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Application of 3D digital technologies in paleontological reconstruction: a systematic literature review

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ABSTRACT

Paleontology, the study of ancient life through fossilized remains, has experienced a transformative shift with the advent of digital technologies. Traditional methods such as manual reconstruction, molding, and casting, though foundational, are often time-consuming and risk damaging valuable specimens. In response, the field has embraced "virtual paleontology," which employs three-dimensional (3D) digital tools to reconstruct, visualize, and study fossils. This study presents a systematic literature review on the application of three-dimensional digital technologies in paleontological reconstruction. The methodology consists of four steps: formulating the research problem, conducting a literature search, selecting studies, and extracting the data. Initially, 1275 peer-reviewed articles were gathered from five databases (ScienceDirect, Scopus, Web of Science, Google Scholar, IEEE), and 48 articles published between 2013 and 2024 were selected. These articles specifically address the use of three-dimensional digital technologies in paleontological reconstruction and research, and despite promising developments, this review acknowledges the challenges and limitations associated with digital restoration. Technical challenges, including data acquisition and software complexity, are discussed. Looking toward the future, the review outlines potential advancements and innovations in digital reconstruction. The importance of collaborative efforts and interdisciplinary approaches has been emphasized as the field pushes the boundaries of digital restoration capabilities.

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1. Introduction

Paleontology was established during the Victorian era, but its roots extend further in history. Paleontological reconstruction is of great interest to people in paleontological research, science communication, and education. The interpretive reconstruction of extinct organisms is the basis of paleontology research and the core link between human interests and the popularization of paleontology. The science-based imagination of extinct creatures, their ecosystems, and their natural environments is fascinating. However, when it comes to restoring ancient life, the only 'props' are fossils. The more complete a fossil is, the closer it is to its original appearance.

In the early stages of fossil restoration, physical methods were used to remove the rocks surrounding fossils. The most basic method involves examining the exposed surface by splitting the rock surrounding the fossil. This fossil repair process requires a variety of tools such as scalpels, needles, hammers, and dental drills. Needle-picking is widely used in fossil restoration, particularly for repairing fossil surface details. When the fossil surface structure is complex, such as thorns and nodules, a needle tip can be used to remove excess surrounding rock. Chemical methods are also effective techniques that leverage the chemical distinctions between fossils and their surrounding rocks. For example, a mild acetic acid

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solution can effectively dissolve limestone from phosphatic fossils (Cunningham et al., 2014). Fossil morphology can be reconstructed by dissolving the fossil, leaving a void in the rock, which can then be used to create a cast. However, these traditional techniques have numerous drawbacks. They are time-consuming, labor-intensive, can irreversibly damage the fragile structure of fossils, result in incomplete data recovery, and are ineffective at the targeted extraction of specific features (Cunningham et al., 2014; Schmidt, 2013).

However, this field has undergone a revolution owing to the emergence of potent methods for digitally visualizing and analyzing fossil materials (Cunningham et al., 2014). With the progress in science and technology, an increasing number of digital technologies have been applied to paleontological research and fossil restoration. Computer-aided visualization and analysis of fossils have revolutionized the examination of extinct organisms (Cunningham et al., 2014). Digital technology has revolutionized paleontological research overall using various computational techniques and methods for the visualization and analysis of fossils (Sutton et al., 2016). The term 'virtual paleontology' was coined with the development of digital technology (Lautenschlager, 2017). Virtual paleontology refers to research on fossils using three-dimensional (3D) digital visualization technologies or methods (Bicknell et al., 2023; Sutton et al., 2016). This combination forms a powerful toolkit for analyzing and disseminating fossil data (Lautenschlager & Rücklin, 2014). The significance of 3D modeling is evident in paleontology (Gaspard, 2013; Lautenschlager & Rücklin, 2014). Noninvasive diagnostic techniques have gained increasing importance in paleontological research (Hoffmann et al., 2014; Lautenschlager & Rücklin, 2014). From a developmental perspective, the use of 3D digital technologies and software has gained momentum in paleontological literature, as scholars have expanded the functionalities and capabilities of open-source software (Hu et al., 2020).

