemporaneous treatments of the same clade (Korshunova *et al.* 2017; see fig. 1 in Ekimova *et al.* 2026 for an overview). In later assessments, some of these entities were difficult to diagnose consistently, relying on character states overlapping interspecific variation, or displaying sensitivity to alternative phylogenetic topologies, occasionally resulting in paraphyletic residual groupings (Furfaro *et al.* 2018, 2021). Subsequent efforts to stabilize the classification (Ekimova *et al.* 2024) were followed by further revisions reinstating earlier taxa (Korshunova *et al.* 2025), resulting in a degree

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of taxonomic volatility that exceeds what is typically encountered in revisionary systematics (see Ekimova *et al.* 2026 for an overview). Such cycles of repeated restructuring can therefore generate uncertainty not only among specialists but also among the wider community of taxonomic users, underscoring the need for calibrated, proportionate responses to phylogenetic results.

We also endorse the principle of sister-group equivalence (Hennig 1966): lineages with comparable evolutionary history should, where appropriate, be treated at equivalent rank, provided this remains compatible with diagnosability, stability, and usability. Elevating one lineage to family level while leaving its sister distributed across multiple genera or, conversely, subdividing a coherent genus into multiple micro-genera based on shallow divergence, tends to introduce rank asymmetry and taxonomic inflation. Adjustments should therefore be applied symmetrically where possible, or deferred until multiple, independent lines of evidence justify them, thereby maintaining internal coherence and interpretability across the classification system. A model of this balanced approach is provided by the recent revision of Acochlidimorpha (Fernández-Simón *et al.* 2025). Using a comprehensive genetic dataset integrated with detailed anatomical comparisons, the authors resolved several deep lineages and revised family boundaries in a way that preserved sister-group equivalence. Some historical families were reinstated (Pontohedylidae, Strubelliidae), while others were newly described (Helicohedylidae). In the Cephalaspidea, at the family (Oskars *et al.* 2015) and genus levels (Oskars and Malaquias 2019), a similarly measured, evidence-driven strategy was adopted, revising familial and generic limits only where molecular results were corroborated by consistent anatomical differentiation, thereby avoiding unnecessary proliferation of poorly diagnosable taxa. Comparable integrative approaches have recently been applied in Chromodorididae: Ribeiro *et al.* (2025) described a new genus, *Neptunazurea* Ribeiro, García-Méndez, Valdés, Schrödl & Padula, 2025, based on molecular phylogenetic evidence, complemented by careful analysis of diagnostic characters in the jaw, radula, and reproductive system. In all these studies, each taxon was defined as a monophyletic, morphologically distinct lineage with clear comparative traits, maintaining both phylogenetic symmetry and practical diagnosability.

Later changes to the aeolidioidean framework (e.g. Korshunova *et al.* 2025) introduced additional layers of rank subdivision by proposing numerous superfamilies and families. Rather than stabilizing the system, these actions further increased nomenclatural complexity and user confusion, particularly where comparable datasets and analytical approaches have not converged on the same higher-rank boundaries. The *Eubranchus* Forbes, 1838/*Amphorina* Quatrefages, 1844 complex provides a concrete illustration of how the absence of convergence through time can generate recursive instability. Fine-scale species delimitation and generic restructuring were proposed on limited molecular and morphological evidence, including the recognition of species such as *Amphorina viriola* Korshunova, Malmberg, Prkić, Petani, Fletcher, Lundin & Martynov, 2020 and *Amphorina andra* Korshunova, Malmberg, Prkić, Petani, Fletcher, Lundin & Martynov, 2020 (Korshunova *et al.* 2020). Subsequent reassessment incorporating broader ecological context and comparative material failed to support the persistence of the diagnostic characters used to separate these taxa, leading to proposed synonymy where evidence did not justify continued separation (Toso *et al.* 2024). Despite this counterevidence, later treatments reinstated these species and further escalated rank subdivision without additional independent evidence. Martynov and Korshunova (2025) subdivided the same lineage into multiple newly erected genera (*Corruptobranchus*, *Eubranchulus*, *Karavellia*, *Longibranchus*, *Nihonbranchus*), many of them monotypic and unsupported by expanded molecular sampling, renewed morphological assessment, or replicated analyses. This pattern illustrates how repeated taxonomic change without evidentiary consolidation can generate instability far exceeding the underlying phylogenetic uncertainty. Conflicts among datasets are inevitable, especially in groups characterized by homoplasy, morphological plasticity, and incomplete sampling. Rather than prompting immediate taxonomic change, such discordance should motivate further sampling and replication until broader consensus emerges.

