

## Review

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# Identifying the Big Questions in paleontology: a community-driven project

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## Abstract

Paleontology provides insights into the history of the planet, from the origins of life billions of years ago to the biotic changes of the Recent. The scope of paleontological research is as vast as it is varied, and the field is constantly evolving. In an effort to identify “Big Questions” in paleontology, experts from around the world came together to build a list of priority questions the field can address in the years ahead. The 89 questions presented herein (grouped within 11 themes) represent contributions from nearly 200 international scientists. These questions touch on common themes including biodiversity drivers and patterns, integrating data types across spatiotemporal scales, applying paleontological data to contemporary biodiversity and climate issues, and effectively utilizing innovative methods and technology for new paleontological insights. In addition to these theoretical questions, discussions touch upon structural concerns within the field, advocating for an increased valuation of specimen-based research, protection of natural heritage sites, and the importance of collections infrastructure, along with a stronger emphasis on human diversity, equity, and inclusion. These questions offer a starting point—an initial nucleus of consensus that paleontologists can expand on—for engaging in discussions, securing funding, advocating for museums, and fostering continued growth in shared research directions.

## Resumen

La paleontología permite conocer la historia del planeta, desde los orígenes de la vida hace miles de millones de años hasta los cambios bióticos de épocas recientes. El ámbito de la investigación paleontológica es tan vasto como variado y está en constante evolución. En un esfuerzo por identificar las “grandes preguntas” de la paleontología, expertos de todo el mundo se reunieron para elaborar una lista de cuestiones prioritarias que el campo puede abordar en los próximos años. Las 89 preguntas aquí presentadas (agrupadas en 11 temas) representan las contribuciones de casi 200 científicos internacionales. Estas preguntas se refieren a temas comunes, entre los que se incluyen los motores y patrones de la biodiversidad, la integración de diferentes tipos de datos a lo largo de escalas espacio-temporales, la aplicación de datos paleontológicos para resolver cuestiones contemporáneas de biodiversidad y clima, y la utilización eficaz de métodos y tecnologías innovadoras para obtener nuevos conocimientos paleontológicos. Además de estos interrogantes teóricos, los debates abordan inquietudes estructurales dentro del campo, y

abogan por una mayor valoración de la investigación basada en especímenes, la protección de los sitios del patrimonio natural y la importancia de la infraestructura de las colecciones; junto con un mayor énfasis en la diversidad humana, la equidad y la inclusión. Estas preguntas representan un punto de partida—un núcleo inicial de consenso que los paleontólogos pueden ampliar—para fomentar debates, obtener financiación, abogar por el apoyo a los museos y estimular el crecimiento continuo en direcciones de investigación compartidas.

### Riassunto

La paleontologia offre spunti fondamentali per comprendere la storia del pianeta, dalle origini della vita miliardi di anni fa fino ai cambiamenti biotici più recenti. L'ambito della ricerca paleontologica è tanto vasto quanto diversificato e rappresenta un campo in continua evoluzione. In questo studio, esperti provenienti da tutto il mondo si sono riuniti per redigere un elenco di "Grandi Domande" prioritarie che la paleontologia potrà affrontare nei prossimi anni. Le 89 domande qui presentate, raggruppate in 11 temi, rappresentano il contributo di circa 200 scienziati internazionali. Queste domande riguardano tematiche come i meccanismi e i pattern di biodiversità, l'integrazione di varie tipologie di dati su scale spazio-temporali multiple, l'applicazione delle conoscenze paleontologiche ai problemi attuali della crisi climatica e della biodiversità, e l'uso efficace di metodi e tecnologie innovative per ottenere nuove intuizioni paleontologiche. Oltre a questi temi teorici, la discussione si focalizza su problematiche strutturali del campo, promuovendo una maggiore valorizzazione della ricerca basata sugli esemplari, la protezione dei siti di interesse culturale e paleontologico, e l'importanza delle infrastrutture per preservare le collezioni, insieme a una crescente enfasi su un apporto multiculturale, equo e inclusivo. Queste domande costituiscono un punto di partenza—un nucleo di consenso iniziale che i paleontologi possono espandere—per avviare discussioni, ottenere finanziamenti, promuovere i musei e favorire una crescita continua verso direzioni condivise di ricerca.

### Non-technical Summary

Paleontologists study the history of life on Earth, from its beginnings billions of years ago to the present day. To unify the discipline and develop a shared research agenda, nearly 200 scientists from more than 30 countries worked together to identify key questions for the future of paleontology. The resulting questions address topics including biodiversity, data integration, application of paleontology to societal issues, and utilizing new technology. Discussions also focus on topics related to improving the field, such as valuing specimen-based research, protecting fossil collecting sites, advocating for museums, and promoting diversity and inclusion among practitioners. These questions are a starting point for paleontologists for future developments of the discipline.

## Introduction

Paleontology offers an important scientific contribution by asking questions about life throughout the billions of years of Earth's history. The field itself has expanded from one based principally on collecting and documenting fossils to a hypothesis-driven, evidence-based field of inquiry using increasingly complex data, analytical approaches, and computational techniques. Paleontologists examine a range of topics about the history of life, including extinction, the evolution of organisms, biodiversity, the impact of climate changes, and the complex dynamics between life and other components of the Earth system. These comprehensive studies of life in the past provide critical context for understanding life on the planet today and the possible responses to ongoing environmental changes.

As in all scientific disciplines, the questions pursued by paleontologists fall on a spectrum, from large overarching questions that are central to the discipline to questions that are more specific and focus on smaller scales or pressing topics or contribute a component for addressing broader questions. The large overarching questions are likely to be persistent, but we can begin to address these grand themes by asking specific questions at various levels of resolution. For example, while a consensus exists on the principal features of the broad trajectory of life preserved in the fossil record, continued and closer examination of the record is required to resolve the details of evolutionary processes, environmental perturbations, and random effects that led to the modern configuration of life on Earth. As the resolution of studies becomes more specific, questions can range from "To which taxon does this specimen belong?" to questions such as "What is the role of abiotic and biotic interactions in driving biodiversity patterns?" Whereas "smaller" questions like the former are foundational to studying paleontology and merit support on their own, it is questions such as the latter

(i.e., a "Big Question") that are the scope of this paper, as they indicate the current state of the discipline and its aims for future scientific development.

Through the Big Questions project detailed herein, we seek to provide a road map for how paleontological research might develop in the coming years, as prioritized by members of the paleontological community. A Big Question (BQ) is defined here as an open-ended question of high scientific importance that can be answered within a reasonable time frame. Defined in this way, BQs become priority questions that can be used to emphasize the importance of the discipline to the larger research community, as well as to direct scientific effort and research funding (Sutherland et al. 2009; Willis and Bhagwat 2010; Parsons et al. 2014; Seddon et al. 2014). For our purposes, we considered a reasonable time frame to be several years, although some questions may require a longer duration to address (e.g., the duration of a career). The amount of time needed to answer a BQ with precision and accuracy is variable and dependent on many factors, including technological advances and available resources.

The answer to a BQ should represent a substantive leap forward in the community's understanding of an issue or address a knowledge gap. "Scientific importance" requires examination of the perceived value of a BQ within the paleontological community, the broader scientific community, and its transference to society at large. Incorporating a diverse set of individuals engaged in paleontological research increases the confidence with which we can present research directions that can justifiably be defined as scientifically important to the international paleontological community. As such, the Big Questions project represents a democratic perspective of the paleontological discipline by individuals conducting germane research; we acknowledge that this effort was influenced by the opinions of those who participated, who represent a small percentage of the global paleontological community.

As the discipline of paleontology continues to grow in scope and application, paleontologists have a responsibility to routinely reflect on, criticize, discuss, and refine research directions, the best practices for conducting professional activities, and the cohesion of the discipline across geopolitical boundaries. Here we present the outputs of such an effort, providing an examination of the current state of paleontological research as expressed by the questions pursued in this discipline.

## Methods

### Project Contributors

The Big Questions project is a community initiative, coordinated through the PaleoSynthesis Project, that sought to engage a broad range of scientists working in paleontology and related disciplines (e.g., archaeology, biology, climate science, geology). Members of the Big Questions coordination team (J.A.S., W.K.) invited participation from the community through three solicitations requesting the submission of BQs in 2020 and 2021 (Fig. 1). The first solicitation was distributed in June 2020 using the PaleoNet listserver and to members of societies including the Palaeontological Association, Paleontological Society, and Paläontologische Gesellschaft. To reach a broader audience, the coordination team issued a second call in January 2021, again using PaleoNet, but expanding to include social media (Facebook; Twitter, now X) and listservers for the Ecological Society of America (Ecolog-L) and the Conservation Paleobiology Network (CPN-L).

In March 2021, the first virtual, plenary meeting was held for those individuals who indicated they would like to contribute to the project. As an outcome, participants in the meeting recognized that the group was dominated by individuals from the United States and Europe (Table 1). Consequently, a third solicitation was distributed in late March 2021 using the same approach as the second solicitation, this time with versions in English, French, Italian, Chinese, and Spanish (reflecting widely spoken language proficiencies in the existing group of participants). Participants involved via the first two solicitations were encouraged to use their personal networks to invite participants from places and with backgrounds not already represented in the project.