Since the inception of paleontology, there has been profound interest in creating interpretive reconstructions of extinct organisms and ancient ecosystems. However, this process is far from simple because of the scarcity of fossil records and the need for a deep understanding of organismal anatomy and refined artistic ability. Virtual reconstruction as a pivotal tool for integrating computer-assisted paleontology with biomedicine, laying the groundwork for digital methodologies (Zollikofer & Ponce de León, 2005). Nevertheless, the convergence of innovative techniques and artistic materials, coupled with the continual surge of new fossil discoveries, which leads to an ever-expanding knowledge of the diversity of ancient organisms, has made these prospects more promising (Eriksson & Horn, 2017).

This is motivated by the need to advance a comprehensive understanding of paleontological reconstruction techniques in a fully digital context. This study reviewed the literature on the application of 3D digital technologies to paleontological reconstruction from the past decade.

Therefore, the research questions of interest are:

- What digital tools and software have been developed for the paleontological reconstruction workflow process over the past decade?
- What are the current limitations and future trends in digital paleontological reconstruction?

Subsequently, a systematic literature review was conducted to identify the roles of 3D digital technologies in the workflow of paleontological reconstruction. While 3D digital technologies have diverse applications in paleontology, including taxonomy, biomechanical modeling, and public education, this review focuses specifically on their use in paleontological reconstructions. This targeted scope allows for a detailed analysis of reconstruction methodologies, their challenges, and their advancements.

2. Methodology

2.1. PRISMA statement

This systematic review adhered to the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Page et al., 2021). Searches were conducted across multiple databases, including ScienceDirect, Scopus, Web of Science, IEEE, and Google Scholar, using a four-step

