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Number 24

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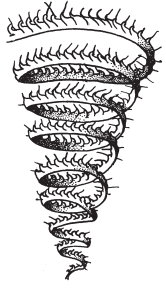
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Cover image: Photographic plate illustrating the representative diversity of extinct and extant marine bivalve genera.



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## THE COMPENDIUM OF THE PHANEROZOIC TYPE SPECIES OF THE CLASS BIVALVIA AND ITS APPLICATIONS

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### ABSTRACT

The detection of synoptical megatrends in the Phanerozoic fossil record requires a robust taxonomic database at the outset. However, large-scale taxonomic data are often unavailable or outdated, or insufficiently standardized, even for major macroinvertebrate groups. Additionally, large-scale syntheses usually require well-resolved genus-level data, which in turn is objectively defined by and anchored to its designated type species, making type species an indispensable part of taxonomic compilations. For the Class Bivalvia, large-scale, systematic compilations are available for all Phanerozoic genera, but a compendium of bivalve type species is lacking. Here, we provide a global, taxonomically standardized, and updated type species compendium of marine bivalves for the entire Phanerozoic. Our type species compilation enlists 2,822 valid genera, their temporal ranges, with details of the methods of typification. We further quantitatively evaluate whether the systematics of bivalve type species have been historically stable or not, using a modified “flux ratio”. Moreover, as type species are representatives of their genera, we statistically compare the longevity of the type species and its parent genus to assess whether the type actually represents the genus’s temporal range. Our results indicate that approximately 63% of original names assigned to bivalve type species have been reassigned. Moreover, only about 38% of bivalve type species span at least 50% of their genus’s temporal range, and the type species had their stratigraphic range at the early phases of the genus’s stratigraphic range. Our findings reiterate that, though type species are the representatives of respective genera, the temporal longevity of the types should not be used as a direct proxy for their generic longevity.

### INTRODUCTION

Synoptic studies of global, large-scale macroevolutionary and macroecological patterns frequently use large taxonomic compilations/compendia (Sepkoski, 1978, 1984; Labandeira, 1994; Benton, 1995; Alroy & others, 2008; Ward, 2010; Zhang, Augustin, & Payne, 2015; Piñeiro & Pichel, 2024). However, compiling a taxonomic

compendium requires considerable time and effort. In the age of “big data” and machine learning algorithms, the availability of global data repositories, such as the Paleobiology Database (PBDB, 2026), the World Registry of Marine Species (WoRMS, 2026), MolluscaBase (2026), or the Global Biodiversity Information Facility (Telenius,

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2011; GBIF, 2026), makes this seemingly onerous task relatively tractable. However, the flexibility to access large volumes of systematic information often comes at the cost of incomplete data or a lack of sufficient spatial and temporal coverage in these databases. Several studies have systematically demonstrated the incompleteness of these global databases while examining different fossil groups (Vilhena & Smith, 2013; Mondal & Harries, 2015; Edie, Smits, & Jablonski, 2017). Even if data are sufficiently available, it is often debatable in which taxonomic hierarchy the study should be conducted, and what should be the standard representative of a taxon. A workaround to this conundrum lies in typically designating the genus as the chosen “unit” of biodiversity, and the most standard representative of every genus is its type species (Raup & Boyajian, 1988; Sepkoski, 1998; Heim & others, 2015; but see Hendricks & others, 2014).

Fortunately, the type species information is not only relatively easily obtained but also serves as an unbiased estimate of the body size of that genus, whereas inferences drawn using nontype species may be over- or underestimated (Kosnik & others, 2006; Heim & others, 2015; Salamon & others, 2023). For morphological analyses, as well, using a random subset of species for quantifying morphological disparity shows considerable increases in morphological variance through time, whereas the morphological variability is much less when only type species are used (Foote, 1989; Kosnik & others, 2006; Salamon & others, 2023). Despite these evidences in support of the claim of the type species being an unbiased representative of a genus, there are certain problems associated with the type species, most prominent among which is the lack of a comprehensive database (for most taxonomic groups), exhaustively enlisting the type species for all (or at least, most) of the genera, and not just the common genera. Consequently, workers often resort to using only a few, commonly available type species, excluding a large part of the group’s taxonomic diversity. Moreover, for long-ranging genera, the temporal range of the type species may be very restricted, representing only a snapshot of the entire temporal range of the genus: The type species might have a temporal range coinciding with the First Appearance Datum (FAD) of the entire genus’s range, whereas the younger end of the genus’s temporal range is not faithfully represented. These shortcomings, based on using type species and nontype species, might question the validity of conclusions drawn from type species-based studies, and also underscore the problems of working with incomplete databases, especially in synoptic studies.