### Working Group Assignments

As a part of the first two solicitations, participants were asked to submit questions they felt were outstanding in the field of paleontology

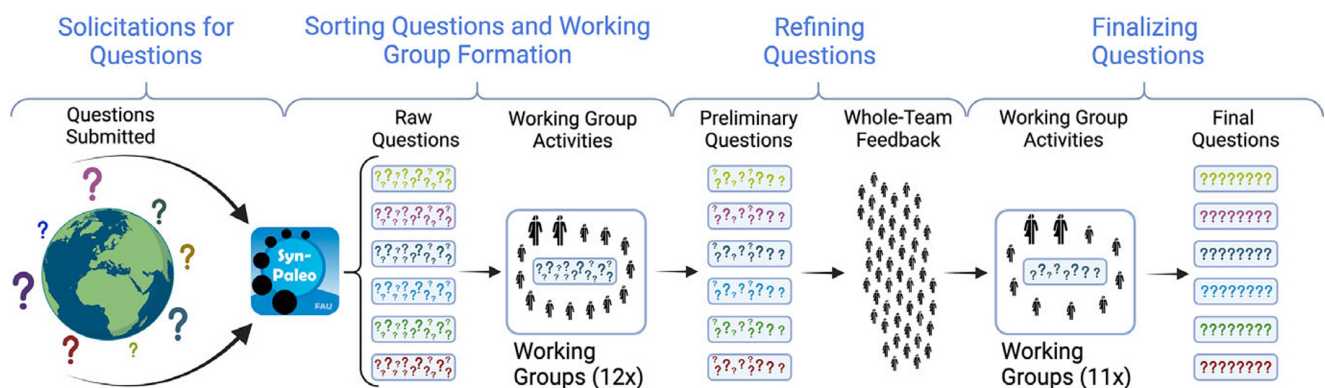
(Table 2). The coordination team then created 12 themes that captured as much of the variation as possible from the submitted questions. Individuals who joined the Big Questions project during the third solicitation were asked to self-select the best category for their questions, as the 12 themes had already been established. All assignments (from all solicitations) were checked for consistency, and when a question pertained to multiple themes, it was assigned to each relevant theme (Fig. 2). Ten of the groups focused on scientific questions (one of which was dropped due to overlaps with questions in related groups; Table 2) and two groups centered on structural issues relating to how paleontology is practiced, as scientific questions and scientific practice are not distinct domains.

All participating individuals were asked to rank their top five theme preferences (Table 2) and assigned to their highest available preference, while attempting to balance numbers and diverse group composition using inferences regarding aspects to participants' identities (e.g., career stage, country, gender identity). Such inferences are undoubtedly flawed (e.g., institutional affiliation may not reflect a participant's nationality), but were an attempt to form diverse groups using incomplete information. Participants were given the additional option to join one of the groups addressing structural issues ("Fundamental Issues," "Looking Inward and Outward"). All participants were given the option to volunteer as a working group leader, and one to three leaders were selected for each group from those volunteers, with consideration for representation of the diverse backgrounds of individuals participating in the project.

### Refinement of Big Questions

Under the direction of working group leaders, the working groups were tasked with refining the set of questions assigned to their themes (Supplementary Material 1) into a condensed set of 8–12 preliminary questions. As a guide for this process, all were asked to consider the following discrete criteria (from Sutherland *et al.* 2009) for what a BQ entails:

1. Addresses an important gap in knowledge
2. More than just a general topic area (e.g., climate change)
3. Answerable through a realistic research design
4. Has a spatial and temporal scale that can be addressed by a research team
5. Has a factual answer that does not depend on value judgments



**Figure 1.** The question pathway in the Big Questions project. Questions were submitted by the global community in one of three solicitations. Submitted questions were assigned to working groups ( $n = 12$ ) composed of self-identified topic experts who chose to participate in the project. Working groups were guided by one to three leaders (larger icons) and refined their assigned questions to a preliminary list. These preliminary questions were assessed by the entire Big Questions team to improve question quality and reduce redundancies in questions from different groups. Using whole-team feedback, working groups (reduced to 11 due to overlaps; Table 2) produced a refined set of final big questions. Created with BioRender.com.

**Table 1.** Countries and administrative regions represented in the Big Questions project by affiliations of the authorship team at the time of manuscript submission, with respect to when individuals joined the project. Note: as countries and administrative regions represented are derived from the institutional affiliations of the authors, this is likely an underestimate of the number of countries and administrative regions represented by individuals in this project

| Country/administrative region (AR) | First solicitation                               | Second solicitation                              | Third solicitation                               | Authorship team                                |
|------------------------------------|--------------------------------------------------|--------------------------------------------------|--------------------------------------------------|------------------------------------------------|
|                                    | Number of affiliations (% of solicitation total) | Number of affiliations (% of solicitation total) | Number of affiliations (% of solicitation total) | Number of affiliations (% of authorship total) |
| Argentina                          | 3 (5.8%)                                         |                                                  | 10 (13.9%)                                       | 13 (8.0%)                                      |
| Australia                          | 1 (1.9%)                                         | 2 (5.1%)                                         | 2 (2.8%)                                         | 5 (3.1%)                                       |
| Austria                            |                                                  | 2 (5.1%)                                         |                                                  | 2 (1.2%)                                       |
| Brazil                             |                                                  |                                                  | 2 (2.8%)                                         | 2 (1.2%)                                       |
| Canada                             |                                                  |                                                  | 1 (1.4%)                                         | 1 (0.6%)                                       |
| China                              |                                                  |                                                  | 4 (5.6%)                                         | 4 (2.5%)                                       |
| Colombia                           |                                                  | 1 (2.6%)                                         |                                                  | 1 (0.6%)                                       |
| Czech Republic                     | 2 (3.8%)                                         | 1 (2.6%)                                         |                                                  | 3 (2.0%)                                       |
| Egypt                              |                                                  | 1 (2.6%)                                         |                                                  | 1 (0.6%)                                       |
| France                             |                                                  |                                                  | 2 (2.8%)                                         | 2 (1.2%)                                       |
| Germany                            | 14 (26.9%)                                       | 4 (10.3%)                                        | 1 (1.4%)                                         | 19 (11.7%)                                     |
| Ghana                              | 1 (1.9%)                                         |                                                  |                                                  | 1 (0.6%)                                       |
| Hong Kong SAR, China               | 1 (1.9%)                                         |                                                  |                                                  | 1 (0.6%)                                       |
| India                              |                                                  |                                                  | 4 (5.6%)                                         | 4 (2.5%)                                       |
| Italy                              | 1 (1.9%)                                         | 2 (5.1%)                                         | 1 (1.4%)                                         | 4 (2.5%)                                       |
| Jamaica                            |                                                  | 1 (2.6%)                                         |                                                  | 1 (0.6%)                                       |
| Madagascar                         |                                                  |                                                  | 2 (2.8%)                                         | 2 (1.2%)                                       |
| Mongolia                           |                                                  |                                                  | 1 (1.4%)                                         | 1 (0.6%)                                       |
| New Zealand                        |                                                  |                                                  | 1 (1.4%)                                         | 1 (0.6%)                                       |
| Norway                             |                                                  | 1 (2.6%)                                         |                                                  | 1 (0.6%)                                       |
| Panama                             | 2 (3.8%)                                         | 1 (2.6%)                                         | 2 (2.8%)                                         | 5 (3.1%)                                       |
| Poland                             | 1 (1.9%)                                         |                                                  |                                                  | 1 (0.6%)                                       |
| Portugal                           | 1 (1.9%)                                         |                                                  | 2 (2.8%)                                         | 3 (2.0%)                                       |
| Singapore                          |                                                  |                                                  | 1 (1.4%)                                         | 1 (0.6%)                                       |
| South Africa                       |                                                  |                                                  | 1 (1.4%)                                         | 1 (0.6%)                                       |
| Spain                              | 5 (9.6%)                                         | 2 (5.1%)                                         | 3 (4.2%)                                         | 10 (6.1%)                                      |
| Switzerland                        |                                                  |                                                  | 4 (5.6%)                                         | 4 (2.5%)                                       |
| Taiwan                             |                                                  | 1 (2.6%)                                         | 5 (6.9%)                                         | 6 (3.7%)                                       |
| United Kingdom                     | 2 (3.8%)                                         | 3 (7.7%)                                         | 4 (5.6%)                                         | 9 (5.5%)                                       |
| United States                      | 18 (34.6%)                                       | 16 (41.0%)                                       | 19 (26.4%)                                       | 53 (32.5%)                                     |
| Venezuela                          |                                                  | 1 (2.6%)                                         |                                                  | 1 (0.6%)                                       |
| Affiliations added                 | 52                                               | 39                                               | 72                                               | 163                                            |
| Countries/AR added                 | 13                                               | 7                                                | 11                                               | 31                                             |

6. Tends not to be situationally dependent (i.e., answerable with “it all depends”)
7. Is not likely to be answerable with “yes” or “no”

Groups accomplished this goal through a combination of strategies, chosen by group leaders, including one or more of: (1) separating questions into subthemes and condensing on common ideas; (2) formation of subgroups to evaluate subsets of questions; (3) virtual

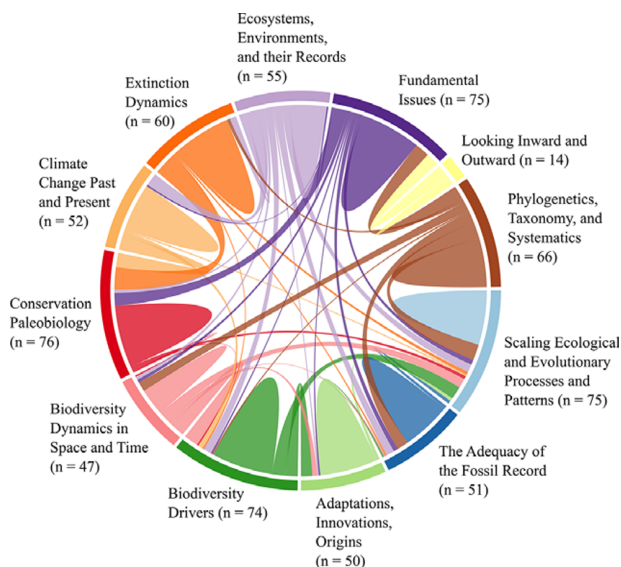
meetings to discuss refinements; and (4) drafting of questions to combine those that existed or cover omitted topics.