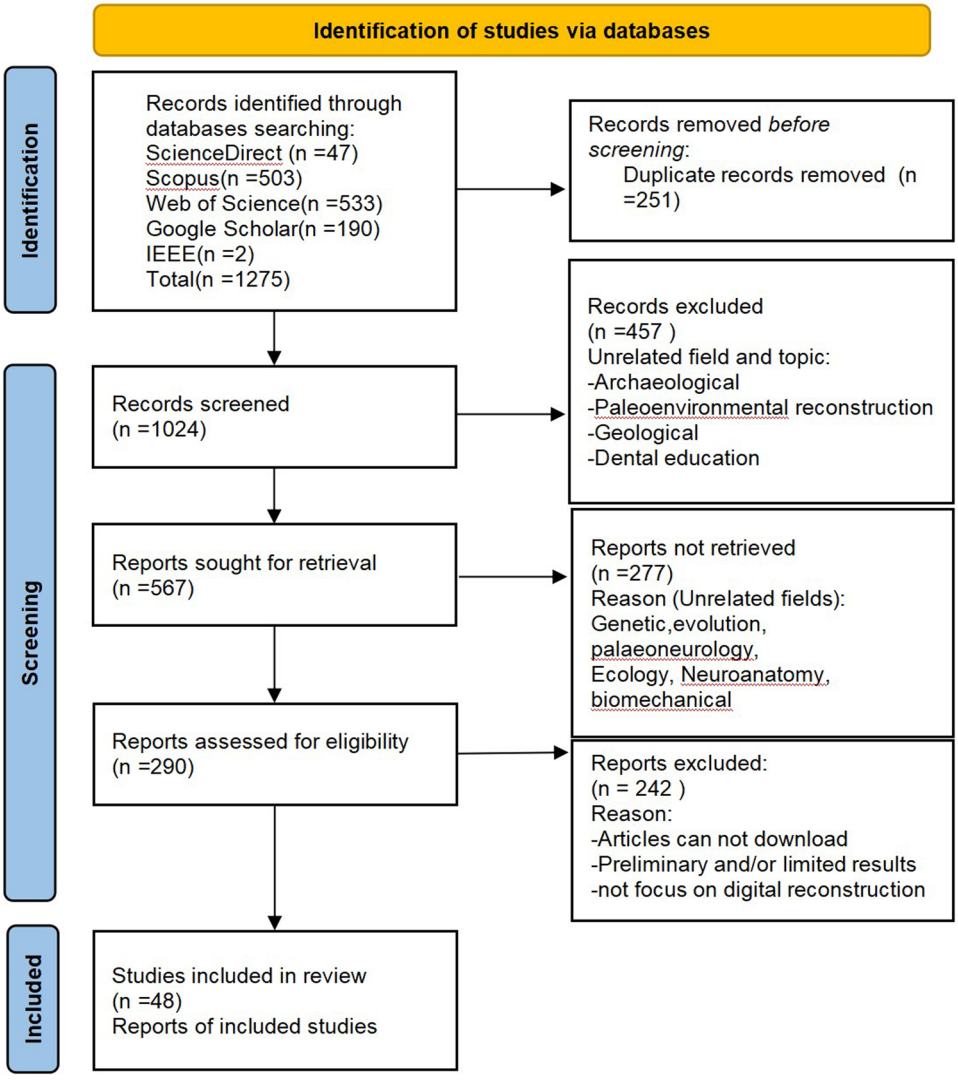

Figure 1. PRISMA flow diagram (Page et al., 2021).

process: (1) identification, (2) screening, (3) eligibility, and (4) data extraction. A comprehensive summary of the documents retrieved at each stage based on the PRISMA guidelines is presented in Figure 1.

2.2. Identification: search strategy and sources

This review concentrates on three overarching themes: (1) 3D digital technology, (2) paleontological reconstruction, and (3) virtual paleontology, based on the objective of understanding the application of 3D digital technologies in paleontological reconstruction. The following terms were selected: ('Paleontological Reconstruction' or 'fossil') and ('Virtual Paleontology') and ('3D visualization tools' or '3D digital technologies'or'computerized tools' or 'digital techniques' in abstract). Specific search term protocols (Boolean logic) corresponded to different databases. The results are shown in Table 1.

This systematic review primarily included articles published in English due to practical constraints such as the availability of translation expertise and access to relevant databases. However, we recognize that this approach may introduce a selection bias, as valuable insights published in other languages might have been excluded. To address this limitation, we included articles with English abstracts and keywords to ensure a broader scope of relevant studies. The focus of this review is to summarize the application of digital technologies in paleontological reconstruction over the last decade; therefore, the search time

Table 1. Search procedure performed in databases.

Database	Search terms protocol	Additional information
ScienceDirect	Paleontology or fossil, and Reconstruction and 3D visualization tools or 3D digital technologies or 3D Year: 2013–2024	–search in all fields –search in Review articles & Research articles –47
Scopus	(TITLE-ABS-KEY (paleontolog* OR fossi*) AND TITLE-ABS-KEY (reconstruction) AND TITLE-ABS-KEY (3d OR digital OR technologies OR virtual)) AND PUBYEAR > 2012 AND PUBYEAR > 2012 AND PUBYEAR < 2025 AND (LIMIT-TO (DOCTYPE, 'ar') OR LIMIT-TO (DOCTYPE, 're')) AND (LIMIT-TO (LANGUAGE, 'English')) Year: 2013–2024	–search in all fields –503
Web of Science	ALL=((Paleontolog* or fossi*) and (Reconstruct*) and (3D visualization tools or 3D digital technologies or Virtual or 3D)) Publication Date: 2013-01-01 to 2024-05-01	–search in all fields –Document Types: Article or Review Article. –533
Google Scholar	(Paleontolog* or fossi*) and (Reconstruct* or Virtual Paleontology or Virtual Reconstruction) and (3D visualization tools or 3D digital technologies or 3D) Return articles dated between: 2013–2024	–search in all fields –190
IEEE	('All Metadata':Paleontolog* or fossil) AND ('All Metadata':Reconstruct*) AND ('All Metadata':3D or virtual) Filters Applied: 2013–2024	–search in all fields –2

Table 2. Inclusion and exclusion criteria.

Inclusion criteria	Exclusion criteria
Using 3D digital technologies	Duplicates from different databases
Focuses on paleontological reconstruction	Studies published in other languages
Written in English	Studies from unrelated areas

frame was set as 2013–2024. Following this, this study conducted a systematic review to identify the roles of 3D digital technologies in the workflow of paleontological reconstruction, outlining the development of cutting-edge applications in the field. The search results were sorted according to relevance, title, abstract, and keywords to encompass as many relevant papers as possible, resulting in 1275 entries.

