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Research Article

Are original biomaterials in vertebrate fossils rare? A global analysis of the scientific literature

Biomateriais originais em fósseis de vertebrados são raros? Uma análise global da literatura científica

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Abstract: The preservation of biomaterials interpreted as original in vertebrate fossils has historically been considered rare in the scientific literature, associated with exceptional taphonomic conditions. In recent decades, however, numerous studies have reported biomolecules, cellular structures, and soft tissues in the scientific literature in different fossil contexts, although these data remain scattered. The research consisted of a documentary study with a descriptive quantitative analysis of the literature, in which documentary records of biomaterials reported in publications over eight decades (1954–2025) were systematized in a database for analysis of distribution patterns. A total of 198 studies were identified, comprising 377 documented records, covering multiple levels of biological organization and different taxonomic, geographic, stratigraphic, and methodological distributions. A correlation was observed between the frequency of published records and the diversity of analytical approaches described, with the recurrent application of multi-method strategies. Taken together, the results indicate that the perception of rarity stems largely from the historical fragmentation of the literature and the absence of integrated quantitative syntheses, rather than from a scarcity of documented reports. The study presents a quantitative synthesis of the distribution of published records and contributes to the understanding of how the preservation of biomaterials has been documented in the paleomolecular literature.

Keywords: Molecular Paleontology; non-mineralized biomaterials; fossil biomolecules; exceptional preservation; descriptive quantitative analysis.

Resumo: A preservação de biomateriais interpretados como originais em fósseis de vertebrados tem sido historicamente considerada rara na literatura científica, associada a condições tafonômicas excepcionais. Nas últimas décadas, contudo, numerosos estudos têm reportado, na literatura científica, biomoléculas, estruturas celulares e tecidos moles em diferentes contextos fósseis, embora esses dados permaneçam dispersos. A pesquisa consistiu em um estudo documental com análise quantitativa descritiva da literatura,

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no qual registros documentais de biomateriais reportados em publicações ao longo de oito décadas (1954–2025) foram sistematizados em banco de dados para análise de padrões de distribuição. Foram identificados 198 trabalhos, totalizando 377 registros documentais, abrangendo múltiplos níveis de organização biológica e diferentes distribuições taxonômicas, geográficas, estratigráficas e metodológicas. Observou-se correspondência entre a frequência dos registros publicados e a diversidade de abordagens analíticas descritas, com recorrente aplicação de estratégias multimétodo. Em conjunto, os resultados indicam que a percepção de raridade decorre, em grande parte, da fragmentação histórica da literatura e da ausência de sínteses quantitativas integradas, mais do que da escassez de relatos documentados. O estudo apresenta uma síntese quantitativa da distribuição dos registros publicados e contribui para o entendimento de como a preservação de biomateriais tem sido documentada na literatura paleomolecular.

Palavras-chave: Paleontologia Molecular; biomateriais não mineralizados; biomoléculas fósseis; preservação excepcional; análise quantitativa descritiva.

1. Introduction

Molecular Paleontology emerged in the 1970s and 1980s as an interdisciplinary field that integrates paleontology, organic geochemistry, and molecular biology to investigate the persistence and transformation of molecules over deep time (Runnegar, 1986; Wörheide *et al.,* 2016). For much of the 20th century, the preservation of original biomaterials in vertebrate fossils was considered rare and restricted to exceptional taphonomic conditions, in line with classical models of fossilization that predicted the rapid degradation of organic components after death and their complete mineral replacement.

In recent decades, however, a growing number of studies have documented remnants of biomolecules, cellular microstructures, and soft tissues in fossils of different geological ages. The development and application of high-resolution analytical techniques, such as mass spectrometry, vibrational spectroscopy, and immunological methods, have expanded the ability to detect preserved organic compounds, pushing back the recognized limits of preservation in the fossil record (Schweitzer, 2003; 2011; Schweitzer *et al.*, 2019; Thomas & Taylor, 2019).

Despite advances, the interpretation of these findings remains a subject of debate, The persistence of biomolecules or their remains for millions of years appears to contradict experimental kinetic estimates for the degradation of proteins and nucleic acids, and some of the literature has attributed certain records to recent contamination or the formation of microbial biofilms (Buckley *et al.*, 2008; Kaye, Gaugler & Sawlowicz, 2008; Peterson, Lenczewski & Scherer, 2010; Saitta & Vinther, 2019). Thus, understanding the actual extent of preservation of biomaterials interpreted as original has become an important issue for both molecular paleontology and the taphonomy of vertebrate fossils.

However, the available knowledge remains scattered throughout the literature. Most of the work consists of case studies, investigations associated with specific depositional contexts, or surveys focused on particular taxonomic groups. Narrative reviews have compiled representative examples of these findings, but were not designed to quantify their frequency or to systematically compare patterns of occurrence on a broad scale.

As a result, it remains unclear whether the preservation of biomaterials interpreted as original is in fact a rare phenomenon or whether this perception stems from the fragmentation of the available data. In particular, the frequency with which such evidence is reported across the scientific literature and how it is distributed among vertebrate clades, geological time intervals, geographic regions, and methodological approaches remains unclear.

The present study does not directly test the preservation of biomaterials in fossil specimens, but rather analyzes how their occurrence has been documented and interpreted in the scientific literature. Therefore, the aim of this study was to provide a comprehensive quantitative synthesis of published reports of biomaterials interpreted as original in vertebrate fossils by compiling and systematizing the available literature, assessing the documentary frequency of published claims, and identifying biological, geographic, stratigraphic, and methodological patterns. By integrating these records into a single analytical framework, this study provides an empirical basis for understanding how the paleomolecular literature documents and interprets such occurrences and their implications for the development of the field.

To contextualize the interpretation of these documentary records, the following presents a conceptual synthesis of the mechanisms proposed in the literature for the preservation and identification of biomaterials in vertebrate fossils.

2. Molecular Paleontology and the Problem of Preserving Original Biomaterials

The interpretation of the records compiled in this study depends on the conceptual framework developed by Molecular Paleontology to explain the preservation of biomaterials in vertebrate fossils. The field is dedicated to the recovery, characterization, and interpretation of endogenous biomaterials preserved in the fossil record, including biomolecules, cellular structures, and soft tissues. A significant portion of this evidence, especially cellular microstructures, is obtained from fossil bones through chemical demineralization assays (e.g., EDTA or diluted acids), which release organic components preserved within the biomineralized matrix (Schweitzer, 2011; Ullmann & Schweitzer, 2023).

Analytical studies have demonstrated that original biomaterials can persist at multiple levels of biological organization and in different classes of organic compounds, challenging fossilization models based on rapid degradation and complete mineral replacement (Schweitzer, 2003; 2004; 2011; Schweitzer *et al.*, 2007; 2014; 2019). In the scientific literature, such evidence has come to be interpreted as a potentially recurring phenomenon, the explanation for which involves complex diagenetic processes.

Reviews have compiled examples of biomaterial preservation interpreted as original in vertebrate fossils, highlighting their taxonomic, temporal, and methodological scope (Schweitzer, 2011; Schweitzer *et al.*, 2007; Thomas & Taylor, 2019). The synthesis by Thomas and Taylor (2019) compiled dozens of studies involving different groups and geological ages, arguing that the findings do not correspond to isolated cases. However, because they are based on representative examples, such reviews have not quantitatively assessed the frequency of the records or their comparative distribution across types of biomaterials, clades, geographic regions, geological time intervals, or analytical techniques.