Following refinement of the preliminary questions by each group, all questions were compiled for cross-group comments. Participants were asked to suggest revisions, evaluate the importance of each question, and identify overlaps. The coordination team then compiled and summarized responses according to the importance of questions and overlaps. Group leaders coordinated

**Table 2.** Working group themes and numbers of questions related to these groups at three stages of the project. The number of individuals assigned to each group is also provided, with the number of group leaders in parentheses. \*The theme “Ecosystems, Environments, and their Records” was included originally, but after the whole-team feedback phase (Fig. 1), considerable overlaps with questions from other groups were apparent, and all questions from this theme were ultimately distributed elsewhere or subsumed by questions in other groups. †Total is greater than the number of submitted questions ( $n = 528$ ), because a question that was relevant to more than one group was assigned to each group for consideration

| Working group themes                                             | Number of assigned participants (group leaders) | Initial questions assigned to group | Preliminary questions | Final questions |
|------------------------------------------------------------------|-------------------------------------------------|-------------------------------------|-----------------------|-----------------|
| Adaptations, Innovations, Origins (AIO)                          | 17 (2)                                          | 50                                  | 4                     | 7               |
| Biodiversity Drivers (BD)                                        | 17 (2)                                          | 74                                  | 9                     | 9               |
| Biodiversity Dynamics in Space and Time (BST)                    | 17 (2)                                          | 47                                  | 8                     | 7               |
| Climate Change Past and Present (CPP)                            | 16 (2)                                          | 52                                  | 10                    | 9               |
| Conservation Paleobiology (CPB)                                  | 17 (2)                                          | 76                                  | 6                     | 8               |
| Ecosystems, Environments, and Their Records                      | 16 (2)                                          | 55                                  | 16                    | 0*              |
| Extinction Dynamics (ED)                                         | 17 (2)                                          | 60                                  | 11                    | 9               |
| Phylogenetics, Taxonomy, and Systematics (PTS)                   | 17 (3)                                          | 66                                  | 11                    | 10              |
| Scaling Ecological and Evolutionary Processes and Patterns (SEP) | 16 (1)                                          | 75                                  | 11                    | 9               |
| The Adequacy of the Fossil Record (AFR)                          | 16 (2)                                          | 51                                  | 11                    | 8               |
| Fundamental Issues (FI)                                          | 22 (2)                                          | 75                                  | 9                     | 5               |
| Looking Inward and Outward (LIO)                                 | 24 (1)                                          | 14                                  | 11                    | 8               |
| Total questions:                                                 |                                                 | 695 <sup>†</sup>                    | 117                   | 89              |

efforts within and among groups to refine the questions further on the basis of this compiled information (Tables 3–13). Finally, each working group drafted text to contextualize their questions, forming the first version of this article.



**Figure 2.** Assignments of originally submitted questions to different working groups. Each question was assigned to at least one group, and many were also assigned to a second group with topic overlap. Width of the outer circle represents the number of questions assigned to each working group (counts also provided in parentheses). Bands connecting different working groups represent the questions assigned to each of the groups, with thicker bands indicating a larger number of questions shared between groups. Created in R Statistical Software (v. 4.3.1; R Core Team 2023) using the circlize package (Gu *et al.* 2014) and the Paired palette from RColorBrewer (Neuwirth 2022).

## The Big Questions in Paleontology

The three solicitations for submission of Big Questions resulted in 528 contributed questions. (Supplementary Material 1: Raw Questions). The number of questions assigned to a given theme ranged from 14 to 76 (Table 2). Groups refined these questions (Supplementary Material 1: Preliminary Questions) to a preliminary list including 4 – 16 questions from each group (Table 2).

After feedback from all BQ participants, working groups again refined their questions, producing 5 – 10 final questions from each group (Table 2; Fig. 1). The BQs are available in Tables 3–13 (in non-ordered lists from each group), clustered in related themes, starting with questions pertaining to topics that might affect any paleontological study (e.g., preservation, scaling, taxonomy). In the eleven sections that follow, explanatory text accompanies the set of questions from each working group, with questions referred to in the text by working group acronyms (see section headers and tables for acronyms) and non-ordered, unranked numbering. Given the strong relationships among different areas of research in paleontology, there are overlaps in the topics of some questions, which can be taken to indicate important, cross-cutting themes within the discipline (Fig. 2).

## The Adequacy of the Fossil Record (AFR; Table 3)

The fossil record is our primary window into the origin and evolution of life on Earth, providing the only direct line of evidence for these events. Yet, the fossil record is composed primarily of organisms with anatomical, behavioral, and ecological attributes that enhance their preservation potential (AFR1, Table 3; Kidwell and Flessa 1996; Behrensmeyer *et al.* 2000; Sansom *et al.* 2010; Klompmaker *et al.* 2017; Saleh *et al.* 2020, 2021). Preservation biases are also often exacerbated by other biases introduced throughout the life of specimens (AFR2; e.g., Seilacher *et al.* 1985;

**Table 3.** Big Questions for the working group on “The Adequacy of the Fossil Record”

| Unique ID | Big Question                                                                                                       |
|-----------|--------------------------------------------------------------------------------------------------------------------|
| AFR1      | How can we best quantify preservation and collecting biases?                                                       |
| AFR2      | How do we develop methods to identify, minimize, and correct data entry biases?                                    |
| AFR3      | How do we account for data loss in historical collections and publications?                                        |
| AFR4      | How do we standardize taxonomic, stratigraphic, and ecological reporting during data acquisition?                  |
| AFR5      | How can we improve the collection of biomolecules from fossils, and what are the limits for biomolecular analysis? |
| AFR6      | How can we correlate marine and terrestrial strata more precisely?                                                 |
| AFR7      | In what ways can we use isotopic systems and geochemical methods to help identify preservation biases?             |
| AFR8      | Which opportunities and threats for fossil discovery will arise as a result of the changing climate?               |

Behrensmeyer et al. 2000; Louys et al. 2017; Krone et al. 2024)—for example, those relating to acquisition and curation, collecting, digitization, geography and geopolitics, publication, specimen preservation, storage, and transport (Flessa et al. 1992; Whitaker and Kimmig 2020; Raja et al. 2022; Johnson et al. 2023). Methods development for evaluating and mitigating these biases continues to be an important area of research (AFR1–AFR3; e.g., Dunhill et al. 2014; Stewart et al. 2021; De Baets et al. 2022; Na et al. 2023; Antell et al. 2024; Hohmann et al. 2024). Adding to the challenge presented by these biases, maintenance of existing collections and capacity for new collections are threatened by a lack of funding, curatorial staff, and adequate storage facilities, both physical and digital (AFR3; Allmon et al. 2018; Marshall et al. 2018).

Differences in data collection and reporting methods can compound biases in paleontological studies, as researchers have specific purposes when they acquire data (AFR4), and these idiosyncrasies can limit future uses of the data. To reduce duplication of data, reduce research costs, and increase versatility, it is imperative to document and clearly communicate data acquisition and management practices (e.g., as through the extended specimen concept; Lendemer et al. 2020; Hardisty et al. 2022; Monfils et al. 2022). Establishing best practices in these areas will benefit paleontology as we move toward a “big data” future (i.e., data characterized by great variety, volume, and/or velocity; Balazka and Rodighiero 2020), and digitization of existing and new specimens is becoming increasingly common (AFR2; Berents et al. 2010; Allmon et al. 2018).

Methodological, imaging, and analytical advances—geochemical approaches in particular (e.g., nontraditional stable isotopes, synchrotron, handheld XRF)—have created new opportunities for evaluating preservational processes (e.g., Gueriau et al. 2016; Teng et al. 2017). For example, advances in organic geochemistry have increased the capacity to extract biomolecules and biomarkers from fossil and sedimentary archives (e.g., Schweitzer et al. 2008; Briggs and Summons 2014; Vinther 2015; Falk and Wolkenstein 2017; Demarchi 2020; Wiemann et al. 2020; McNamara et al. 2021). However, it remains to be seen how deep in time biomolecules can be found and with what accuracy and resolution the methods can be applied through geological time (AFR5). Inorganic geochemistry has also advanced fundamentally in the last decades, as stable isotope (traditional and nontraditional) and clumped isotope

systems provide new insights in studies of  $p\text{CO}_2$ , pH, paleophysiology, mass extinctions, and the paleobiology and paleoenvironment of fossil taxa (e.g., Casey and Post 2011; Cook et al. 2015; Kimmig and Holmden 2017; Martin et al. 2017; Chen et al. 2018; Kral et al. 2022; Jung et al., 2024). Geochemical advances and continuing improvements to technology and equipment also are expanding the scope of paleontology by enhancing our understanding of diagenesis, morphology, paleoecology, and paleoclimate (AFR6, AFR7; e.g., Smith et al. 2021; Abdelhady et al. 2024; Comans et al. 2024).

The changing global environment also presents new challenges and opportunities for sampling the fossil record (AFR8). For example, as sea level rises and extreme weather events become more common, some existing fossil collecting sites along the coasts may be submerged (e.g., chalk deposits in Europe), while the same processes might lead to the exposure of new sites (e.g., Reimann et al. 2018; Voudoukas et al. 2022). It is also likely that rising temperatures causing the loss of permafrost and glacial ice will expose previously inaccessible outcrops that offer new opportunities for research, even as the changing climate alters erosional processes that may influence fossil exposure and quality (AFR8; e.g., Clark et al. 2021).

### Scaling Ecological and Evolutionary Processes and Patterns (SEP; Table 4)

The scale of an investigation influences the observation and interpretation of ecological and evolutionary processes (SEP1–SEP4, Table 4). In paleontology, scale often relates to the temporal and spatial dimensions of taxa, patterns, or processes (SEP2, SEP3).