2.3. Screening and eligibility

At this stage, we determined the inclusion and exclusion criteria as outlined in Table 2. We evaluated various factors, including language, topic, and content of each paper.

We initially evaluated whether each article met the necessary criteria to support the objectives of this review. Duplicate articles from different databases were excluded from the analysis. Subsequently, we identified and retained studies that focused on the application of 3D technology in paleontological reconstruction. Studies related to archaeology, cultural heritage monuments, medical fields, engineering, vegetation, dental education, and similar areas were excluded. Finally, a comprehensive verification and validation process was conducted on all selected articles to ensure the relevance of their categories and content.

2.4. Data extraction

We revisited the final list of selected articles to ensure alignment with the pertinent criteria and verified the suitability of our selection process. In Appendix A, the articles are chronologically organized by year of publication, with information extracted from each article based on the objectives of this review. The application of 3D digital technologies in paleontological reconstruction is detailed, encompassing term categories, methods, and objectives. This review focused on peer-reviewed literature to ensure methodological rigor. While gray literature, such as (e.g., state evaluation reports, conference proceedings, technical reports, and theses, was not systematically included due to challenges in accessibility and evaluation, we acknowledge its potential to provide valuable insights into emerging research and practices.

A detailed checklist summarizing how each item from the PRISMA 2020 framework has been addressed is provided in Appendix B. This checklist includes essential aspects such as the identification, screening, eligibility, and inclusion of studies, ensuring that the methodology is systematic and reproducible.

3. Results

The digital paleontological reconstruction process consists of three stages: data acquisition, preprocessing of raw fossil data to remove noisy points and matrices virtually, and reconstruction of the preprocessed fossil data. Based on this, and depending on the technologies under investigation or utilized in the study, we categorized the articles into 'Raw 3D Fossil Data Acquisition Methods,' 'Fossil Data Preprocessing and 3D Reconstruction Software,' and 'Usability' (expanding application after visual reconstruction, including areas such as 3D printing for display purposes and establishing comprehensive databases) for review. The primary research contribution of each article served as the basis for categorization into one of these three domains, ensuring clarity and preventing overlap between the categories.

Ultimately, 48 articles were selected and categorized based on their relevance to the research objectives. Among them, 38% corresponded to raw 3D fossil data acquisition methods, and 29% focused on Fossil Data Preprocessing and 3D Reconstruction Software. Finally, 33% were related to the usability of the reconstructed fossil data (as shown in Figure 2).

Appendix A summarizes the objectives and strategies of the selected papers, detailing their key focus areas, methodologies, and an assessment of their quality and relevance. This comprehensive overview enables readers to understand how the included studies align with the broader goals of this systematic review, emphasizing their significance in addressing the research objectives.

3.1. Raw 3D fossil data acquisition methods

Many physical or chemical isolation and preparation methods can damage the specimens and are unable to recover data from inside a fossil. Virtual paleontology provides a set of tools that enables more complete data extraction from such materials (Cunningham et al., 2014; Ogihara et al., 2015; Sutton et al., 2016). In recent years, 3D surface digitization tools for fossils have been extensively used in paleontology. These innovative techniques allow researchers to produce digital replicas of fossils using computed tomography (CT), laser scanning, or photogrammetry, a technique involving a series of photographs (Lautenschlager, 2017). The following sections describe the various data acquisition methods utilized in paleontological research over the past decade.