The Class Bivalvia, spanning the entire Phanerozoic, has a rich (both quantitatively and qualitatively) fossil record and global spatiotemporal distribution, leading to its consideration as a model macroevolutionary group (Miller & Sepkoski, 1988; Jablonski & others, 2003; Mondal & Harries, 2015, 2016, 2025; Collins & others, 2019). Unfortunately, there is no single comprehensive type species database available for this well-studied group. Existing studies relying on/utilizing bivalve type species are primarily taxonomic descriptions of the genus’s morphological features (McAlester, 1968; Huber, 2010, 2015; Carter & others, 2011) or are molecular phylogenetic reconstructions, using DNA data from type species (Tëmkin, 2010). Moreover, most of these studies focus on certain lineages or sublineages only and/or are temporally restricted (McAlester, 1968; Tëmkin, 2010; Ros-Franch, Márquez-Aliaga, & Damborenea, 2014; Lopes-Lima & others, 2017; Crouch & others, 2021). For example,

the work of Ros-Franch & others (2014) provides a detailed critical assessment of several bivalve genera, listing their type species, FADs, Last Appearance Datum (LADs), and paleobiogeographic distributions; however, their database caters only to Triassic to Early Jurassic bivalves. Moreover, even though comprehensive studies like those of Heim & others (2015), analyzing the body size evolution in marine vertebrate and invertebrate groups (including bivalves), used type species, the list of bivalve taxa with the type information included was vastly incomplete. In this contribution, we provide a novel, global compendium of the type species of all taxonomically valid genera of the Class Bivalvia for the entire Phanerozoic. We also assess if the systematics of bivalve type species have been historically stable or not, using a modified version of Alroy’s (2002) equilibrium proportion of valid taxa metric (the “flux ratio”). Afterwards, we assess whether the temporal ranges of type species and their respective genera are congruent by quantitatively comparing the temporal distributions of each genus with its corresponding type.

## METHODS

### Data collection

For the present study, we have used an updated compendium of taxonomically valid marine bivalve genera, primarily based on Fang & others (2009), Mondal & Harries (2015) and Zhou & others (2023). The temporal ranges of these genera and their types have been meticulously updated using 1,275 sources such as PBDB (primary source for temporal ranges), WoRMS, GBIF, the Bivalve Treatise (Cox & others, 1969, 1971; Carter & others, 2011; Neveeskaja & others, 2013), and a host of other published literature (see Appendix 1 for the complete list). Although online databases (i.e., GBIF, MolluscaBase, and WoRMS) contain relevant systematic information across different groups, the information on the type species is either not available or scattered across websites (i.e., updated systematic information on WoRMS/MolluscaBase/GBIF; temporal information on PBDB), or the temporal spans of several type species are missing or highly ambiguous. This problem is further exacerbated for endemic genera, especially those reported from Asian or Southeast Asian countries (but see Fang & others, 2009), or Central and Eastern Europe. Among published literature, the Bivalve Treatise provides a comprehensive list of most Phanerozoic invertebrate taxa, but these volumes also require several updates in terms of ages of different genera and their systematics (Cox & others, 1969, 1971; see Carter & others, 2011). In recent decades, handbooks on Phanerozoic bivalves, such as those made by Neveeskaja & others (2013), serve as a valuable resource; however, their original material was published in Russian, which may limit accessibility to non-Russian speakers. Additionally, this handbook is primarily made for bivalves from the extratropical regions of Eurasia, thereby limiting its spatial resolution. Therefore, additional systematic and temporal range information for both genera and their corresponding type species was amassed from diverse sources (Table 1; Appendix 1), allowing for the determination of the temporal ranges of the genera and their representative types.