**Table 4.** Big Questions for the working group on “Scaling Ecological and Evolutionary Processes and Patterns”

| Unique ID | Big Question                                                                                                                                                                                                                                       |
|-----------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| SEP1      | Which evolutionary and ecological processes (local to global) can be best evaluated using the fossil record?                                                                                                                                       |
| SEP2      | In the fossil record, how do we interpret and measure ecological and evolutionary trends at different taxonomic, spatial, and temporal scales to infer directionality or causality?                                                                |
| SEP3      | How do we address the spatial, temporal, and taxonomic incompleteness of the fossil record to be able to interpret ecological and evolutionary processes and patterns at different scales?                                                         |
| SEP4      | How can we identify and counteract spatial and temporal transmutations (a change in the relationship between variables caused by crossing data scales, leading to interpretive error) within ecological and evolutionary models?                   |
| SEP5      | Given incompleteness of the fossil record and spatiotemporal averaging, how do we estimate rates of change in taxonomic composition, community structure, ecosystem function, niches, traits, life modes, turnover, etc., using the fossil record? |
| SEP6      | What drives metacommunity composition and community assembly over time and space?                                                                                                                                                                  |
| SEP7      | How do external environmental drivers (e.g., plate tectonics, global temperature, sea level) influence the structure of biological systems at different spatiotemporal scales?                                                                     |
| SEP8      | What are the signatures of emergent processes at macroevolutionary timescales (e.g., species sorting, species selection, clade competition)?                                                                                                       |
| SEP9      | How do biological systems impact the abiotic systems and the feedback between them at different scales?                                                                                                                                            |

Ecological and evolutionary processes occur at multiple spatiotemporal scales, but identifying or demonstrating their significance at all scales is challenging and rare (SEP4; Jablonski 2008; Price and Schmitz 2016; Rapacciuolo and Blois 2019; Louys *et al.* 2021; Liow *et al.* 2023). Evaluating the effects of scaling in the fossil record is further complicated by the need to identify and address the incompleteness of the record (SEP3, SEP5; Peters and Heim 2011; Benson *et al.* 2021; and see “The Adequacy of the Fossil Record”). The data captured in the fossil record are imperfect and biased, providing only a glimpse of longer and shorter processes, patterns, and interactions (SEP3, SEP5–SEP7; Faith *et al.* 2021; Flannery-Sutherland *et al.* 2022; Dunne *et al.* 2023).

Paleontological research into the ecological and evolutionary drivers of observed patterns is flourishing, as emergent research areas—for example, conservation paleobiology (Dietl *et al.* 2015; Dillon *et al.* 2022), geobiology (Knoll *et al.* 2012), and phylogenetic paleoecology (Lamsdell *et al.* 2017)—bridge subdisciplines and broach connections between the micro- and macroevolutionary scales (SEP2, SEP5 – 7; e.g., Machado *et al.* 2023; Rolland *et al.* 2023). Paleontologists must grapple with demonstrating links to the biology of modern organisms (i.e., neontology) in studies at various scales in the fossil record (Dietl *et al.* 2019; Rapacciuolo and Blois 2019). Unifying paleo- and neontological data can reveal more about the natural world than either could in isolation (e.g., Hlusko *et al.* 2016; Smith *et al.* 2023c); however, the efficacy of cross-scale analyses needs continued examination. Macroecology (Brown 1995; McGill 2019) may provide one option to incorporate a conceptual basis for this work as, for example, studies of the metacommunity concept—a set of local communities that are linked by dispersal of multiple, potentially interacting species (Leibold *et al.* 2004)—provide a framework for examining scale-based problems. A tenet of this concept is that the study of local patterns and processes is not sufficient to understand the structure and dynamics of a metacommunity (Leibold *et al.* 2004). Studying metacommunity composition and community assembly over space and time acknowledges the fluidity and connection of communities and seeks common patterns across metacommunities (SEP6; e.g., Muscente *et al.* 2018, 2022; Eden *et al.* 2022; Gibert *et al.* 2022). The relationship between the processes on evolutionary scales, their relative influence, and fluctuations through time continue to be important topics (SEP2, SEP4, SEP8).

Over the course of Earth’s history, the biosphere has had a profound impact on the geosphere in ways that we are still working to fully comprehend (SEP9). Studying the interaction from an abiotic perspective highlights the feedback mechanisms and interactions within the Earth–life system, as traces of life are ubiquitous from Earth’s mantle to the atmosphere (Pawlik *et al.* 2020; Giuliani *et al.* 2022).

### Phylogenetics, Taxonomy, and Systematics (PTS; Table 5)

The fossil record contains unique information on the diversity of previous life-forms and their relationships to one another, which provides retrospective context for cataloging and understanding life on the planet today. Phylogenetics is often perceived simply as a tool for inferring evolutionary relationships or organizing biodiversity but also can be seen more broadly as a framework for hypothesis testing and reconstructing past events that are not directly observable in the fossil record (Bromham 2016). This can include estimating species divergence times, studying trait evolution, or quantifying diversification dynamics. Although speciation and extinction have a long history of study, these processes

**Table 5.** Big Questions for the working group on “Phylogenetics, Taxonomy, and Systematics”

| Unique ID | Big Question                                                                                                                                                                                            |
|-----------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| PTS1      | What causes the mechanism of speciation or character evolution to change over time?                                                                                                                     |
| PTS2      | Which abiotic and biotic factors determine species longevity (stratigraphic duration)?                                                                                                                  |
| PTS3      | Which aspects of the macroevolutionary process are identifiable in the molecular or fossil records using phylogenetic methods, and under which circumstances?                                           |
| PTS4      | How can traditional taxonomy be used to inform the process of selecting the best operational taxonomic unit for a particular phylogenetic analysis (e.g., diversification, disparification, phylogeny)? |
| PTS5      | How can taxonomic practice help to harmonize boundaries between taxa in fossil and extant groups?                                                                                                       |
| PTS6      | How can we collect and integrate developmental data observable in the fossil record (e.g., timing of organogenesis, gene expression) into phylogenetic approaches?                                      |
| PTS7      | How much phylogenetic information can be gained from combining different types of data (e.g., morphology, stratigraphy, biogeography, environmental)?                                                   |
| PTS8      | How can we improve the performance of phylogenetic inference through the development of better methods?                                                                                                 |
| PTS9      | How do we improve the representation of uncertainty and bias from the fossil and geological records in phylogenetic inference?                                                                          |
| PTS10     | What can we learn about environmental and geological processes using phylogenetic methods?                                                                                                              |

are complex, and some aspects require further study to improve our understanding (PTS1, PTS2, Table 5). By adopting new methodologies, improving data collection practices, and integrating various types of data centered around current, carefully constructed taxonomies, we can unlock the full potential of hypothesis testing using phylogenetic approaches (PTS3).

Phylogenies are often constructed using molecular data, but there are many benefits to including information from other sources, such as the fossil record (PTS4, PTS5; Parham *et al.* 2012; Lee and Palci 2015; Mongiardino Koch *et al.* 2021; Wright *et al.* 2022). Other data sources, such as developmental biology (Wright 2015), may also prove useful in phylogenetic inference (PTS6). The field requires a multidisciplinary perspective informed by computer and data science, ecology, geology, geochronology, phylogenomics, and statistics (Parham *et al.* 2012; Liow *et al.* 2023). Phylogenomics and deep learning can help to discern and organize biodiversity, but their accuracy will always depend on the quality of their input data, which necessitates reliable systematics and taxonomic identifications (e.g., Bortolus 2008). The accuracy of phylogenetic analyses that include fossils relies on information about taxonomies and their associated uncertainties (Bortolus 2008; Parham *et al.* 2012; Soul and Friedman 2015; Barido-Sottani *et al.* 2023). Taxonomy and comparative anatomy are invaluable in understanding diversification history and character evolution, establishing homologies, quantifying variability, and generating testable hypotheses using phylogenetics and species delimitation methods (Barido-Sottani *et al.* 2023). These research fields must be supported in their own right (Agnarsson and Kuntner 2007; Löbl *et al.* 2023; Smith *et al.* 2023b).

Integrating different data types requires explicit process-based models (PTS7, PTS8), such as the fossilized birth–death model,

which models speciation, extinction, and fossilization simultaneously (Stadler 2010; Heath et al. 2014). Combined with models of molecular and morphological evolution, this framework allows for statistical inference of dated phylogenies that include extant and fossil taxa. Most existing models treat speciation and character evolution as independent (Warnock and Wright 2020), but further refinement of this framework can illuminate the tempo and mechanisms of speciation (PTS1). Comprehensive analyses also require approaches that capture uncertainty and biases while concurrently allowing for varied approaches to weighting of molecular and morphological data (PTS9). We can construct explicit Bayesian hierarchical models to incorporate different data types while accounting for uncertainty in a principled and intuitive way (e.g., Höhna et al. 2016; Bouckaert et al. 2019; Ronquist et al. 2021). It is also imperative to assess the trade-off between data availability, computational efficiency, and model complexity. Simulations play an important role in confronting this challenge and parameter identifiability issues associated with phylogenetic models by helping to explore the performance of available methods, potential limitations of data, and the expectations under null hypotheses (Barido-Sottani et al. 2019; Louca and Pennell 2020; Höhna et al. 2022; Mulvey et al. 2024).

Environmental and geological processes influence the course of evolution (e.g., Arakaki et al. 2011; Hannisdal and Peters 2011; De Baets et al. 2016; Kocsis et al. 2021). Incorporating these processes into phylogenetics will elucidate their interaction with biological events, linking large-scale processes, such as the extent and timing of climatic change, continental breakup, or changes in depositional rates through time with evolutionary phenomena (PTS10).

Biodiversity Dynamics in Space and Time (BST; Table 6)

Quantifying and interpreting biodiversity dynamics over time is a long-standing theme in paleontology (Phillips 1860; Sepkoski et al. 1981; Benson et al. 2021), leading to questions such as whether there are constraints on global biodiversity (BST1, Table 6; Alroy et al.