In response to this limitation, studies focusing on specific clades have begun to examine the literature in a targeted manner. Surveys involving non-avian dinosaurs (Alves & Machado, 2020), non-dinosaurian Mesozoic reptiles (Cadena & Schweitzer, 2012; Alves & Machado, 2021a), Avialae (Alves & Machado, 2021b), and Cenozoic mammals (Gomes *et al.*, 2022) have indicated that the available records are more numerous and geographically extensive than traditionally recognized, suggesting that the perception of rarity stems largely from the dispersion of evidence across the literature and the absence of integrative syntheses. Independent evidence supports this interpretation: microstructural analyses of dinosaur bones without macroscopic signs of exceptional preservation (Bertazzo *et al.*, 2015) and observational surveys with systematic sampling (van der Reest & Currie, 2020) indicate that the frequency of these microstructures interpreted as organic may be higher than traditionally assumed, depending on the investigative effort and the methodological repertoire employed.

Although they represent an important advance, the first attempts at quantification applied statistical methods to the available literature, including a meta-analysis based on demineralization assays to investigate taphonomic factors associated with the recovery of cellular microstructures (Ullmann & Schweitzer, 2023). However, by restricting itself to a single type of proxy and a taxonomically biased sample set, this approach does not allow for estimating the global frequency of occurrence of biomaterials interpreted as original specimens nor for comparing different categories of evidence.

Consequently, it is not yet possible to recognize cross-cutting patterns in the literature on vertebrate fossils or to comprehensively assess how the records are distributed across biomaterials interpreted as original, clades, geographic regions, geological time intervals, and analytical techniques. The absence of a comprehensive quantitative synthesis therefore remains a central gap in the empirical understanding of Molecular Paleontology. The present study seeks to help fill this gap by compiling, systematizing, and quantitatively analyzing the scientific literature on biomaterials interpreted as original in vertebrate fossils.

3. Materials and Methods

3.1 Study Design

This research is configured as a quantitative documentary survey of the scientific literature. The empirical object of the study is not directly the fossils, but the scientific literature that presents claims of endogenous recovery of original biomaterials in deep-time vertebrate fossils (> 1 million years [Ma]).

In scientific mapping studies and quantitative documentary analyses, the literature constitutes the empirical unit of analysis itself, requiring the construction of a documentary corpus representative of the field under investigation (Zupic & Čater, 2015; Donthu *et al.*, 2021). In these designs, the *corpus* is typically constructed through combined strategies of targeted searches in bibliographic databases, continuous monitoring of specialized publications, and reference tracking, with the progressive inclusion of studies throughout the research process. Thus, the analysis focuses on the patterns of documentation of biomaterial claims in the literature—their frequency, distribution, and association with biological, geographical, temporal, and methodological contexts.

3.2 Search Strategy and Study Selection

The *corpus* was constructed through a targeted literature review of scientific publications. The studies were identified through three complementary procedures: (i) regular monitoring of journals specializing in paleontology and related fields via bibliographic alerts and periodic review of newly published issues; (ii) searches in academic bibliographic databases (primarily Google Scholar, Web of Science, and Scopus) using combinations of terms associated with biomaterials preserved in vertebrate fossils (e.g., *soft tissue preservation*, *endogenous biomolecules*, *ancient proteins*, *fossil* *biomolecules*, *fossil cells*, *molecular paleontology*); and (iii) retrospective and prospective tracking of references from relevant studies. We primarily considered studies in English, while also including publications in Portuguese and Spanish when relevant.

The compilation was continuously updated and considered complete in January 2026. This was not a systematic review, but a curated literature survey focused on studies with explicit claims of endogenous recovery of biomaterials in deep-time vertebrate fossils (>1 Ma). The 1 Ma threshold was adopted to exclude subfossil and Late Quaternary materials, thereby focusing the analysis on deep-time fossils in which long-term biomolecular preservation constitutes the central scientific question. The studies were read in full to verify eligibility; after consolidating the set, duplicate records were removed, and the remaining studies were subjected to the inclusion and exclusion criteria described below. Similar targeted compilation procedures, combining bibliographic searches and reference tracking, have been employed in reviews and syntheses within the paleomolecular literature itself (e.g., Schweitzer, 2011; Thomas & Taylor, 2019), and are recognized as a valid strategy for *corpus* construction in scientific mapping studies (Zupic & Čater, 2015; Donthu *et al.*, 2021).

The final *corpus* comprised 198 studies. The primary unit of analysis was the documentary record of biomaterial, defined as the association between a type of biomaterial and a taxon reported in a study. A single study could generate multiple records when it presented more than one biomaterial, taxon, or geological context, totaling 377 documentary records treated as coding units. The frequencies presented therefore refer to the documentary recurrence of claims in the literature, and not to the number of publications or fossil samples analyzed.

3.3 Inclusion and exclusion criteria

Peer-reviewed studies and technical papers with analytical rigor that claimed the presence of *original biomaterials* in vertebrate fossils were included; for the purposes of this study, these are understood as the varied set of biological materials interpreted or claimed to be original, preserved at different levels of structural organization — including tissues, cells, biomacromolecules, and/or their degradation products (biomarkers) — capable of being recovered from deep-time fossil samples (Schweitzer, 2003; 2004; Schweitzer *et al.*, 2014; Alves & Machado, 2020; 2021a; 2021b; Gomes *et al.*, 2022).

The following were excluded:

(a) studies claiming the presence of mineralized soft tissues, i.e., tissues that were originally flexible but were completely replaced by autogenous minerals during fossil diagenesis;

(b) studies that reported only the identification of endogenous biominerals associated with originally biomineralized tissues, i.e., hard parts (e.g., bones and shells);

(c) studies that were limited to the identification of trace elements or elemental biomarkers (e.g., S, P, Ca, Zn, Sr), when not accompanied by claims of direct molecular tracing;

(d) studies that initially claimed original biomaterials, but in which the authors themselves attributed the traces to the formation of microbial biofilms, recent contamination, or exogenous geochemical precipitates;

(e) studies that reported biomaterials preserved in amber or coprolites;

(f) studies that reported the recovery of original biomaterials without providing detailed information about the finding;

(g) studies that did not use at least one of the appropriate groups of analytical techniques—optical, biological, or chemical—to support their conclusions.

3.4 Database Construction

Based on the selected studies, a relational database was constructed in which each record corresponds to the occurrence of biomaterial interpreted as original and reported in the literature regarding vertebrate fossils. Coding was performed manually through a full reading of the articles. Biomaterial categories were defined according to the interpretation reported by the original authors, regardless of the analytical technique used for their identification. Accordingly, records assigned to a given biomaterial category (e.g., collagen) may include evidence obtained through different analytical approaches, such as morphological observations, immunological assays, chromatographic analyses, spectroscopic techniques, or mass spectrometry. Analytical methods were coded independently from biomaterial type. When a single study reported multiple biomaterials, different taxa, more than one geological interval, or various analytical techniques, each occurrence was recorded separately as a coding unit to preserve the complexity of the reported information.

The extracted records were subsequently categorized and standardized for comparative analysis, as described in the following sections. The complete *corpus*, corresponding to the full database, is provided as Supplementary Dataset S1, accompanied by a glossary of acronyms and abbreviations (Supplementary Table S1), ensuring transparency and reproducibility.

3.5 Standardization and Data Processing

The data extracted from the studies were standardized to allow comparisons between heterogeneous records and to operationalize the analytical variables in the database. Taxonomic categories were organized into broad vertebrate clades, with more specific identifications retained as sublevels and the original name recorded as metadata; nomenclatural inconsistencies were adjusted to the currently accepted nomenclature in the systematic literature.

Stratigraphic information was recorded as described in the studies and grouped into comparable chronostratigraphic units (geological age), while localities were standardized by country and continent for geographic analysis. Biomaterials were classified according to their biochemical nature and level of biostructural organization, preserving the specific names reported. Analytical techniques were grouped into general methodological classes, while also maintaining a record of the individual techniques used in each study.