Good examples of this approach come from the families Polyceridae and Onchidoridiidae. Within the family Polyceridae, early analyses based on multilocus molecular data already suggested that Okadaiidae and Gymnodorididae were nested within Polyceridae (Hallas *et al.* 2017, Korshunova *et al.* 2020), despite their pronounced morphological distinctiveness. Subsequent expansion of taxon sampling and the inclusion of genomic-scale data independently confirmed this placement, leading to their formal synonymy (Canet-Miralda and Moles 2024, Prieto-Baños and Layton 2025). A comparable outcome is seen in Onchidoridiidae, where the establishment of the genus *Idaliadoris* Furfaro & Trainito, 2022 was supported by concordant multilocus molecular evidence, detailed anatomical study, and a diagnostic egg-mass morphology, providing an example of taxonomic separation justified by convergent lines of evidence (Furfaro *et al.* 2022). Together, these cases illustrate that taxonomic decisions are most robust when independent datasets converge on the same evolutionary hypothesis, allowing classifications to evolve through evidentiary consolidation rather than repeated revision.

Diagnosable, usable taxa

Beyond molecular evidence, new taxonomic names should, wherever possible, be grounded in the direct examination of specimens suitable for study and include documentation of the living animal (where available), a detailed account of its morphology, and a concise diagnosis that enables comparison with closely related or externally similar species. These standards safeguard reproducibility and help ensure that names remain interpretable by both specialists and non-specialists. Taxonomic decisions should preferably rely on the evaluation and integration of evidence from morphological, anatomical, ecological, and molecular data, among others. Such convergence provides a particularly robust basis for defining taxa, linking phenotypic traits to evolutionary lineages, and

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allowing subsequent re-evaluation across independent datasets. In genuinely cryptic species complexes, diagnosability may rest primarily on explicitly defined molecular diagnostic characters (MDCs, e.g. fixed nucleotide substitutions), provided these are reproducible and anchored to voucher material. The cryptic meiofaunal acochlidian *Pontohedyle* A. N. Golikov & Starobogatov, 1972 provides a clear example: combined molecular species delimitation and DNA barcoding revealed multiple lineages that could not be reliably distinguished by traditional morphology alone (Jörger *et al.* 2012, Jörger and Schrödl 2013).

Descriptions based primarily on a single line of evidence, whether molecular or morphological, can stretch the limits of reproducibility when they are not supported by adequate voucher material and explicit diagnostic criteria. A cautionary example is the description of *Cadlina vavilovi* Korshunova & Martynov, 2024 under a 'phyloperiodic' framework (Korshunova and Martynov 2024), where the absence of fresh, verifiable material limited the reproducibility of the proposed taxonomic hypothesis and hindered comparisons with related taxa. The issue is therefore not the type of evidence used, but whether the taxonomic hypothesis can be independently evaluated, traced to physical material, and compared with related taxa. Such cases underscore why integrative frameworks remain valuable, as they enhance the credibility of new descriptions and reinforce long-term stability by anchoring phylogenetic lineages in reproducible, interpretable biological evidence.