Table 6. Big Questions for the working group on “Biodiversity Dynamics in Space and Time”

| Unique ID | Big Question                                                                                                                                                                                                                             |
|-----------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| BST1      | What is the global diversity trend through time, and how is diversity constrained, if at all?                                                                                                                                            |
| BST2      | How have large-scale spatial diversity patterns (e.g., latitudinal diversity gradient, distribution of diversity hotspots) changed across deep time?                                                                                     |
| BST3      | What are important drivers of global trends in taxonomic diversity or ecological disparity, and has their relative importance changed through time?                                                                                      |
| BST4      | What is the relationship between deep-time biodiversity (e.g., taxonomic richness, ecomorphological disparity) and ecosystem function (the combination of all biological interactions and physical processes occurring in an ecosystem)? |
| BST5      | What are the drivers of origination in space and time?                                                                                                                                                                                   |
| BST6      | What is a common basis (e.g., taxonomic units, morphological traits) that can be used consistently to bridge modern and fossil biodiversity research?                                                                                    |
| BST7      | In what ways is the “Anthropocene” creating a unique signature in biodiversity over geologic time (both direct and indirect effects; e.g., changes in climate and in connectivity)?                                                      |

2008; Harmon and Harrison 2015; Rabosky and Hurlbert 2015; Close et al. 2020). Given the challenge of fully documenting modern biodiversity (Mora et al. 2011), we cannot expect to know absolute biodiversity in the past, but we can estimate relative changes in biodiversity. Genuine trajectories of biodiversity through time can be uncovered only if we can account for spatial differences and temporal changes in preservation potential, as well as other biases particular to the fossil record (e.g., Smiley 2018; Krone et al. 2024; and see “The Adequacy of the Fossil Record”). By dissecting the components of these trajectories, we can identify drivers of originations and extinctions in deep time (BST5; and see “Adaptations, Innovations, Origins”). To fully understand biodiversity, we must first agree on the most effective methods for measuring biodiversity over different timescales (BST6; see “Scaling Ecological and Evolutionary Processes and Patterns”). Such a consensus can help address pressing questions, including whether modern biodiversity is an outlier in geological time (BST7).

Spatial aspects of biodiversity, such as the latitudinal diversity gradient (Humboldt 1808), are as important as temporal patterns. An extensive literature explores causes of the latitudinal diversity gradient, including its dynamics over geological timescales (Jablonski et al. 2006; Allen et al. 2020, 2023; Zacaï et al. 2021; Fenton et al. 2023; Quintero et al. 2023). Evidence points to a close link between the intensity of the latitudinal diversity gradient and paleoclimate (Mannion et al. 2014; Yasuhara et al. 2020; Yasuhara and Deutsch 2022), but exactly how the latitudinal diversity gradient changed over time remains an open question (BST2).

Biodiversity patterns are the result of extinctions, originations, and the intricate interactions between living organisms and their environment. Identifying the specific factors that drive global changes in biodiversity and disentangling the individual and combined effects of these factors require careful research and analysis (BST3; and see “Biodiversity Drivers”). Approaches leveraging new tools—including mechanistic models (e.g., Saupe et al. 2019), machine learning (e.g., Raja et al. 2021), and network analysis (e.g., Muscente et al. 2018, 2022; Woodhouse et al. 2023)—can identify key drivers of global and regional biodiversity and biodiversity hotspots through time (Cermeno et al. 2022) or at least provide testable hypotheses. We are only beginning to understand and quantify the role of biodiversity as a driver of ecosystem function in the paleontological record (BST4), underscoring the need for consistent units of measure across spatiotemporal scales (BST6; McGuire et al. 2023).

Biodiversity Drivers (BD; Table 7)

In paleontology, documenting patterns of biodiversity is a central theme, but understanding the factors that drive these patterns is a large task (Jablonski 2008, 2017; Ezard et al. 2016; Di Martino et al. 2018). We can, however, begin to address this challenge by decomposing the task into more manageable questions and hypotheses that extend across taxonomic levels. Comparing taxa with differing ecological characteristics (BD1, Table 7) may help disentangle prevailing drivers—including anthropogenic drivers—under shared and disparate environmental conditions or times of perturbation (BD2; Harnik 2011; Klompmaker et al. 2013; Hull et al. 2015; Trubovitz et al. 2023). To compare the potential drivers across taxonomic groups and to do so on different spatial and temporal scales, it is crucial to standardize, harmonize, and clearly communicate study design and methods (Hayek et al. 2019). Doing so will help us establish broader principles that transcend specific taxonomic, spatial, and temporal contexts (BD3).

**Table 7.** Big Questions for the working group on “Biodiversity Drivers”

| Unique ID | Big Question                                                                                                                                                         |
|-----------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| BD1       | How do the ecological niches of species influence their response to perturbation?                                                                                    |
| BD2       | How does the prevailing climate state experienced by species and communities influence their response to perturbation?                                               |
| BD3       | How do methodological choices influence the outcome of studies investigating the relative importance of abiotic and biotic drivers in driving biodiversity dynamics? |
| BD4       | How do the rate and magnitude of environmental change impact diversification?                                                                                        |
| BD5       | How did biological evolution affect the evolution of other Earth systems (e.g., lithosphere, atmosphere, and hydrosphere)?                                           |
| BD6       | How has the relative importance of biotic and abiotic drivers of biodiversity and extinction changed through time?                                                   |
| BD7       | What is the relative role of biotic and abiotic drivers in increasing ecosystem complexity?                                                                          |
| BD8       | To what extent do population-based characteristics determine resilience to extinction through geological time?                                                       |
| BD9       | How do changes in community structure observed at the population level relate to evolutionary changes in ecosystems through time?                                    |

Abiotic and biotic conditions change through time at varying rates and magnitudes, and their effects on biodiversity and ecosystem dynamics warrant further study (BD4, BD7). It has been suggested that abiotic drivers act over broad spatiotemporal scales (e.g., Court Jester model; Barnosky 2001), whereas biotic drivers are more applicable on local and shorter scales (e.g., Red Queen model; Benton 2009; Vermeij and Roopnarine 2013; Wisz *et al.* 2013). The relative significance of these sets of drivers remains uncertain (BD6; e.g., Eichenseer *et al.* 2019; Bush and Payne 2021; Spiridonov and Lovejoy 2022), underscoring the importance of conceptual models for how biodiversity responds to them (Vrba 1985, 1992, 1993; Mancuso *et al.* 2022). There is evidence that diversification patterns observed at higher taxonomic levels (e.g., family) are not always replicated at lower levels (e.g., species; Jablonski 2007; Hendricks *et al.* 2014; Balisi and Van Valkenburgh 2020). Across each of these variables, the effects of scale on which hypothesis is supported (i.e., biotic or abiotic drivers) merit further consideration—in some instances, relationships may be reversed when comparing shorter ecological and longer evolutionary timescales (BD3; e.g., De Baets *et al.* 2021). Further exploration with differing spatiotemporal scales, taxonomic groups, and ecologies is needed, as it remains a challenge to dissect the complex interplay between ecology, microevolution, and macroevolution on geological timescales (BD8, BD9; e.g., Liow and Taylor 2019; Liow *et al.* 2023). Examining the reciprocal effects of biological evolution as an actor, as well as in feedbacks and as a primary driver in other Earth systems, is a promising research direction (BD5).

### Adaptations, Innovations, Origins (AIO; Table 8)

The evolutionary history of many species (and higher taxa) is demarcated by adaptive novelties and innovations along with repeated migration, dispersal, and colonization events as species have evolved and survived through morphological adaptation, ontogenetic shifts, and novel behaviors (AIO1, Table 8; e.g.,

**Table 8.** Big Questions for the working group on “Adaptations, Innovations, Origins”

| Unique ID | Big Question                                                                                                                                                                                                                                                    |
|-----------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| AIO1      | What were the geological and biological drivers of the origin of life and major groups of organisms such as eukaryotes, plants, animals, and fungi?                                                                                                             |
| AIO2      | How were major life transitions (e.g., origins of biomineralization, early Paleozoic diversifications, terrestrialization, evolution of planktonic lifestyle) in Earth's history associated with major changes in the geological and/or biological environment? |
| AIO3      | How is our understanding of the origination of novelties and innovations affected by fossil preservation, the global quality of the fossil record, and stratigraphic completeness?                                                                              |
| AIO4      | What are best practices for integrating different analytical tools and techniques to improve our interpretation of the ecological context and timing of the origin of adaptations and features?                                                                 |
| AIO5      | How have changes in ontogeny (i.e., life-history traits such as larval/juvenile ecology, growth, and developmental patterns, including heterochronies) influenced macroevolution or themselves been influenced by environmental change?                         |
| AIO6      | Which common patterns of morphological or behavioral responses to environmental change on evolutionary timescales can be identified and how do these compare with modern systems on ecological timescales?                                                      |
| AIO7      | Which observable differences in the origin and fixation of features at different scales of biological hierarchy can be identified, and what generated these patterns?                                                                                           |

Nylin *et al.* 2018; Stigall 2019). Colonizing regions in new environments and adapting to cope with the challenges induced by new environmental pressures has led to the development and emergence of advantageous novelties over time. These novelties increase the capacity of individuals to survive, thrive, and reproduce (AIO1, AIO2; e.g., Patton *et al.* 2021; Tihelka *et al.* 2022; Woehle *et al.* 2022). Observing modern species and their responses to stimuli provides paleontologists with a means to connect microevolutionary processes and patterns to those observed over evolutionary timescales in the fossil record (AIO6), which are obscured by taphonomic processes (AIO3). Improving data integration across scales, leveraging new methods, and better accounting for biases can help us answer long-standing questions on topics relating to phylogenomic conflict (Parins-Fukuchi *et al.* 2021), evolutionary patterns (e.g., phyletic gradualism vs. punctuated equilibrium; Gould and Eldredge 1972; Hunt 2007; Hunt *et al.* 2015; Tsuboi *et al.* 2024), and phylogenetic relationships (Wright *et al.* 2022).