3.6 Data Analysis

The data analysis was descriptive and comparative in nature, focusing on evaluating the frequency of occurrence of the reported variables. Distribution patterns of records on biomaterials interpreted as original were examined in relation to five analytical axes: biological (biomaterial type and level of biostructural organization), taxonomic, geographic, stratigraphic (geological age), and methodological (analytical techniques employed). The analyses were conducted in an integrated manner, allowing for the identification of recurring trends and gaps in the literature. Data processing, organization, and tabulation were performed using *Google Sheets* (Google LLC).

The results are presented through textual summaries, tables, and graphical representations, organized into analytical axes that reflect the main dimensions of the database. No inferential statistical analyses were performed, since the central objective of the study was to characterize the frequency and distribution of published records, rather than to test causal hypotheses.

As the study is based on published literature, the results reflect patterns of scientific research and are subject to publication bias, availability of material, research tradition, and access to analytical techniques, and do not necessarily represent the actual frequency of preservation in the fossil record.

4. Results and Discussion

The results presented below are based on the analysis of *the* documentary *corpus* constructed in this study and refer to the patterns of record of biomaterial claims interpreted as original in the scientific literature, not to the direct verification of the preservation phenomenon in the fossil record. The results are presented according to five analytical axes: biological (biomaterial type and level of biostructural organization), taxonomic, geographic, stratigraphic (geological age), and methodological (analytical techniques employed). Information on the temporal evolution of scientific production is included only as a complementary characterization of the corpus. The analytical axes are described below according to the main structural dimensions of the database.

4.1 Characterization of the Literature Corpus

The compiled corpus allows for a quantitative and comparative characterization of claims regarding biomaterials interpreted as original in vertebrate fossils. As the first analytical axis, we examine the temporal distribution of publications and the number of records over the decades (Fig. 1). For analytical purposes, the total number of records corresponds to the set of biomaterial traces claimed in the studies, considering that a single study may report multiple biomaterials interpreted as preserved. This distinction allows us to evaluate, by decade, not only the evolution of the number of publications but also the frequency and diversity of the claims documented in the literature.

The quantitative turning point in scientific output clearly occurs starting in the 2001–2010 decade, when significant growth is observed in both the total number of records and the number of works actually published, breaking the pattern of slow and irregular growth observed in previous decades. The highest concentration of production is found in 2011–2025, with the 2011–2020 decade standing out as the absolute peak of production (46.5%). Although 2021–2025 is an incomplete period, it maintains a high level of productivity (21.0%), exceeding all decades prior to the 2000s, indicating the continued expansion of the field.

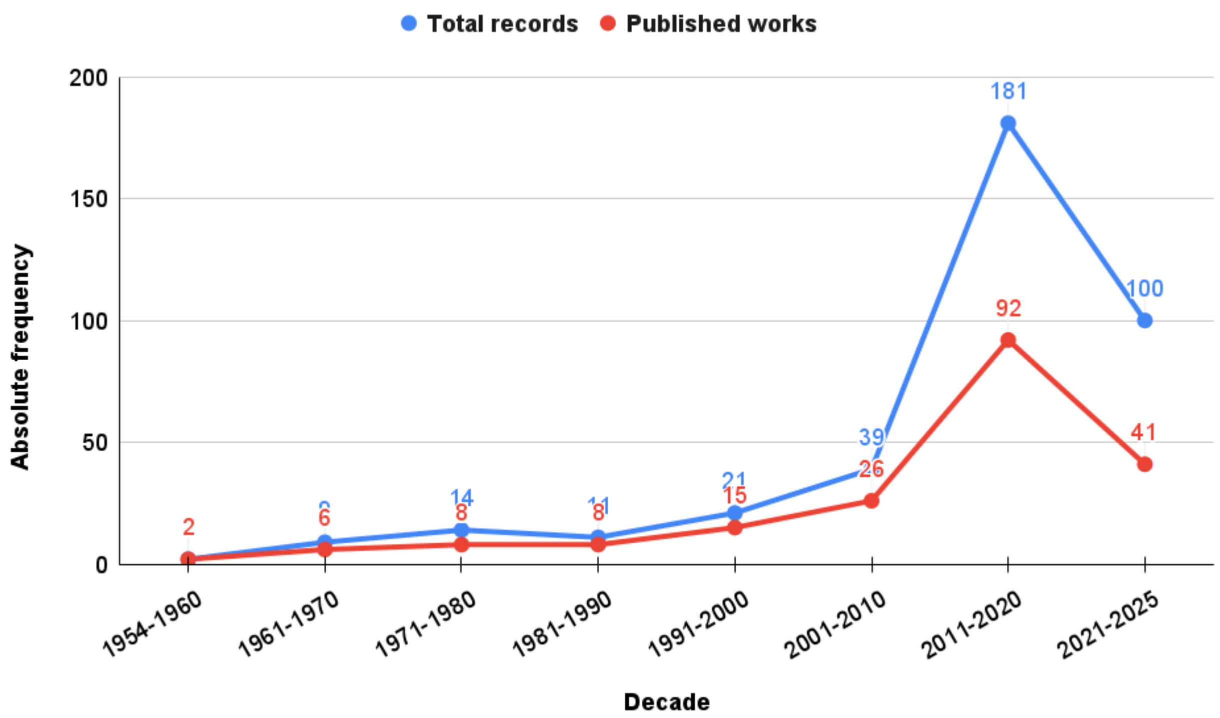

Figure 1. Decennial distribution of published works (n = 198) and total records (n = 377) relating to claims of original biomaterials in vertebrate fossils.

Figura 1. Distribuição decenal dos trabalhos publicados (n = 198) e do total de registros (n = 377) relativos a reivindicações de biomateriais originais em fósseis de vertebrados.

Biological dimension

This dimension describes the distribution of biomaterial claims interpreted as original according to biomaterial type and level of biostructural organization. The distribution by biomaterial type reveals strong asymmetry, with a predominance of remains interpreted as structural biomacromolecules and cellular components associated with bone tissue (Fig. 2).

Collagen-related remains constituted the most frequently reported biomaterial category (13.8%), followed by osteocytes (10.3%) and blood vessel-like structures (9.5%). This predominance may partly reflect the frequent investigation of mineralized skeletal tissues and the molecular stability generally attributed to collagen. However, the collagen category includes different forms of evidence reported in the literature, including collagen fibers and molecular detections obtained through different analytical approaches. Together, these findings indicate that biomineralized tissues (e.g., bones) and their cellular constituents represent the main focus of the claims investigated.