Reproducibility also depends on the correct interpretation of reference material. Caution must be exercised when using molecular data stored in public databases, as taxonomic instability can arise when the species name assigned to a sequence and its locality of collection are inconsistent with topotypical material or fall outside the known biogeographic range of the taxon (e.g. Martín-Hervás *et al.* 2021, Paz-Sedano *et al.* 2022). Such mismatches can propagate errors through downstream phylogenetic and taxonomic analyses, especially when database sequences are reused without critical evaluation of their provenance. The same level of care is required when proposing new genera, which should remain anchored to the taxonomic history and documented provenance of the group to ensure continuity and interpretability (Furfaro *et al.* 2022). Without explicit attention to provenance, sampling context, and topotypical reference, molecular evidence risks amplifying uncertainty rather than resolving it.

Transparency and community trust

Beyond the scientific importance of describing and organizing biodiversity, taxonomy also serves the public good by providing names that form the connective infrastructure of biodiversity science, linking databases, conservation frameworks, and environmental policy. Because nomenclatural acts extend far beyond systematics, decisions about scope and rank should consider their impact on users who are not taxonomic specialists. When several rank assignments are equally consistent with phylogeny, the preferred solution is generally the one that maximizes communication, continuity, and interoperability. Each revision should ideally include clear documentation linking old and new names, with comprehensive synonym lists, to support consistent use across platforms such as the World Register of Marine Species (WoRMS) (WoRMS Editorial Board 2026), MolluscaBase (MolluscaBase eds. 2026), the Global Biodiversity Information Facility (GBIF) (GBIF 2026), and other biodiversity information systems. Stable nomenclature underpins the credibility and interoperability of biodiversity data. Frequent or opaque nomenclatural change can frustrate citizen scientists, divers, educators, photographers, resource managers, policymakers, and legislators. Accordingly, taxonomic changes should be both well justified and clearly communicated to maintain confidence in classifications and facilitate the integration of biodiversity information across research, conservation, education, and public engagement.

Taxonomy provides the shared infrastructure through which biodiversity information is documented, communicated, and reused, and this depends fundamentally on transparency and reproducibility. Each taxonomic act should be anchored to verifiable material, including holotypes, paratypes, or topotypical vouchers housed in public repositories. Similarly, all sequence data should be explicitly linked to voucher numbers. Complete metadata at publication, including ZooBank LSIDs, type repositories, and diagnoses, enables immediate synchronization with databases such as WoRMS and MolluscaBase. The ICZN distinguishes clearly between availability and acceptance. Availability concerns whether a name has been established in accordance with the provisions of the Code, whereas acceptance depends on the strength of the supporting evidence and subsequent use by the scientific community. A name can enter formal use only if the work itself meets Article 8 publication criteria. For printed works, material copies must be publicly distributed beyond a few private exchanges (Art. 8.1.2); for electronic works, the publication must be registered in ZooBank at or before release, with fixed, publicly accessible content (Art. 8.5; ICZN 2012 amendment). Neither ZooBank registration alone nor a single library deposition suffices. Authors should therefore provide verifiable documentation (e.g. print-run details, distribution lists, dates of availability, and URLs/DOIs) to facilitate database synchronization and avoid later disputes over status. Once availability is established, broader community practice will determine acceptance.

Depositing type material in a public institution does not, by itself, guarantee reproducibility if access to specimens is substantially restricted. Repositories may limit loans, examination, or minimally destructive sampling for legitimate reasons, including institutional policy, legal restrictions on international transfer of biological material, carrier and customs regulations, or formalin fixation that precludes DNA/RNA extraction, which can impede independent verification, particularly in taxa where molecular data are central to species delimitation. When molecular evidence is central to the taxonomic hypothesis, however, such limitations can constrain independent verification. Best practice, therefore, requires that type deposition balances long-term conservation with scientific reproducibility. Where primary types cannot be sampled, authors should ensure that sequenced reference vouchers are deposited in collections that permit molecular verification, and that these are explicitly cross-referenced

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in the original description. These measures help ensure that taxonomic hypotheses remain independently testable, even when the name-bearing type itself cannot be reanalysed.