### Structure of the database and data validation

This database includes the taxonomic affinities (i.e., subclasses, orders, suborders, families, and type species) and the FADs and LADs of each genus and type species, the total temporal ranges of

the genus, and their representative type species (Table 1; Appendix 1). While collecting type species data, we observed that certain bivalve genera were represented by multiple type species in different data sources. An exhaustive literature search was conducted in these cases to resolve issues arising from synonymy, typographic errors, and taxonomic reassignments reflecting systematic revisions, and ultimately, the most recently accepted type species was retained as the type in the database. Similarly, we also screened the database for misspellings of genus names, invalid junior subjective homonyms, objective synonyms, alternative spellings, replacement names, and unjustified emendations. The nomenclature of these genera and type species, including their original names, synonyms, and accepted names, were cross-verified from the online databases, and only those taxa that are currently recognized as valid under International Commission on Zoological Nomenclature (ICZN, 1999), following the taxonomic consensus reflected in MolluscaBase and WoRMS databases, were retained. The method of designating the types has also been provided: whether types are designated via original designation (OD), by monotypy (M), or subsequent designation (SD), or retypification, or subsequent monotypy (SM), and absolute tautonymy/orthotypy (ICZN Code, Article 68.4, 69).

To assess whether the systematic assignments for any taxonomic group have been historically stable and valid to date, Alroy (2002) devised a quantitative scheme known as the “flux ratio.” Although originally intended to provide conservative estimates of biodiversity by accounting for species synonymies, the flux ratio assesses how many species names have been taxonomically revised and are still valid (i.e., currently accepted). To calculate the flux ratio, information on the number of times a species name has been invalidated and revalidated, and detailed lists of synonymies, are required (Alroy, 2002; Benton, 2008). Because collecting this information falls beyond the scope of our research, we used a modified version of this approach, wherein instead of calculating the ratio of taxonomic name invalidations and revalidations, we estimate how “historically stable” bivalve type species-level systematics is. For this, we first matched the original type species names (i.e., names given when the type species was first described) with the currently accepted type species names, and counted the number of instances for which the original and currently accepted names match—a change of name from the original reflects a case of name invalidation, whereas unchanged species names are indicative of stable taxonomic assignment. Moreover, in cases of name changes, we counted the number of years passed between the original name and the currently accepted name. For example, the currently accepted name of the type species of the genus *Bakevella* King 1848 is *Bakevella binneyi* (Brown 1841); however, its original name is *Avicula antiqua* Münster in Goldfuss 1836 (Table 1). This change of name suggests that the original name has been invalidated, and this was invalidated five years after the initial name proposition.

To compare the temporal distributions of genus and type-species longevity, we evaluate whether the temporal range of the type species encompassed the majority of the genus’s total span (>50%) or was more temporally restricted, using a binomial test. To evaluate whether type species are more likely to originate in particular portions of their genus’s temporal range, we divided each genus’s stratigraphic range into three intervals: “early” (from the genus’s origination to one-third of its total duration), “middle” (from one-

third to two-thirds of the total duration), and “late” (from two-thirds to the extinction of the genus). The midpoint of each type species’ temporal range was calculated and placed into one of these three bins, thereby standardizing comparisons across genera of different temporal longevities. Furthermore, we used a Chi-squared test to evaluate whether the origination timing is uniformly distributed across the early, middle, and late portions of genus lifespans. In addition, we used a randomization analysis (Foote 1996; Wagner & Marcot, 2010), which generated a null distribution of type species frequencies across the early, middle, and late phases of their genus’s range. This was accomplished by shuffling type species within their genus ranges across 10,000 iterations, thereby accounting for variation in genus durations. These statistical approaches assess whether the observed pattern of type species origination departs from both a uniform expectation and from expectations affected by genus longevity.

## RESULTS AND DISCUSSION

Our reanalysis of Phanerozoic bivalve systematics resulted in a compilation of 2,822 genera, six subclasses, 37 orders, and 255 families (Table 1; Appendix 1). The systematics of this model macroevolutionary group is quite complete at the generic level (Foote & Sepkoski, 1999; Valentine & others, 2006; Mondal & Harries, 2015; Troudet & others, 2017). The low percentage of singletons (5.5%) is also within the acceptable range, as reported previously (Mondal & Harries, 2015). Additionally, when tabulating the durations of the type species, information was available for 2,708 species (i.e., a coverage of about 96%; Table 1). Out of these 2,708 type species, cumulatively, 1,721 species are defined as original designations, 453 are types by monotypy, 41 are both original designations and monotypy; 414 have been assigned as types by subsequent designation, 21 as subsequent monotypy, 10 are designated by absolute tautonymy, five are reassigned, and 40 are typification of replaced names. Furthermore, one species (*Archivesica gigas* [Dall 1896]) is an original combination, another (*Arca samanensis* [Olsson, 1929]) is designed by orthotypy, and one species (*Cornucardia hornigii* [Bittner 1901]) is both designated by monotypy and is a retypification of a replaced name. Information on type species designation was not available for a total of 143 species, despite checking different sources. Additionally, for one genus (*Striatoceramus* Heinz 1932), no type species has been designated (Table 1; Appendix 1).