3.1.1. Computed tomography

Among the many available digital methods, CT has emerged as a widely used, nondestructive, and accurate tool for collecting fossil data. It is an advanced nondestructive technique used to investigate the internal structure of fossils by acquiring thousands of serial images to produce accurate internal morphological 3D reconstructions (Abel et al., 2012; Bicknell et al., 2022; Heřmanová et al., 2020; Racicot, 2016; Yan-Fang et al., 2019). Falkingham et al (2018) stated that CT is one of the most powerful analytical tools available for investigating the anatomy and morphology in paleontological contexts. Pérez-Ramos and

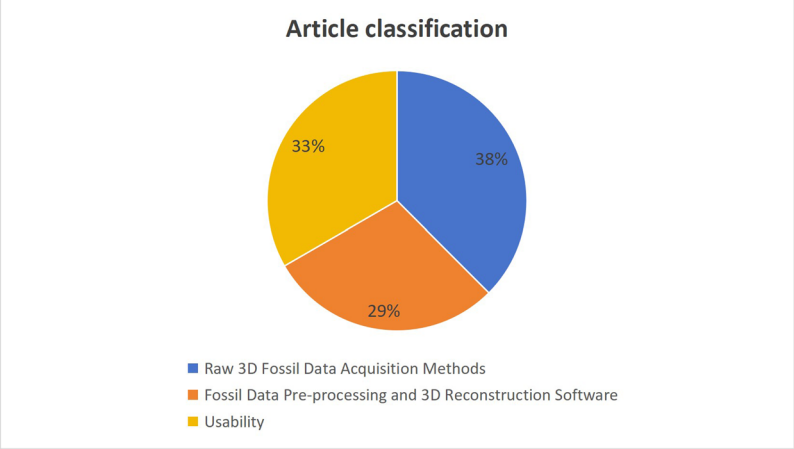

Figure 2. Division of articles in each category.

Figueirido (2020) highlighted that recent advancements and improvements in CT technology have significantly enhanced the analysis of fossils, offering detailed internal information without requiring invasive methods. Gaspard (2013) asserted that X-ray CT, when compared to traditionally used transverse serial sections, is a promising tool for the 3D modeling of the brachidium. This advancement has been crucial for brachiopod classification. CT technology has significantly improved over the past decade, enabling rapid scanning of larger and denser objects (Abel et al., 2012). Studies (e.g., Bartolini-Lucenti & Rook, 2023) highlight the practical implementation of CT scanning and surface scanning to digitize significant museum specimens, underscoring their utility in advancing paleontological research. Since its inception in the 1970s, CT has significantly impacted numerous fields (Uldin, 2017). For example, paleoanthropology has greatly benefited from this efficient and noninvasive method for conserving, reconstructing, and analyzing fossilized human remains (Uldin, 2017).

3.1.2. Micro-computed tomography

X-ray micro-computed tomography (μCT), developed in the late 1980s, has become an invaluable technique for fossil imaging, offering high-resolution (sub-millimeter) detail. This technique is suited for small subjects and can simultaneously image both the external and internal morphologies, offering significant benefits in invertebrate research (e.g., Peris et al., 2022). X-ray μCT enables the scanning of extremely small structures at the micron scale (Schmidt, 2013). For example, Knyaz et al (2022) used X-ray μCT to examine human teeth and demonstrated the efficacy of image-processing techniques in reconstructing their morphology. Similarly, Liu et al. (2021) demonstrated that μCT can noninvasively reveal the structures inside the Chengjiang fossil slab. They also utilized μCT to achieve high-quality 3D reconstruction of a 2-mm-long larva of the arthropod Leanchoilia illecebrosa from 520-million-year-old early Cambrian Chengjiang biota in China. This technology has three-dimensionally preserved Chengjiang fossils and other biota with similar types of preservation, particularly those with comparable iron concentrations.

The advantage of μCT over conventional CT is its significantly higher achievable resolution (Hoffmann et al., 2014). Peris et al. (2022) described a novel genus and species within the relatively uncommon beetle family Thanerocleridae (Cleroidea). They underscored the fact that the observation of specific traits, such as mouthparts and intricacies on the ventral side of the thorax, became feasible only after 3D reconstruction of the fossil using X-ray μCT scanning. Noninvasive methods yield supplementary information concerning external features, such as ornamentation irregularities while preserving the integrity of the fossil (Hoffmann et al., 2014). These case studies underscore the effectiveness of employing this nondestructive technique in studies involving fossils.