Taxonomy depends on credibility across the scientific community. Each name represents a hypothesis about evolutionary history that enters legal, ecological, and educational frameworks upon publication. Its authority, therefore, rests on transparency and reproducibility. Publishing in reputable, peer-reviewed journals remains essential, as journals lacking appropriate taxonomic expertise may be less able to assess ICZN compliance, evidentiary support, or collateral taxonomic effects. Names described without accessible material, verifiable data, peer review, or adequate diagnosis can erode confidence in the discipline. Taxonomic debate should remain evidence-focused and collegial, with open access to datasets, alignments, imagery, and methods enabling disagreement to function as a cumulative process of testing and refinement rather than personal conflict.

An additional source of instability lies not in data or intent, but in the practical constraints of contemporary peer review. As taxonomic expertise becomes increasingly scarce, journals face growing difficulty in securing reviewers with both systematic and nomenclatural competence. As a result, formal taxonomic acts may pass review without thorough scrutiny of ICZN compliance, voucher accessibility, or downstream phylogenetic consequences, and taxonomic changes introduced or modified during late production stages may not always receive equivalent expert scrutiny. This is not a failure of individuals, but a structural challenge for the discipline. Strengthening editorial safeguards, such as ensuring access to nomenclatural expertise when formal acts are proposed and maintaining review oversight through the publication process, would help align publication practices with the standards of rigor and responsibility that taxonomy requires.

Conclusion

Taxonomy is not a static catalogue but an evolving framework for understanding life's history. Its evolution must, however, be guided by replication, diagnosability, proportionality, and usability, rather than by novelty alone. Recent heterobranch research has demonstrated both the transformative power of molecular and phylogenomic data and the unintended instability that can arise when taxonomic action outpaces evidentiary consolidation. Multilocus and genomic datasets have corrected long-standing misconceptions and resolved deep relationships, but the rapid proliferation of names without sufficient replication or usable diagnoses has introduced avoidable instability. Stability is not resistance to change, but the disciplined alignment of taxonomic decisions with convergent, independently verifiable evidence.

The purpose of this *point of view* is not to assign blame or deepen existing divisions, but to articulate a shared set of principles that can guide taxonomic practice across groups and research traditions. Some problematic precedents in the literature reflect structural constraints, such as limited training, uneven access to mentorship, and diminishing institutional support for taxonomy, rather than individual intent. These constraints should not be used to justify continued practice but should motivate collective improvement. By making expectations explicit, transparent, and operational, we aim to support a more consistent and collegial taxonomic culture.

Within this framework, we explicitly reaffirm Nudibranchia *stat. rest.* in its long-standing, inclusive sense, as it has been understood and applied for more than two centuries (e.g. Bergh, Cuvier, Gray, Odhner, Pelseneer, Vayssière). Both major constituent lineages, Doridina and Cladobranchia, are robustly supported as monophyletic and together form a natural evolutionary unit. No replicated phylogenetic evidence demonstrates that retaining Nudibranchia *s.l.* obscures evolutionary relationships or introduces paraphyly. Restricting the name to a subset of this clade would therefore offer no explanatory or predictive gain, while imposing substantial disruption on a term that is deeply embedded in scientific literature, education, biodiversity informatics, and public engagement. Consistent with the principles outlined here, the conservation of Nudibranchia reflects a proportionate, evidence-calibrated decision that preserves both phylogenetic meaning and communicative stability.

We argue that the evidence-calibrated principles summarized in Table 1 provide a practical framework for translating phylogenetic hypotheses into stable and usable classifications. Taxonomic action should follow a cautious path, undertaken only when independent molecular, morphological, and/or ecological datasets yield concordant results, and deferred when such signals cannot be harmonized. Classifications should remain proportional to the available evidence, preserving phylogenetic coherence while minimizing unnecessary disruption to long-established names. These principles must be paired with procedural transparency, including verifiable type material, explicit voucher–sequence linkage, open access to data and imagery, and civil, evidence-focused debate. Ultimately, taxonomic progress depends not on the proliferation of names but on the production of classifications that remain robust, reproducible, and useful as evidence accumulates.

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Conflicts of interest

None declared.

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