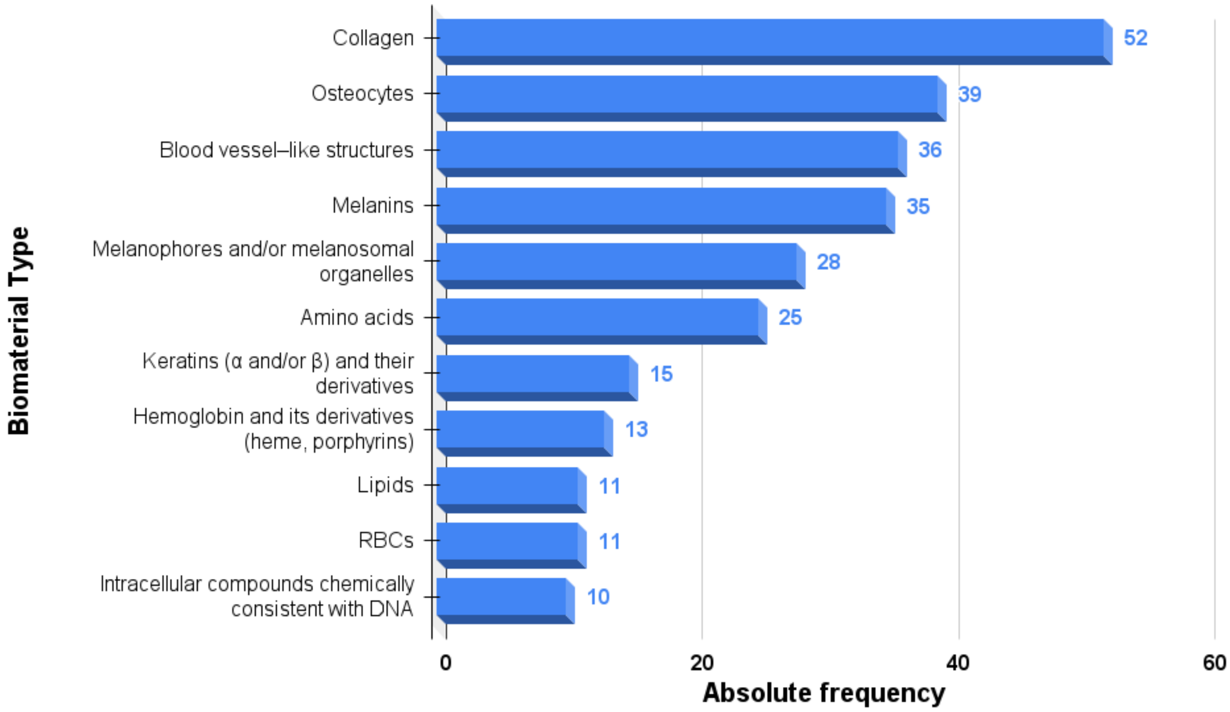

Figure 2. Distribution of records by type of biomaterial interpreted as original in vertebrate fossils (n = 377).

Figura 2. Distribuição dos registros por tipo de biomaterial interpretado como original em fósseis de vertebrados (n = 377).

Abbreviations: DNA, deoxyribonucleic acid; RBCs, red, round, and nucleated microstructures, consistent in size and morphology with red blood cells. Note: Biomaterials were ordered by decreasing frequency of reported occurrences. The graph omitted biomaterials mentioned fewer than ten times.

Together, the predominance of collagen-related evidence, osteocytes, and blood vessel-like structures indicates that biomineralized tissues (e.g., bones) and their cellular constituents represent the main focus of the claims investigated. Records associated with biological pigments, such as melanins and melanophores/melanosomes, also exhibit high frequency, reflecting both the recent consolidation of approaches aimed at reconstructing coloration and soft tissues and the recognized chemical stability of the melanin molecule (Prado *et al.*, 2025), which is frequently cited in the literature as favoring its preservation in the fossil record.

In contrast, biomolecules such as lipids, hemoglobin, and intracellular compounds chemically consistent with DNA occur in smaller numbers, suggesting lower frequency of published claims, greater analytical complexity, or more restrictive identification criteria. Taken together, these results indicate that current paleomolecular research has primarily focused on biomineralized tissues, their cellular constituents, and chemically stable biomaterials that are more amenable to investigation using complementary analytical techniques.

The distribution of records according to the level of biostructural organization reveals a predominance of biomacromolecules *and/or their degradation products* (61.8%), which account for the largest share of the analyzed records (Fig. 3).

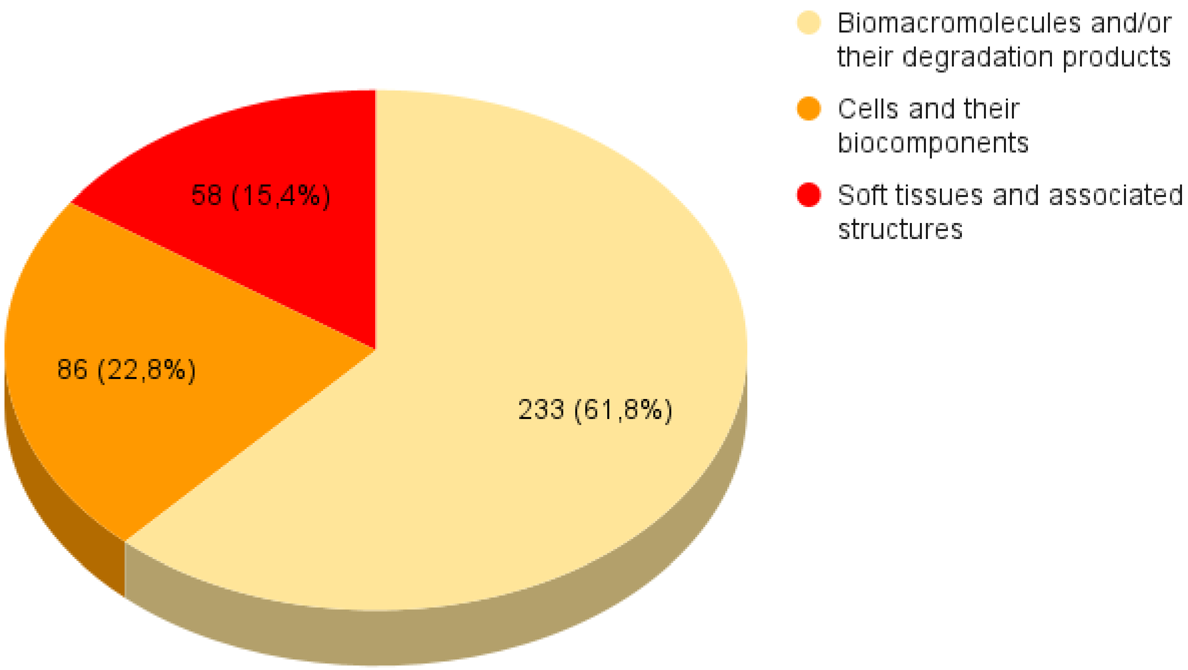

Figure 3. Distribution of records of biomaterials interpreted as original according to the level of biostructural *organization (n = 377).*

Figura 3. Distribuição dos registros de biomateriais interpretados como originais segundo o nível de organização bioestrutural (n = 377).

This distribution shows that the records are not restricted to isolated molecular residues—although these are more frequent—but include different levels of biological complexity, encompassing cellular and tissue records. Records attributed to *cells and their biocomponents* (22.8%) represent an intermediate fraction of the set, while *soft tissues and* associated *structures* (15.4%) constitute the smallest proportion. Taken together, the observed pattern indicates that, although records at the cellular and tissue levels are present in the literature, scientific output favors reports at more fundamental biostructural levels, where preservation over geological time is more frequently claimed.

In broader interpretive terms, these results corroborate, now on a quantitative scale, observations previously discussed conceptually by Schweitzer (2011), according to which the literature has interpreted exceptional preservation as involving multiple biological components traditionally considered highly labile. The coexistence of broadly dominant categories and a long tail of rare, specific biomaterials suggests a continuously expanding field, in which new modes of preservation are progressively proposed in the literature as the analytical and instrumental scope broadens.

4.2 Taxonomic dimension

The distribution of records by clade reveals a strong taxonomic asymmetry in the analyzed literature (Fig. 4), with a clear predominance of *Dinosauria*, which accounts for the highest frequency of reported occurrences (44.3%). For analytical purposes, the term *Dinosauria* is used in this study in a strictly operational sense, referring to non-avian dinosaurs. Fossil birds were treated separately within the Avialae clade, despite their phylogenetic inclusion in Dinosauria, since the specialized literature tends to investigate them using distinct methodological traditions, comparative frameworks, and analytical approaches—often closer to paleornithology, the comparative biology of extant birds, and specific taphonomic approaches to pneumatized skeletons. This distinction reduces interpretive overlap in the database and allows for a more precise evaluation of association patterns between types of biomaterials and distinct anatomical-histological contexts, preventing the large volume of studies on non-avian dinosaurs from masking trends specific to the avian record.