3.1.3. Surface scanning

The external features of the fossils were digitally visualized through surface scanning. Over the last decade, laser scanners, optical scanners, and other surface scanning methods have become increasingly accessible (Bastir et al., 2019). In case studies on paleontological reconstruction, Reolid et al. obtained morphometric data from digitized 3D models of scientifically accurate theropod reconstructions from eight representative families using 3D scanning devices (Reolid et al., 2021). Das et al. (2017) demonstrated a cost-effective and rapid method for the 3D scanning of large paleontological specimens by utilizing time-of-flight depth sensing with a Kinect scanning module. This method is advantageous because of its low cost compared to industrial scanners and photogrammetric techniques, while maintaining scanning accuracy over a wide range of volumes, making it particularly well-suited for large specimens (Das et al., 2017). Bastir et al. (2019) outlined the primary steps involved in 3D surface scanning using portable equipment suitable for transportation of osteological collections. They specifically concentrated on describing and providing handling suggestions for small (Next Engine HD Laser scanner) and handheld (Artec Spider, MHT, and EVA) scanning devices. These surface scanners, which are widely utilized in paleoanthropology, are known for their accuracy in obtaining high-resolution 3D models (Bastir et al., 2019). PaleoScan is another cost-effective and high-throughput methodology for fossil scanning, providing a practical solution for digitizing large fossil collections (Silva et al., 2024).

3.1.4. Photogrammetry

Photogrammetry, which was initially utilized in mapping and architecture, is a technique that creates a 3D model using photographs of an object. It has been adopted across various scientific disciplines and is extensively employed in paleontology as an economical and straightforward technique for 3D reconstruction (Fahlke & Autenrieth, 2016; Profico et al., 2019). Among the methods tested, manual photogrammetry showed a high degree of reproducibility and was the most efficient and cost-effective option. Special emphasis was placed on ensuring adequate overlap, consistent lighting, and focus because these factors are crucial for capturing suitable photographs (Fahlke & Autenrieth, 2016). Photogrammetric 3D models offer morphometric information that is not available from bone studies alone, including the surface/volume ratio. This technique, applied to accurate dinosaur models, provides extensive and accurate data that are useful in various areas of dinosaur paleontology and paleobiology (Reolid et al., 2021). Photogrammetry is valuable for illustrating the overall specimen morphology, excelling in surface reconstruction with high accuracy in texture, color, and morphology. However, it lacks the capability to capture internal structures and requires postproduction scaling (Profico et al., 2019). Despite these limitations, this method remains useful, particularly when internal exploration is unnecessary (Bicknell et al., 2022; Kouraiss et al., 2019).

3.1.5. Stereo camera

Stereo cameras are open-source technologies that generate high-resolution 3D surface models of objects by capturing multiple images (Fahlke & Autenrieth, 2016). Olsen and Westneat (2015) described a method for capturing landmarks and curves in fossil specimens using stereo cameras. Once the cameras are calibrated, any point visible in both camera views can be reconstructed in 3D using pixel coordinates and a set of calibration coefficients. Building on this approach, Olsen and Westneat (2015) developed an R package called StereoMorph, which efficiently and accurately collects 3D landmarks and curves using two standard digital cameras. However, this method requires at least 20 images and several hours of computational processing per specimen, making it unsuitable for capturing a small number of landmarks from numerous specimens.

3.2. Fossil data preprocessing and 3D reconstruction software

After acquiring the original 3D fossil data using various technical methods (as mentioned above), preprocessing of the original 3D data is required. Consequently, the primary challenge in analyzing raw 3D fossil data has shifted from scanning to data preprocessing. This process involves transforming 3D CT data into a virtual representation of the fossil, isolating it from the matrix and dissecting it into anatomical components (Abel et al., 2012). Thus, various software and methods have been employed to preprocess the original fossil data. This preprocessing virtually removes the surrounding rock and matrix of the fossil to obtain processed 3D fossil data. However, the process of labeling and segmenting CT images is frequently labor-intensive, error-prone, and subject to the discretion of the researchers. Setting a standard for CT image processing of fossils is essential for reducing the time consumed by manual processing (Yu et al., 2022). Therefore, identifying and developing existing 3D segmentation software for fossil 3D data is of particular importance. This section provides an overview of common software used for fossil data preprocessing and 3D fossil model reconstruction.