The interdependence among ecological determinants and biological features requires thorough examination to reveal the inextricable relationship between micro- and macroevolutionary processes, environmental change, and preservation (AIO4–AIO6; e.g., Lamsdell *et al.* 2020; Alméjida *et al.* 2021; and see “The Adequacy of the Fossil Record”). To develop these research directions (AIO5–AIO7), hypotheses on the emergence of major features (e.g., Naranjo-Ortiz and Gabaldón 2019; Murdock 2020), changes in morphology (e.g., Anderson and Ruxton 2020; Hopkins and To 2022), ontogeny (e.g., Chevalier *et al.* 2021; Friend *et al.* 2021; Lanzetti *et al.* 2022), and behavior (e.g., Berbee *et al.* 2020; Yamamoto and Caterino 2023) require contextualization with spatiotemporal, taphonomic, and preservational constraints (AIO3, AIO4). Answering these questions can facilitate the examination of

overarching patterns in biotic developmental and community responses to perturbation throughout the history of life and can possibly be projected to the future (AIO6). Studies on the emergence of adaptations, innovative features, ontogenetic strategies, behaviors, and the development of novelties can provide paleontology with crucial insights into the processes of evolution and extinction, as well as the interactions between individuals, species, and communities (AIO5–AIO7; Barido-Sottani et al. 2020; Brocklehurst and Benson 2021; Stansfield et al. 2021; Dunhill et al. 2024).

Extinction Dynamics (ED; Table 9)

The understanding that species are ephemeral and will eventually become extinct is now a fundamental principle of paleontology (Cuvier 1813; Darwin 1859; MacLeod 2014; Marshall 2017)—and potentially scales up from species to faunas and paleocommunities (e.g., Muscente et al. 2022). This concept is integral to the study of the history of life on Earth, as it helps to explain changes in biodiversity observed in the fossil record (Jablonski 1991; McKinney 1997). At the same time, extinction is a major theme in modern bioscience relating to impacts of anthropogenic stressors (e.g., climate change, habitat change, pollution; McKinney 1997; Dirzo et al. 2014). As is usual for comparisons of the modern and fossil records, attempting to bridge the differences in study characteristics (e.g., evolutionary history of ecosystems; spatiotemporal completeness, extent, and resolution; taxonomic completeness; Foote 2000; Eichenseer et al. 2019; Foster et al. 2023; Pohl et al. 2023; Finnegan et al. 2024) over which extinction can be observed necessitates reflection on which data types are suitable to facilitate cross-scale studies and comparisons (ED1, Table 9; Lotze et al. 2011; Andréoletti and Morlon 2024).

The “BigFive” mass extinctions originally were defined using the concept of statistical outliers (Raup and Sepkoski 1982) at a high taxonomic level, using a specific rate metric, and based on

skeletonized marine organisms. An updated definition of mass extinction is long overdue, as is a dialogue on how pattern and process should be included in the definition (ED2; Marshall 2023). This definition would precipitate the reexamination of whether mass extinctions are associated with consistent vulnerabilities of specific morphological and ecological traits (ED3, ED4; Foster et al. 2023) and whether their phases and recovery patterns are comparable (ED6, ED7; Hull et al. 2015).

Another aspect of extinction dynamics, pertaining to the ecological impact of the event, is whether functional diversity is maintained across mass extinction events (ED5; Bambach et al. 2007; Foster and Twitchett 2014; Aberhan and Kiessling 2015; Dunhill et al. 2018; Muscente et al. 2018; Cribb et al. 2023). Mass extinctions are often attributed to abiotic changes (e.g., changes in temperature, oxygen content, pH), and finding thresholds relating to magnitudes and rates of such changes remains a priority (ED8; Song et al. 2021). Species also are likely to experience secondary extinction cascades due to the loss of critical biotic interactions (e.g., predator–prey relationships) in trophic or other biological interaction networks (Roopnarine 2006; Dunne and Williams 2009). If we are to truly understand the dynamics of extinction events in the fossil record and use them to predict extinction risk in our human-dominated world (Barnosky et al. 2011; Braje and Erlandson 2013; Song et al. 2021; Vahdati et al. 2022), we need to understand the interplay between primary and secondary extinction events via the inclusion of biotic interactions in studies of extinction selectivity (e.g., Sanders et al. 2018; Mulvey et al. 2022; Dunhill et al. 2024).

Climate Change Past and Present (CPP; Table 10)

Paleontologists often reconstruct past climates using fossils or geochemical proxies, and this remains a major theme in the biogeosciences (CPP1, Table 10). For example, examining stable oxygen isotopes in fossils can reveal climate change across temporal scales, from the life span of individual organisms (e.g., Nützel et al. 2010; Alberti et al. 2013) to the eon scale (e.g., Song et al. 2019;

Table 9. Big questions for the working group on “Extinction Dynamics”

| Unique ID | Big Question                                                                                                                                                                 |
|-----------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| ED1       | Which data types can be used to most effectively compare past extinctions to the current biodiversity crisis?                                                                |
| ED2       | With our changing understanding of extinctions, how should the definition of “mass extinction” be updated to reflect a unified concept?                                      |
| ED3       | Which, if any, biotic traits associated with survival through a mass extinction (e.g., body size, trophic mode, species associations) are universal across taxa and/or time? |
| ED4       | Which, if any, ecological impacts of extinction are generalizable across time?                                                                                               |
| ED5       | To what extent are ecological functions maintained following the extinction of species?                                                                                      |
| ED6       | To what extent are the phases of events (e.g., collapse, recovery) during extinctions consistent across different biotic crises?                                             |
| ED7       | Which, if any, patterns in the process and timing of recovery following extinction events are universal across clades?                                                       |
| ED8       | At what threshold can climate or other abiotic change cause an extinction?                                                                                                   |
| ED9       | What is the role of cascading biological effects in extinction dynamics?                                                                                                     |

Table 10. Big Questions for the working group on “Climate Change Past and Present”

| Unique ID | Big Question                                                                                                                    |
|-----------|---------------------------------------------------------------------------------------------------------------------------------|
| CPP1      | How can fossils best be used to reconstruct climate change over different timescales?                                           |
| CPP2      | Which climate factors are the proximate drivers of extinction?                                                                  |
| CPP3      | How can we best use the fossil record to predict climate change impacts on the modern biota?                                    |
| CPP4      | What is the “ecosystem sensitivity” of ecosystem structure in response to climate change?                                       |
| CPP5      | How have the spatial distributions of organisms shifted in response to climate change?                                          |
| CPP6      | How have organisms’ tolerances changed in response to climate change?                                                           |
| CPP7      | Which cascading effects of climate change can be identified from the fossil record?                                             |
| CPP8      | What adaptation and management options for conservation biology can be derived from past biosphere responses to climate change? |
| CPP9      | How has climate change affected the evolution of life?                                                                          |

Grossman and Joachimski 2022). However, smoothly integrating data across these temporal scales remains challenging (CPP1). Assessing biotic responses to changing climates is becoming a major theme in paleontology, with several pertinent questions (CPP2–CPP9; e.g., Rita *et al.* 2019; Piazza *et al.* 2020; Nätscher *et al.* 2023). Nevertheless, it is critical to avoid circular reasoning where climate reconstructions based on fossil proxies subsequently are used to interpret fossils.

A host of variables—including direct and indirect measures of nutrient levels, temperature,  $p\text{CO}_2$ , precipitation, salinity, pH, and, oxygen and other isotopes—can be used to examine the influence of climate on biodiversity (Bijma *et al.* 2013; Saupe *et al.* 2019; Jane *et al.* 2021; Jackson and O’Dea 2023; Lin *et al.* 2023; Yasuhara and Deutsch 2023; Malanoski *et al.* 2024). Elucidating the relative importance of these variables on biodiversity can guide conservation efforts (CPP2, CPP8), although best practices for bridging the mismatch in temporal scales studied in paleontology and those of interest to policymakers remain elusive (CPP3; Smith *et al.* 2018; Pimiento and Antonelli 2022; Groff *et al.* 2023; Kiessling *et al.* 2023; and see “Scaling Ecological and Evolutionary Processes and Patterns”). Bridging these gaps can benefit from studies leveraging conservatism of physiology (Reddin *et al.* 2020), simulations (e.g., Hunt 2012; Barido-Sottani *et al.* 2019; Raja *et al.* 2021; Smith *et al.* 2023a), and the pursuit of higher-resolution paleontological datasets (Smith *et al.* 2023c). The application of paleontological observations to conservation practice remains primarily aspirational (Groff *et al.* 2023); however, leveraging the need for temporal context to understand climate change is a promising avenue for integrating paleontological data (Smith *et al.* 2018; Dietl *et al.* 2019; Kiessling *et al.* 2019, 2023).

Climate sensitivity has been defined as the global mean temperature increase when atmospheric  $\text{CO}_2$  equivalent concentration is doubled (IPCC 2021), and we can use this framework to define “ecosystem sensitivity” (CPP4). For example, how much will ecological structure—a concept challenging to objectively measure (e.g., Parrott 2010; LaRue *et al.* 2023)—change on average with a given increase in temperature? A more straightforward assessment of shifts in spatial distribution is also possible, as there is modern (Lenoir *et al.* 2020) and past (Wing *et al.* 2005; McElwain 2018) evidence of species ranges tracking climate. Still, the signal is complex (Reddin *et al.* 2018, 2020), primarily due to sampling constraints and limited temporal resolution, and merits further examination (CPP5). In isolation from or in combination with range shifts, the degree to which species can adapt their niches over time is crucial to predicting how they will respond to ongoing climate change (CPP6). Fossil data support niche stability at low taxonomic levels (Hopkins *et al.* 2014; Saupe *et al.* 2014; Stigall 2014; Antell *et al.* 2020); however, thermal tolerances have evolved across the domains of life (Storch *et al.* 2014), suggesting that the rate and relative frequency at which tolerances evolve are key features in niche evolution.