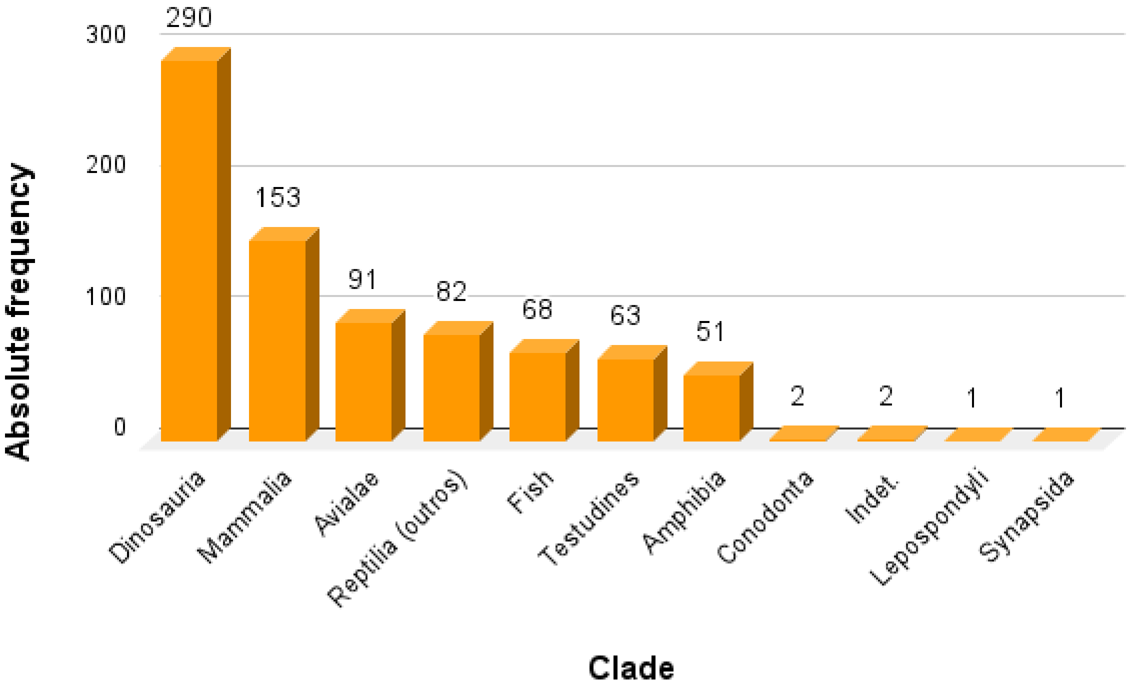

Figure 4. Distribution of records by taxonomic clade of vertebrates in the analyzed corpus (n = 377).

Figura 4. Distribuição dos registros por clado taxonômico de vertebrados no corpus analisado (n = 377).

Note: “indet.” indicates indeterminate taxonomic identification.

From a methodological standpoint, taxonomic clades were recorded only once per article and per identified biomaterial type, and were treated as taxonomic representatives in the database. Thus, the frequencies presented do not correspond directly to the total number of publications, nor to the absolute total of empirical occurrences derived from multiple fossil samples analyzed in a single study. Instead, they reflect the frequency with which certain clades are associated with different types of biomaterials throughout the analyzed *corpus*, allowing for a comparative assessment of the taxonomic diversity involved in claims of original biomaterials.

At an intermediate level are *Mammalia* (17.8%) and *Avialae* (15.6%), while *Reptilia (others)* (13.5%), *Fish* (9.5%), *Testudines* (8.0%), and *Amphibia* (6.6%) exhibit progressively lower frequencies. This pattern indicates that the literature tends to favor groups traditionally associated with exceptional preservation contexts, greater availability of material investigated in the literature, and greater historical and methodological interest, especially regarding studies on soft tissues, cells, and biomacromolecules. Thus, the observed distribution reflects not only biological interpretations proposed in the literature but also sampling, historical, and analytical biases, converging with the synthesis by Thomas & Taylor (2019), and reinforcing, through systematic quantification, that the concentration observed in certain groups stems more from historical research biases and material availability than from an intrinsic preservational exclusivity proposed for certain clades (Ullmann & Schweitzer, 2023). Additionally, clades with residual occurrence were recorded—such as *Conodonta*, *Lepospondyli*, and indeterminate *Synapsida*—whose extremely low frequencies indicate only marginal representation within the analyzed corpus. These occurrences are not sufficiently expressive to support robust comparative inferences, but are retained in the graphical representation for the sake of sample completeness.

The category *Reptilia (others)* encompasses non-avian reptiles distinct from *Dinosauria* and *Testudines*, including Squamata, Crocodylomorpha, Pterosauria, and Mesozoic marine reptiles (Ichthyosauria, Plesiosauria, and Mosasauria), as well as records generically attributed to undetermined Reptilia.

Following the same taxonomic-operational criteria adopted for the distinction between *Dinosauria* and *Avialae*, we chose to treat *Dinosauria* and *Testudines* independently of the general *Reptilia* (others) grouping, due to historical, methodological, and epistemological specificities associated with these clades as noted below. In the case of non-avian dinosaurs, this is one of the most intensively studied groups in the context of molecular paleontology and the preservation of organic microstructures, attracting analytical investments, methodological development, and sustained attention from the scientific community (Ullmann & Schweitzer, 2023). This prominence is associated both with their central role in the popular imagination (Alves *et al.*, 2022), which fosters funding and visibility, and with the fact that, in the specialized literature, they constitute a particularly attractive field for early-career researchers interested in applying innovative analytical approaches to materials widely represented in the fossil record (Jones, 2019). Furthermore, Mesozoic dinosaurs offer methodologically favorable conditions for paleomolecular testing, as they combine great geological age, an abundance of bone tissue potentially containing biomolecules, and the availability of modern phylogenetic analogues (birds) for comparative validation (Schweitzer *et al.*, 2005; 2016).

As for *Testudines*, their distinction stems from the consistent growth of studies focused on this group, particularly in South America, driven by the ongoing work of specialized research groups—notably investigations based on materials from Colombia—that systematically explore claims of cellular, tissue, and molecular preservation in fossil chelonians (Cadena & Schweitzer, 2012; 2014; Cadena, 2020). Furthermore, anatomical and histological characteristics specific to turtles, such as the structure of their bones and shells, make this group particularly informative for comparative preservation studies, justifying its separate analysis from other reptiles.

Finally, although some taxa such as *Temnospondyli* appear in the database, they were not included in *Reptilia (others)*, as they correspond to basal tetrapods traditionally treated as amphibians and are therefore consistently allocated to the *Amphibia* category, in accordance with the taxonomic criteria adopted in this study.

4.3 Geographic Dimension

Regarding geographic distribution (Fig. 5), records reported in the literature were counted based on the country of origin associated with each sample species identified in *the corpus* (n = 377). Each species linked to a type of biomaterial contributed one occurrence to the respective country (total = 771). Records without precise identification of geographic origin (n = 41) were not assigned to any country and, therefore, were not included in the cartographic representation. A single sample may have been analyzed in different studies, not necessarily representing new findings but rather new investigations of the same material; additionally, some studies gathered specimens from multiple locations.

The distribution by continent reveals a strong concentration: North America (36.3%), Europe (20.8%), and Asia (19.6%) account for the majority of published records, followed by Africa (11.4%) and South America (3.5%). The Eurasia category (2.7%) includes transcontinental countries, such as Russia and Georgia, which are treated separately to avoid double counting. At the national level, a marked asymmetry is observed: the United States accounts for 30.1% of the records, surpassing the combined total of several countries in *the corpus*.