Regarding species-level systematics, our analysis reveals that out of the 2,822 Phanerozoic genera, the originally assigned names of the type species still hold for only approximately 32% of species, whereas about 63% of types have their original names revised/changed (the remaining genera [~5%] do not have complete information on either their original names or the currently accepted names). The average temporal span for when an original name has been changed to the currently accepted one in literature is 25.3 years. Therefore, although the over two-decade-long timeline for name revision would be indicative of historically stable type species-level systematics, the markedly higher proportion of name changes is strongly suggestive otherwise. Additionally, of all the type species in our compendium, 230 have their original names revised to a species name erected earlier than the original name. For example, the original name of *Byssosarca divaricata* G. B. Sowerby I, 1833 (type of *Acar* Gray 1857) is currently accepted as *Acar plicata* (Dillwyn, 1817) (see Appendix 1 for more examples).

In general, a type species spans approximately 27% of its genus's stratigraphic range. Interestingly, the temporal ranges of some of the type species are often longer than those of their respective genus. However, this incongruence between the temporal spans of genus and species is exacerbated in cases where the species has been transferred to another genus—for instance, *Propeamussium zitteli* (Hutton 1873) under *Entoloides* Allasinaz 1972 (Table 1). Additionally, when we quantified whether types span a substantial proportion of the genus's ranges (using 50% of the genus's temporal duration as a cut-off), our analyses show that only about 38% of type species span more than half of their generic duration (680 of 1,813 genera), significantly fewer than the null expectation of 50% (binomial test,  $p < .001$ ). Similarly, the Wilcoxon signed-rank test showed that the median distribution of type species spans is significantly lower than the expected value of 50% ( $p < .001$ ). Therefore, for Class Bivalvia, the type species rarely matches its genus's stratigraphic range. Our results further show that the type species are not randomly distributed within the stratigraphic range of the genus (Chi-square,  $p = .004$ ): the majority of the type species originate early ( $n_{\text{Early}} = -69\%$ ), with about 14% originating in the middle and about 17% in the late phases of their genus's history. Therefore, overall, type species show shorter average durations than genera, with occasional cases of incongruence in which species outlast their assigned genera, probably reflecting erroneous taxonomic assignments. However, once species were reassigned to their currently accepted genera, these incongruences were resolved—for example, the type species of *Newaagia* Hertlein 1952 (*Spondylus obliquus* Münster, 1841) appears to span more than 100 Myr, and the genus itself ranges for 48 Myr. In its current classification, *Spondylus obliquus* is accepted as *Newaagia obliquus* (Münster, 1841), with a much shorter temporal range of 3.4 Myr. Such discrepancies are particularly common in the PBDB, largely because synonymized species are often lumped under type species, thereby artificially inflating the age ranges. Importantly, the temporal origins of types are nonrandom: They are under-represented in middle and late phases and significantly enriched in the early phase of their genus's history. However, the lack of temporal congruence between generic- and type species-level durations, along with the multiple instances of original type species names no longer being valid, further reinforces the notion of species not being true proxies of generic-level patterns (Hendricks & others, 2014).

Our results reinforce the view that type species primarily serve as nomenclatural “anchors,” fixing a genus name to a particular species under the ICZN rather than reflecting its biological or evolutionary breadth, and thus their stratigraphic spans should not be used as direct proxies for the temporal duration of genera. Genera are collections of species in which attributes (including temporal ranges) can vary widely among their constituent species, and using type species alone to infer generic-level temporal patterns can therefore introduce systematic bias into macroevolutionary inference (Allmon, 1992; Hendricks & others, 2014).

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## Table 1

**Table 1.** Phanerozoic compendium of bivalve genera and their type species (currently accepted names only; for original names, see Appendix 1), along with their systematic information, and method of type designation. Abbreviations: OD, original designation; SD, subsequent designation; M, monotypy; SM, subsequent Monotypy. For details of First Appearance Datum, Last Appearance Datum, and longevity of genus and type species, and the supporting references, see Appendix 1.

## Supplementary Data

**Appendix 1.** Phanerozoic compendium of bivalve genera and their type species (original names and currently accepted names), along with their First Appearance Datum, Last Appearance Datum, and temporal ranges.

## Code availability

No custom code was used in this study. All statistical analyses have been performed using standard functions in the R software (version 4.2.2).

## Ethics declaration

The authors declare no competing interests.

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