The impacts of climate change on biotic systems are numerous (Pörtner 2021), but cascading effects are less well known (CPP7; e.g., Pecl *et al.* 2017; Słowiński *et al.* 2018). For example, differential range shifts of species in response to climate may lead to novel communities, with new biotic interactions and elevated potential for secondary extinctions (ED9; Pecl *et al.* 2017; Chiarenza *et al.* 2023). Identifying cascading effects in the fossil record is likely difficult but important to reveal the interplay of abiotic and biotic drivers under climate change (O’Keefe *et al.* 2023).

## Conservation Paleobiology (CPB; Table 11)

Conservation paleobiology, which seeks to apply the methods and theories of paleontology to the conservation and restoration of biodiversity and ecosystem services (Dietl *et al.* 2015), has emerged as a pathway for paleontologists to engage with conservation issues. A key theme in these questions is the integration of multiple types of data and methods across scales (CPB2, CPB4, CPB6, Table 11) to provide insights about biodiversity change (CPB3–CPB5, CPB8). Questions in this section crosscut many of the other sections—especially “Climate Change Past and Present”—as conservation paleobiology is an emergent area of research in paleontology that is informed by the entire discipline.

Many paleontologists are seeking ways to more directly connect their science to practice (CPB1, CPB2, CPB8; Dillon *et al.* 2022). Although there are several success stories of paleontological data application (e.g., Everglades restoration; Marshall *et al.* 2014), only 10.8% of published conservation paleobiology studies have had a demonstrable effect on conservation practice (comparable to other areas of conservation science; see Groff *et al.* 2023). A cultural shift in the norms and practices of the paleontological community is required to produce research results that more closely align with the needs and concerns of practitioners (Dietl *et al.* 2023). How to get there is a big question (CPB1). At the same time, questions that form the theoretical basis for conservation paleobiology (CPB3–CPB7) remain research priorities, offering opportunities for scientific progress while highlighting gaps in our understanding of biodiversity and ecosystem function and, by extension, ecosystem services (Dillon *et al.* 2022). For example, it remains a significant challenge to untangle the different drivers that push ecosystems

**Table 11.** Big Questions for the working group on “Conservation Paleobiology”

| Unique ID | Big Question                                                                                                                                                                                                                 |
|-----------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| CPB1      | What translational science strategies could be adopted to ensure that conservation paleobiology research remains relevant and aligned with the priorities of environmental resource managers and conservation practitioners? |
| CPB2      | How do we integrate multiple types of paleontological data (e.g., molecular, environmental, ecological) with planning and decision support tools for guiding ecosystem management?                                           |
| CPB3      | How can our understanding of past episodes of environmental change be used to develop scenarios of biological responses to modern and future environmental stressors?                                                        |
| CPB4      | How can we use paleontological data to define meaningful ecological baselines that are relevant to conservation across spatial and temporal scales?                                                                          |
| CPB5      | How can the fossil record inform our ability to diagnose and mitigate the effects of multiple interacting human and nonhuman drivers of environmental change on biodiversity and ecosystem functioning?                      |
| CPB6      | How can we compare rates of biodiversity change (e.g., extinction, adaptation, geographic range shifts) across ecological, historical, and paleontological timescales?                                                       |
| CPB7      | How can recent sedimentary records expand the temporal scope over which ecological resilience can be evaluated?                                                                                                              |
| CPB8      | In what ways can paleoenvironmental reconstructions improve the accuracy and scope of ecosystem services risk assessments?                                                                                                   |

beyond their natural limits and to understand the resulting responses over time (CPB5). The extent to which paleoecological records can be utilized to broaden the temporal perspective for detecting critical transitions in ecosystems and signals of changing resilience (CPB7) is also not fully understood. Nor is it known how, and under which circumstances, looking to the past can contribute productively to setting baselines for ecosystem recovery (CPB4) or anticipating a climate-changed future (CPB3). Such knowledge could support conservation management and planning efforts designed to help reduce the loss of biodiversity and ecosystem services (CPB8) in the face of environmental change. Theoretical development in these areas is foundational for paleontology and is essential for the discipline to grow as an applied area of research to provide insights about future changes in the human-dominated world (Dietl and Flessa 2011; Dietl et al. 2015, 2019; Barnosky et al. 2017; Dillon et al. 2022; Pimiento and Antonelli 2022; Groff et al. 2023; Kiessling et al. 2023; Kowalewski et al. 2023; Zuschin 2023).

Fundamental Issues (FI; Table 12)

Every scientific discipline relies on a dedicated community and supportive infrastructure. To protect paleontology’s foundational resources, infrastructure updates are needed (FI1, FI3, FI5, Table 12). Best practices for collecting, curating, and archiving paleontological data and heritage are developing, but a consensus remains a work in progress (FI1). Assigning specimens an accurate taxonomy in a sound systematic framework is critical for their utility and inclusion in a shareable resource (e.g., GBIF, iDigBio, the Paleobiology Database, FI3; Marshall et al. 2018). The accuracy and resolution of taxonomic identifications strongly affect biodiversity measurements and interpretation, but this fundamental work is consistently undervalued in the current system for rewarding academics (FI3; Agnarsson and Kuntner 2007; Mabry et al. 2022; Salvador et al. 2022; Smith et al. 2023b). As a result, taxonomic expertise is under threat (e.g., Agnarsson and Kuntner 2007; Salvador et al. 2022). Even so, novel methods for taxonomic analysis (e.g., machine learning; Romero et al. 2020; De Baets 2021; Punyasena et al. 2022; Abdelhady et al. 2024; Adaimé et al. 2024) hold the potential to make taxonomic work more efficient, reproducible, and sustainable. Reliable taxonomic, locality, and stratigraphic information are essential for building physical (e.g., samples) and digital

(e.g., metadata, imagery) storage infrastructure that allows comparison and integration among researchers and scientific disciplines (Löbl et al. 2023). These improvements require a community effort that is supported by sustainable long-term funding—particularly in the Global South (e.g., Valenzuela-Toro and Viglino 2021; Raja et al. 2022). This funding can enable expanded accessibility, use, and combination of data, all of which are critical for facilitating interdisciplinary research (Allmon et al. 2018; Kaufman et al. 2018; Smith et al. 2023b). Through interdisciplinary research and study programs, the field can continue to expand (FI3). For example, studies of prehistory demonstrate long-standing human collection and use of fossils from the middle Pleistocene onward, creating new opportunities to understand human behavior through interactions with fossils (Cortés-Sánchez et al. 2020). Interdisciplinarity will continue to generate new creative approaches with valuable perspectives from other disciplines (e.g., archaeology, biology) while providing new insights on long-pursued questions in paleontology (FI2–FI4).

Paleontology is also economically and societally important (FI4, FI5). Economic contributions include resource exploration, regional tourism (Perini and Calvo 2008; Kibria et al. 2019), and diverse products based on paleontological research (e.g., books, clothing, film and television works, theme parks, toys, video games). Aside from these outputs, paleontology requires greater valorization within the scientific community and broader public (FI4, FI5; Plotnick et al. 2023). Geosites are non-renewable areas important for understanding Earth’s history through the observation of biological and geological phenomena. Protecting and conserving important outcrops (e.g., Atkinson et al. 2005; Maran 2014; Mexicana 2020; Neto De Carvalho et al. 2021; Carvalho and Leonardi 2022) and access to them necessitate transparent discussion among all who interact with and care about the sites (e.g., paleontologists, landowners, traditional custodians of the land, universities, industrial companies, museums, government). Additionally, collection spaces are the physical repositories of our geoheritage (e.g., museums, geological surveys) and require sustained support from governments, academics, and the public. The primary evidence that paleontologists rely on (physical specimens) is under threat due to restructuring in funding models and museum closures, which removes from the public a pathway for engagement with geoheritage. Public engagement provides a valuable means to increase the profile of paleontology. This work and the people involved in it require significant investment to draw together science, economy, and culture to care for Earth and life’s heritage (FI1, FI4, FI5).

As scientists, we have a responsibility to communicate with the public about our work, yet many researchers receive no formal training on how to perform this duty (e.g., Salvador et al. 2021), and these activities are secondary in hiring and promotion decisions (FI2, FI4; e.g., Davies et al. 2021; Raja and Dunne 2022). Without an informed public, policymakers cannot craft legislation that benefits the greatest number of people, and individuals cannot make accurate data-driven decisions. The roles of paleontologists continue to diversify, with a large proportion of graduates working outside academia in settings with variable skill requirements (FI2; e.g., industry, conservation, education, government; Keane et al. 2021). Paleontologists need skills to make them academically, economically, and socially valuable so they can share information about the long-term changes and variability that life on Earth has experienced with increased proficiency.