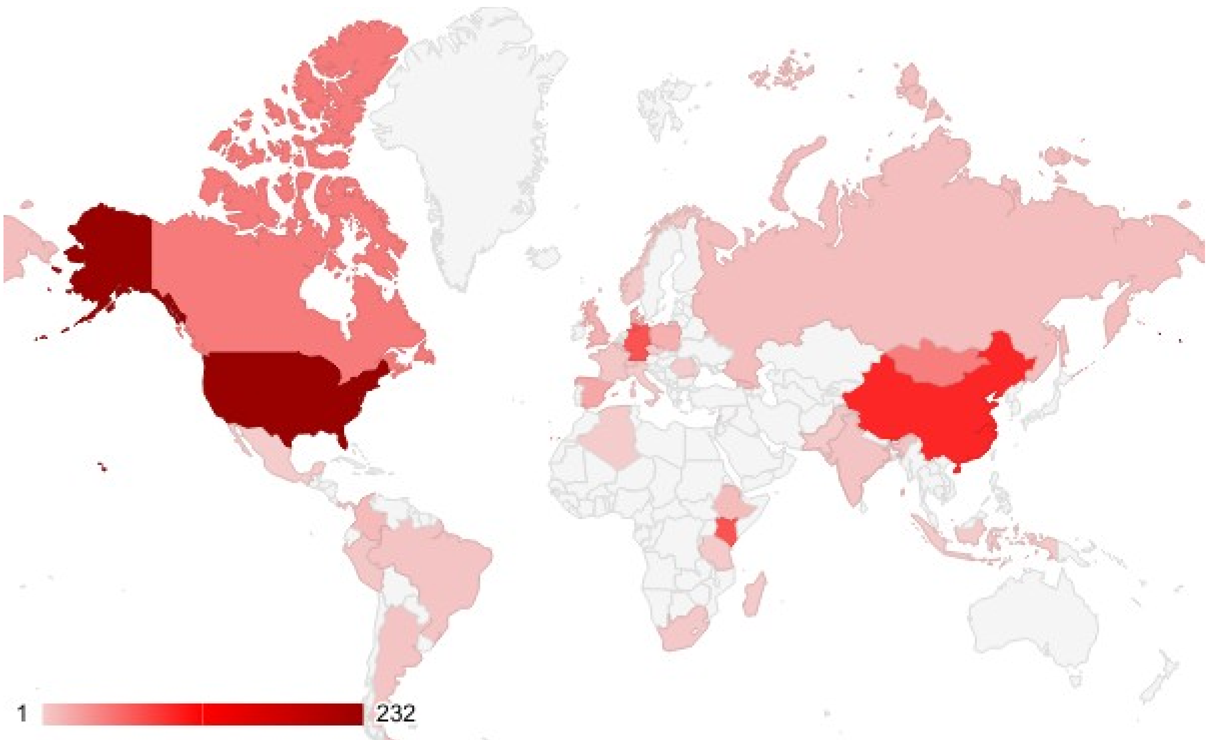

Figure 5. Distribution of records of biomaterials interpreted as original in vertebrate fossils in the 35 countries of origin (n = 771).

Figura 5. Distribuição dos registros de biomateriais interpretados como originais em fósseis de vertebrados entre os 35 países de procedência (n = 771).

In a second tier are China (12.3%), Germany (9.0%), and Kenya (9.0%), followed by Canada (6.1%) and Mongolia (5.8%), while the remaining countries exhibit progressively lower frequencies, resulting in a long-tail distribution. Together, these six countries account for approximately 73% of all occurrences documented in the *corpus*, highlighting a strong geographic concentration of the records reported in the literature.

The North American predominance is frequently associated in the literature with the concentration of analytical infrastructure (mass spectrometry, electron microscopy, synchrotron radiation, and proteomic approaches), to continuous funding and intensive investigation of major fossil-bearing formations (e.g., Hell Creek, Lance, and Judith River) since the late 1990s, factors that favor greater scientific output and a consequent frequency of published records. China's position reflects the recent expansion of paleontology in the country, linked both to the exploration of exceptionally well-preserved deposits and to the strengthening of its analytical capabilities. Kenya, Canada, and Mongolia are frequently associated with international collaborations involving laboratories based in North America and Europe.

Countries with fewer published records do not necessarily have less fossil potential. England and Poland, for example, are home to groups specializing in paleomolecular research, suggesting that the low representation in the literature is related more to the scale of the research and the size of the collections studied than to a lack of technical capacity. In other cases, the lower frequency of reported records likely results from a combination of multiple factors, including the availability and accessibility of fossil material, the intensity of research effort, the availability of analytical infrastructure, and the continuity of research programs in Molecular Paleontology.

In South America, Colombia has the highest frequency (1.4%), being the only country on the continent among the main ones in *the corpus.* This pattern may be associated with the systematic work of a research group dedicated to cellular, tissue, and molecular investigations of fossil vertebrates, particularly chelonians (Cadena & Schweitzer, 2012, 2014; Cadena, 2020; Alves, 2021a). At lower levels are Brazil (0.8%), Argentina (0.8%), and Peru (0.5%), whose reduced representation appears to reflect the lower continuity of specific molecular research programs and more restricted access to high-resolution techniques (Alves, 2021b).

The presence of published records across all continents indicates that paleomolecular investigations have been conducted in different geographic regions, albeit with significant research asymmetry. The recurrence of reports from tropical, arid, temperate, and cold regions suggests that scientific investigation of these materials is not restricted to specific climatic zones. This pattern is consistent with previously published regional surveys, which also report biomaterials in different depositional contexts (Gallucci *et al.*, 2024). Thus, the global distribution of records published in the literature is broad, while the observed inequality primarily reflects the intensity of scientific effort directed toward these materials.

Although the distribution corresponds to the country of origin of the fossil samples, the pattern observed in the literature cannot be interpreted solely in terms of natural taphonomic processes. The recurrence of records in certain countries is strongly associated with the analytical effort applied by national and international teams focused on molecular prospecting. Thus, the frequency of records documented in the literature results primarily from the interaction between the availability of material accessible to research and the intensity of investigative effort applied, indicating that their geographic representation depends both on conditions of access to fossiliferous material and on the scientific attention dedicated to these deposits.

Consequently, the geographic distribution documented in the literature should not be interpreted solely as a reflection of preservation potential, but rather as the result of the interaction among fossil availability, research effort, analytical infrastructure, and publication bias.

4.4 Stratigraphic Dimension

Regarding temporal distribution (Fig. 6), the total number of records reported in the literature was obtained by accounting for the geological interval associated with the species identified in each record of *the corpus* (n = 377). Each species linked to a specific type of biomaterial contributed one occurrence to the corresponding period, and a single study could generate multiple occurrences when it involved species or samples from different stratigraphic units (total occurrences = 715). It should also be noted that the analysis of the same sample in more than one study does not represent new findings, but rather new investigations of the same material, indicating that the records described in the studies span multiple intervals along the geological column.