Looking Inward and Outward (LIO; Table 13)

Whereas paleontologists are keenly aware of the taphonomic biases constraining our view of past biodiversity, we have not systematically studied the biases linked to the identities and practices shaping how

Table 12. Big Questions for the working group on “Fundamental Issues”

| Unique ID | Big Question                                                                                                                                                                                                                                 |
|-----------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| FI1       | How can we efficiently collect, store, and combine different paleontological data types in an openly accessible and inclusive way?                                                                                                           |
| FI2       | What are best practices for training paleontologists to have a broad set of skills (e.g., data analyses, research skills, soft skills) that are transferable to an increasingly wider range of job requirements inside and outside academia? |
| FI3       | How can we best motivate taxonomic and systematic work and facilitate crosstalk and collaboration with other paleontological disciplines?                                                                                                    |
| FI4       | How can paleontologists communicate findings and foster critical thinking skills so that the public can understand the utility of paleontological information and differentiate valid scientific ideas from other ideas?                     |
| FI5       | What are the best practices for the protection and valorization of geosites and unique fossil heritage?                                                                                                                                      |

**Table 13.** Big Questions for the working group on “Looking Inward and Outward”

| Unique ID | Big Question                                                                                                                                                                                                                                                              |
|-----------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| LIO1      | How is our understanding of past ecological and evolutionary processes shaped by biases in publication by location, authorship, language use, and funding availability?                                                                                                   |
| LIO2      | Which processes drive turnover in diversity trends (e.g., gender identities, different geographic regions) of academic paleontologists over time, and how could increased diversity lead to increasingly diverse products and outcomes?                                   |
| LIO3      | Which socioeconomic and identity factors—and their intersections—underlie variability in publication rate, professional advancement, and grant awards among the global paleontology community, both historically and in the present day?                                  |
| LIO4      | To what extent are paleontological specimen collecting and repository practices built on a legacy of colonial economic structures and how can we avoid recapitulating these interactions today across individual and institutional collaborations?                        |
| LIO5      | How should qualities of fossil origin (e.g., country, sovereignty, collection process, local collaborative involvement, political conflict) be considered when designing research and navigating potential trade-offs in ethics and scientific value?                     |
| LIO6      | Which settings (e.g., economic, cultural, physical) govern the biogeography of where paleontological fieldwork occurs and who (e.g., gender/ethnic identity) carries out—and benefits from—that work?                                                                     |
| LIO7      | Which institutional and mentorship attributes, such as accountability mechanisms, facilitate equitable collaboration among paleontologists, avoid bias, and promote the retention of students from backgrounds and identities currently underrepresented in paleontology? |
| LIO8      | How do we integrate and sustain a commitment to diversity, equity, and inclusion initiatives into the foundations of hiring, promotion, and funding schemes in paleontology?                                                                                              |

we collect, analyze, and interpret the fossil record. Presently, socioeconomic factors disproportionately influence the sampling coverage of both modern ecosystems and past biodiversity (Cisneros *et al.* 2022; Monarrez *et al.* 2022; Raja *et al.* 2022). Many perspectives and data are missing, which contributes to an incomplete understanding of past and present global biodiversity and restricts the development of ecological and evolutionary theory (LIO1, Table 13; Mohammed *et al.* 2022; Raja *et al.* 2022). Identifying and addressing these biases and challenges in paleontology (e.g., dominance of the English language; Cisneros *et al.* 2022; Raja *et al.* 2022) and incorporating as many diverse perspectives as possible will lead to a better understanding of all aspects of life on Earth (LIO2, LIO3).

Though many people globally have undertaken the study of past life, including within Indigenous traditions and local communities (Mayor 2007; Benoit *et al.* 2024), the earliest data points of Western academic paleontology are tied to the expansion of colonial empires (Monarrez *et al.* 2022; Scarlett 2022). Current research infrastructure is often built on these colonial legacies, including specimens held in museum collections (LIO4; Bradley *et al.* 2014; Cisneros *et al.* 2022; Mohammed *et al.* 2022; Monarrez *et al.* 2022; Raja *et al.* 2022). Digitization efforts are making museum collections and exhibits more accessible internationally to those with internet access, but digital representations do not necessarily provide the same research and engagement opportunities as physical specimens and have their own complications (e.g., compliance with sharing

policies, digital quality and resolution, large file sizes, internet access and bandwidth; Falkingham 2012; Lewis 2019). Natural history specimens and geosites are often considered to be natural heritage items (including status as UNESCO sites, <https://whc.unesco.org/en/list>), and calls for repatriation are growing in number (Bradley *et al.* 2014; Vogel 2019), making evaluating this issue in paleontology a priority (LIO4; see “Fundamental Issues”).

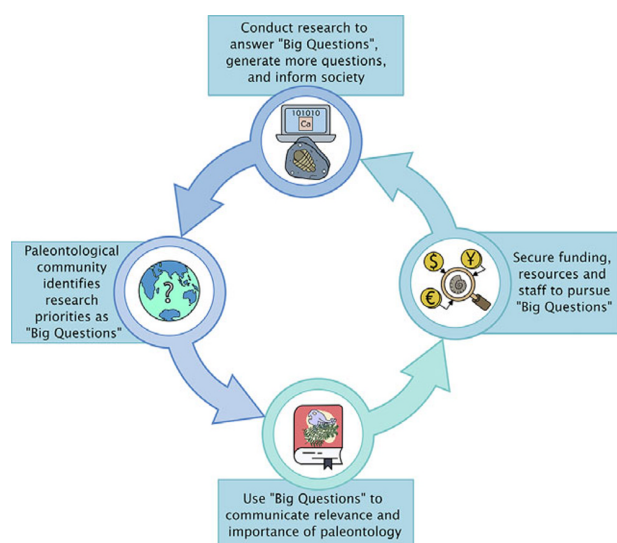
Researchers, institutions, and funding bodies must make proactive decisions to avoid contributing further to colonial legacies by evaluating the power dynamics of international collaborations while contending with the curation of specimens collected in the past (LIO5; e.g., Dunne *et al.* 2022). These decisions can run counter to incentives for publication on “novelty” and unique specimens, which are often gleaned from fieldwork in key geographic regions (e.g., Myanmar; LIO6; Dunne *et al.* 2022; Raja *et al.* 2022).

More broadly, fieldwork is not equally accessible to everyone despite its high value as a component of science education (e.g., Shinbrot *et al.* 2022). As in all the sciences with fieldwork components, paleontologists must grapple with safety and equity considerations, including mechanisms for reporting sexual harassment and assault (Clancy *et al.* 2014), explicit discussions about the safety of people of marginalized identities in field conditions (Demery and Pipkin 2021; Rudzki *et al.* 2022), and accessibility and inclusive design of field experiences for people with disabilities (LIO6; Stokes *et al.* 2019).

The exclusion and attrition of groups of people with particular identities and affinities (i.e., minoritized or marginalized groups) from academia have previously been described as a passive, leaky pipeline; however, this metaphor downplays the challenges posed by racism, colonial legacies, and systemic bias at institutional levels, which are now more accurately described as a “hostile obstacle course” (e.g., Bernard and Cooperdock 2018; Valenzuela-Toro and Viglino 2021; Berhe *et al.* 2022; Carter *et al.* 2022). Recognizing that these challenges exist, paleontologists must identify and embrace practices that create a more inclusive and equitable culture (LIO7; Valenzuela-Toro and Viglino 2021; Carter *et al.* 2022; Cisneros *et al.* 2022; Raja *et al.* 2022). Current diversity, equity, and inclusion tasks fall disproportionately on minoritized individuals, yet often are not considered in tenure and promotion assessments (LIO8; Jimenez *et al.* 2019). Although individual actions are important, support for diversity, equity, and inclusion must come from the highest levels of leadership (e.g., those making funding decisions) to signal their value (Dutt 2021; Chen *et al.* 2022). In implementing these changes, we can iteratively add to our dataset of changing outcomes in paleontology to evaluate whether such actions are effective (LIO2) and how this affects our understanding of both past and future worlds (LIO1).

### Concluding Remarks

The present state of paleontological research is complex and constantly changing. Considering the limited number of paleontologists employed professionally in comparison to other scientific fields (e.g., Keane *et al.* 2021; Plotnick *et al.* 2025), it is prudent to develop a shared research agenda that the paleontological community can jointly address (Fig. 3). The questions presented here are unavoidably influenced by the perspectives of those participating and by the initial set of questions submitted. However, we have attempted to minimize this influence through our strategy for an inclusive approach to question submission, project participation, and authorship. Doing so gives us confidence that these BQs faithfully represent a forward-looking agenda for the discipline of paleontology.



**Figure 3.** The Big Questions project can be used as a tool to guide research in paleontology and to advocate for the importance of funding paleontological research.

Whether this list of questions is taken as a whole, separated by theme, or examined piecemeal as individual questions, we encourage all in the paleontological community to use these BQs as a tool for communicating the importance of paleontology and securing research funding. Indeed, as the questions presented here have emerged from a community-wide effort, they likely are more representative of the state of the field than if the exercise was conducted with a top-down approach by a select few individuals, and this element may add credibility and power to arguments for funding in paleontology, broadly. As in other endeavors to define priority questions (e.g., Sutherland et al. 2009; Seddon et al. 2014), we expect a variety of uses (e.g., development of research projects, spurring discussion on the importance of different BQs) and audiences (e.g., other scientists, funding bodies, students, the general public). We anticipate these BQs will be used by researchers as framing and inspiration for new research directions and as a tool they can use to justify paleontological research to funding organizations (Fig. 3). The BQs reiterate the substantive contributions of museums and physical collection spaces, making clear a need for sustained funding of the repositories of our geoheritage. The BQs highlight the breadth and vitality of paleontology and the important and substantive role the discipline will continue to play in pushing the frontiers of understanding throughout the life sciences.

Many of the questions included here are directed at pursuing long-standing hypotheses on how life has evolved and responded to environmental change. A large portion also pertains to the application of paleontological data to the biodiversity and environmental crises that permeate the modern world. Questions in each of these areas share common considerations, including the effects of scale on observations and the ever-present challenge of assessing the adequacy of the fossil record to address these questions. Reflecting larger ongoing discussions in science and society, there is also an emphasis on conducting paleontological research more inclusively and equitably as a community. Through efforts like this Big Questions project that bring together groups of people with many backgrounds, expertise, and motivations, we aspire to grow and strengthen the global paleontological community. Our collective understanding of the history and future of life on Earth will only be

improved by creating a cohesive discipline where all interested individuals can contribute.

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