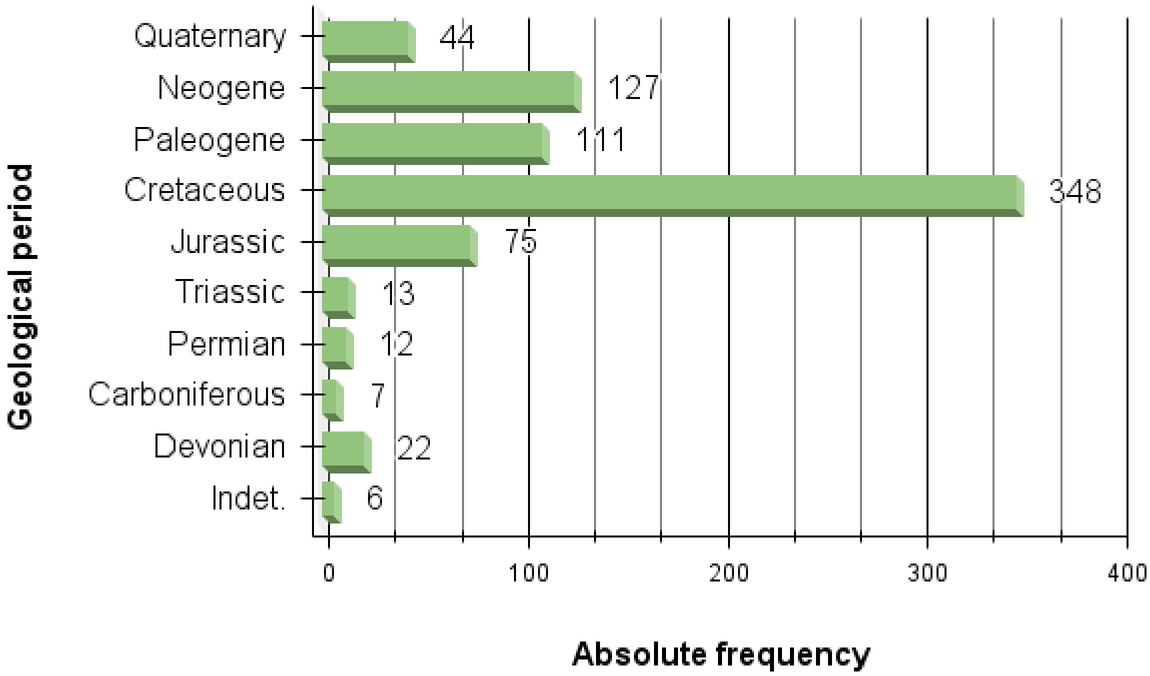

Figure 6. Distribution of biomaterial records interpreted as original in vertebrate fossils by geological period (n = 715).

Figura 6. Distribuição dos registros de biomateriais interpretados como originais em fósseis de vertebrados por período geológico (n = 715).

Notes: In publications that omitted the geological age, it was inferred by matching the published age to the International Commission on Stratigraphy (ICS, 2024). The periods were organized according to their chronological position in the geological time scale, from oldest to youngest. “Indet.” indicates indeterminate stratigraphic attribution.

The records documented in the literature regarding claims of original organic components are distributed across a broad temporal range of the geological column. On a macro-temporal scale, published records are distributed throughout the Phanerozoic Eon, concentrating more frequently in the Mesozoic Era (54.1%), compared to the Cenozoic (40.3%) and Paleozoic (5.7%) Eras. The predominance of the Mesozoic in the literature is likely related to the greater investigative attention devoted to fossils from this interval and their strong representation in molecular paleontology studies, particularly those involving Dinosauria (Ullmann & Schweitzer, 2023), in addition to the fact that many Mesozoic deposits correspond to *Konservat-Lagerstätten* and contexts of relatively rapid burial, which are frequently interpreted in the literature as favorable for the preservation of organic microstructures (Briggs, 2003; Schweitzer *et al.*, 2007; Ullmann & Schweitzer, 2023; Prado *et al.*, 2025).

On a more detailed temporal scale, the distribution by geological periods shows a strong concentration in the Cretaceous (42.8%), followed by the Jurassic (10.2%). Among the Cenozoic intervals, the Neogene (17.6%) and Paleogene (15.2%) stand out, while in the Paleozoic, the Devonian (3.1%) and Permian (1.7%) have the highest relative frequencies. An independent survey conducted by Thomas & Taylor (2019) reveals a convergent trend, bringing together records distributed throughout the entire geological column, but with a Mesozoic predominance—especially in the Cretaceous—and a smaller, though consistent, share of Cenozoic occurrences. This correspondence indicates that the temporal pattern identified in the present study does not stem solely from the composition of *the* analyzed *corpus* but reflects a broader trend in the paleomolecular literature.

The recurrence of reports of original biomaterials in fossils attributed to different geological ages is not unexpected, since experimental and geochemical evidence and comparative analyses indicate that geological time alone is not a direct predictor of molecular preservation (Thomas & Taylor, 2019; Anné *et al.*, 2023; Ullmann & Schweitzer, 2023; Gallucci *et al.*, 2024; Rogoff & Ullmann, 2025). In the paleomolecular literature, preservation has been interpreted as dependent on local taphonomic and geochemical factors, such as matrix mineralogy, matrix permeability, iron availability, pH, hydrothermal history, and diagenetic history (Schweitzer *et al.*, 2014; Wiemann *et al.*, 2018; Boatman *et al.*, 2019). Processes such as mineral binding, iron-mediated molecular cross-linking, and early encapsulation have been proposed in the literature as mechanisms capable of stabilizing biomolecules and allowing their persistence in very old rocks (Schweitzer *et al.*, 2014; Wiemann *et al.*, 2018). Thus, geological age, on its own, is not always treated in the literature as an absolute impediment to the identification of biomaterials interpreted as original, and the recurrence of reports indicates that published evidence spans a broad temporal range of the geological record. This pattern extends, within the scope of the analyzed literature, the observations previously described for Mesozoic and Paleozoic vertebrates (Schweitzer, 2011; Schweitzer *et al.*, 2019; Thomas & Taylor, 2019; Voegele *et al.*, 2022; Anné *et al.*, 2023; Ullmann & Schweitzer, 2023; Rogoff & Ullmann, 2025).

The limited number of reported records for the Paleozoic can be explained, in part, by the reduced investigative effort directed toward these fossils, historically influenced by the previous paradigm that original biomaterials could not persist over long geological time intervals (Schweitzer *et al.*, 2007; Schweitzer, 2011). This scenario created a scientific exploration bias, in which older deposits were less frequently investigated using molecular methodologies (Cleland & Schroeter, 2018; Saitta & Vinther, 2019; Ullmann & Schweitzer, 2023). According to discussions in the literature, older rocks tend to exhibit a higher average degree of diagenetic alteration and thermal maturation, generally reducing the detectability of some preserved biomolecules (Wiemann *et al.*, 2018; Demarchi *et al.*, 2016), although certain biomolecules are thermally more stable (Saitta *et al.*, 2024).

In this sense, the observed distribution indicates that the frequency of records documented in the literature is not homogeneous across geological time, being influenced by taphonomic factors discussed in the literature as well as by historical and methodological biases inherent to scientific practice itself (Parry *et al.*, 2018; Boatman *et al.*, 2019; van der Reest & Currie, 2020; Ullmann *et al.*, 2019; 2021; 2022; 2023; 2024).

4.5 Methodological Dimension

The distribution of analytical techniques highlights the recurrent use of complementary approaches in the investigation of biomaterials interpreted as original in vertebrate fossils. The techniques were grouped into three categories—optical/morphological (n = 660; 45.7%), biological/molecular (n = 203; 14.1%), and chemical/spectroscopic (n = 581; 40.2%)—according to the type of information obtained from the fossil material. Studies rarely rely on a single procedure; it is common to combine multiple techniques applied to the same specimen (Schweitzer, 2004; Schweitzer *et al.*, 2008). Since certain instruments combine more than one instrumental principle, the classification presented is operational and adopted solely for analytical purposes.

The names and abbreviations have been standardized, since the literature employs heterogeneous instrumental nomenclatures; equivalent variations have been grouped under the same designation while preserving distinctions with relevant analytical implications (e.g., SEM-EDS or LC-MS/MS).

Table 1. Main analytical techniques employed in the investigation of biomaterials interpreted as original in vertebrate fossils, organized by methodological groups.

Tabela 1. Principais técnicas analíticas empregadas na investigação de biomateriais interpretados como originais em fósseis de vertebrados, organizadas por grupos metodológicos.

Group of techniques	**Analytical techniques**	**Frequency (n)**	**% of total**	**Main information obtained**
Optical / Morphological (n=660)	OM	163	24.7	Observation of histological morphology and cellular structures.
	SEM	151	22.9	Characterization of tissue and cellular microstructure and microtextures.
	TEM	97	14.7	Identification of cellular ultrastructure and subcellular organization at the nanoscale.
	FESEM	45	6.8	High-resolution imaging of microstructures and organic components.
	SEM-EDS	36	5.4	Microstructure associated with the determination of local elemental composition.
	FM	17	2.6	Detection of fluorescent organic compounds.
	AFM	16	2.3	Nanoscale topographic characterization of surfaces and fibers.
	ESEM-EDS	15	2.3	Observation of microstructures with *in situ* elemental analysis.
Biological / Molecular (n=203)	IHQ	46	22.7	Detection of specific proteins by antigen-antibody binding.

	CH	31	15.3	Identification of biochemical classes by selective staining.
	ARA	30	14.8	Characterization of the state of amino acid preservation.
	ELISA	21	10.3	Specific detection of protein antigens by immunoenzymatic reaction.
	IF	14	6.9	Spatial localization of fluorophore-labeled proteins.
	WB	10	4.9	Confirmation of protein presence and molecular mass.
Chemical / Spectroscopic (n=581)	EDS	83	14.3	Determination of the elemental composition of organic structures.
	ToF-SIMS	81	13.9	Mapping of organic molecular fragments.
	FTIR	47	8.1	Identification of organic functional groups.
	LC-MS/MS	46	7.9	Direct identification of protein sequences.
	XRD	32	5.5	Determination of associated mineral phases.
	SRS-XRF	28	4.8	High-resolution elemental mapping.
	RS	23	3.9	Identification of organic compounds and pigments.
	HPLC	23	3.9	Separation and characterization of soluble biomolecules.
	MS/MS	17	2.9	Structural characterization of molecular fragments.
	Py-GC/MS	16	2.7	Identification of degraded organic macromolecules.
	XANES	13	2.2	Determination of the chemical state of elements.
	RP-HPLC	13	2.2	Separation of amino acids and peptides.
	EBSD	11	1.9	Characterization of the mineral crystal structure.

Note: The techniques were presented according to standardized nomenclature (see text) and ordered by decreasing frequency of use. The table omits techniques used fewer than ten times: AAR, AHPO, AHPO-HPLC, ATR-FTIR, BCA, BSE, CAE, ChemiSTEM, CL, CLSM, CM, CP, CT Scan, DDC-SEM, DIBA, DIC, EDPA, EDS, EDX, EELS, EFM, EPMA, ESEM, ESI-MS, EXAFS, FEG-ESEM, FESEM-BSE, FESEM-EDS, FIB-SEM, FLEEMS, FUV Photography, X-ray Photography, FPLC, GC, GC/MS, HPLC-ESI-Q-TOF-MS, HQ, HRMS, IEC, IFI, LA-ICPMS, LC-ESI-MS, LC-MS, LSF, MALDI, MALDI-MS, MALDI-ToF, micro-CL, micro-CT, Microthermometry, MS, nano-TC, NanoSIMS, PAGE, PCR, proton NMR, Py-GC×GC-TOFMS, Q-TOFMS, RIA, NMR, RPE, RR. The complete glossary of acronyms is available in Supplementary Table S1.

Optical and morphological techniques constitute the most frequently used group, with OM (24.7%) and SEM (22.9%) standing out, accounting for a large portion of the occurrences. These methods are primarily employed for the identification of microstructures interpreted as compatible with biological tissues, such as osteocytic lacunae, fibers, vessels, and possible cellular structures. Higher-resolution techniques, such as TEM (14.7%) and FESEM (6.8%), appear with intermediate frequency and allow for the observation of ultrastructures at the nanoscale, frequently used as initial evidence interpreted as indicative of the preservation of organic material.

The group of biological and molecular techniques mainly includes IHC (22.7%), CH (15.3%), and immunological assays (ELISA [10.3%], IF [6.9%], and WB [4.9%]), employed to detect specific classes of biomolecules through antigen-antibody interactions or selective biochemical reactions in fossil tissues. These procedures allow for the spatial localization of compounds compatible with structural proteins and other organic components interpreted as preserved, functioning as biological affinity tests applied to structures previously identified by microscopy.

Finally, chemical analytical techniques exhibit a high degree of instrumental diversity. Among the most frequently used are EDS (14.3%), ToF-SIMS (13.9%), FTIR (8.1%), and RS (3.9%), employed in studies to characterize the elemental and molecular composition of the described structures. Chromatographic methods (HPLC [3.9%], Py-GC/MS [2.7%], and RP-HPLC [2.2%]) and additional mass spectrometry methods (LC-MS/MS [7.9%] and MS/MS [2.9%]) are also frequently used in molecular investigation and in the interpretation of potential biomolecules, amino acids, and organic fragments. In this context, such analyses are utilized in the studies as the level of analytical evidence with the highest specificity to support the organic interpretation of the reported materials.

Taken together, the results indicate that the investigation of original biomaterials is based on a progressive and complementary analytical strategy: initially, morphological techniques allow for the recognition of structures interpreted as compatible with biological tissues; next, biological methods assess their biochemical affinity; finally, chemical analyses seek to molecularly characterize the described compounds. This pattern suggests the existence of a recurring investigative protocol in the literature, in which different levels of evidence are integrated to test the proposed interpretation of organic preservation in vertebrate fossils. This pattern is consistent with the survey presented by Thomas & Taylor (2019) and Anné *et al.* (2023), which demonstrate that studies in molecular paleontology employ multiple independent analytical approaches—morphological, chemical, and immunological—as a strategy for cross-validating interpretations of biomolecules in fossil materials.

The distribution of analytical techniques follows patterns already observed by clade. Mesozoic reptiles rely primarily on morphological and chemical evidence (Alves & Machado, 2021a), while Cenozoic mammals, especially in exceptional contexts, show greater use of biological techniques (Gomes *et al.*, 2022). In Avialae, a combination of complementary methods predominates (Alves & Machado, 2021b). Thus, the methodological choice appears to be conditioned by the taphonomic potential attributed to the material in the literature, in accordance with the need for cross-validation indicated by Thomas & Taylor (2019).

5. Conclusion

This study does not directly investigate the preservation of biomaterials in the fossil record, but rather the way in which such preservation has been documented and characterized in the scientific literature. By compiling publications from 1954 to 2025, it was possible to identify recurring patterns in the distribution of reports regarding biological, taxonomic, geographic, stratigraphic, and methodological aspects. The results indicate that the recurrence of published reports of biomaterials interpreted as original is greater than traditionally recognized in previous syntheses, and that the perception of rarity may be related, at least in part, to the historical dispersion of these records and the absence of integrated quantitative syntheses.

In general, the observed biological, taxonomic, geographic, stratigraphic, and methodological patterns suggest that the documented distribution of reports across these dimensions reflects both the taphonomic explanations proposed in the studies themselves and the intensity of research directed at specific materials and contexts. This methodological analysis highlighted the recurrent use of multiple, independent techniques that gather morphological, biological, and chemical information.

As a limitation, this research was based on published claims rather than direct verification of the samples, so the results express documentary frequency rather than the actual frequency of preservation in the fossil record. The coverage of *the corpus*, resulting from its progressive construction, also reflects historical, analytical, and geographical biases inherent in scientific activity itself.

Future investigations may integrate quantitative reviews and standardized empirical analyses of fossil samples in different taphonomic contexts. Meta-analytic approaches with uniform validation criteria and greater sharing of analytical data will allow for a more rigorous assessment of the actual frequency of preservation of biomaterials interpreted as original. Overall, this study fulfills its objective by providing the first comprehensive quantitative synthesis of published reports of biomaterials interpreted as original in vertebrate fossils. The database compiled here establishes a documentary foundation for future empirical investigations into the preservation mechanisms discussed in the paleomolecular literature.

Data Availability: The dataset supporting the findings of this study is available as Supplementary Dataset S1, and the glossary of acronyms and abbreviations as Supplementary Table S1.

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