After acquiring raw 3D fossil data through various methods and preprocessing, the resulting fossil data often lack completeness, necessitating further reconstruction. The digital reconstruction of fossils using CT and other scanning methods is now a standard practice in paleontology. This procedure includes two aspects: the transformation and reconstruction of fossil specimens. The transformation process involves altering the raw 3D model to correct for postmortem brittle and plastic deformation. In contrast, reconstruction involves filling in fractures, adding missing parts, and smoothing the mesh surface. Nevertheless, documenting and reproducing digital edits from the restoration can be challenging (DeVries et al., 2022).

Several 3D software options have proven convenient for this task. Additionally, virtual reconstruction is beneficial for preserving the original fossil structure. Three-dimensional reconstructions can examine the entire structure of the fossil data without requiring additional imaging. Furthermore, they allow for the

creation of 3D pixels (voxels) that can be used for extremely accurate volume calculations. This feature is particularly useful for type specimens or exceptionally rare materials for which destructive analyses of structures are not feasible (Schmidt, 2013). A critical aspect of paleontological research is the development and utilization of advanced 3D modeling and reconstruction software. In recent years, the field has seen significant advancements aimed at enhancing the visualization and analysis of fossil specimens.

3.2.1. 3D segmentation software

Among the numerous 3D segmentation software options, Drishti Paint has been frequently cited and appears to be a relatively powerful tool for preprocessing raw fossil data. Hu et al. (2020) introduced Drishti version 2.7, which is open-source software for volume exploration, rendering, and 3D segmentation. This update enhances the accuracy and precision of digital reconstruction, 3D modeling, and printing (Hu et al., 2020). As noted in the literature, in addition to Drishti, numerous software options are available for preprocessing fossil data. For example, engineering 3D software packages such as Polyworks, Amira and Avizo can enhance the comprehension of paleobiological aspects across various fossil groups following scanning (Hoffmann et al., 2014). In the study of Reolid et al. (2021), after generating meshes and exporting them in the OBJ file format, CloudCompare V2 was employed for additional data processing. CloudCompare is an open-source software program specializing in 3D point clouds and mesh processing. This process primarily involves adjusting the scale of the models to their actual size, as proposed by Therrien and Henderson (Reolid et al., 2021). Similarly, Mimics software demonstrated effective performance in CT data visualization and virtual segmentation. It facilitates the easy manipulation of CT slices and allows for manual segmentation of the original fossil data across three planes, enabling the removal of matrices and artifacts (Bicknell et al., 2022; Sharp, 2014). However, labeling and segmenting CT images involve laborious tasks, are susceptible to errors, and rely on the subjective judgments of the researchers. Establishing a standard protocol for processing raw 3D fossil data is crucial for minimizing the time required for manual processing (Yu et al., 2022).

3.2.2. Blender

Blender (BlenderORG) is an open-source, cross-platform 3D computer graphics application that was developed and maintained by the Blender Foundation. Offering versatility, it allows users to create, import, and modify 3D objects; manipulate lighting, color, and texture; and conduct ray tracing on the resulting models. In addition, it facilitates the animation of 3D objects, video editing, and various complex options tailored for detailed, photo-realistic ray tracing, often surpassing the requirements of most paleontological applications. Blender has become integral to the paleontological community and serves two main functions. First, it manually models meshes, creates ray-traced, ideal reconstructions of fossil organisms, and produces high-quality images. Secondly, it is employed to publish CT scan data, which are subsequently processed using other software suites (Garwood & Dunlop, 2014).

Blender integrates an animation tool known as an 'armature', enabling the precise manipulation of sections within a surface mesh while recording changes. During the retrodeformation of a fossil, an armature is created and linked to it to manage the displacement and distortion of its fragments. DeVries et al. (2022) utilized this aspect of the software to document reconstructive modifications and capture the movement and distortion of each fragment. This workflow and its results provide valuable insight into the previously opaque digital restoration process in paleontology. Although the utility of 3D reconstruction, including Blender, is being increasingly recognized within the paleontological community, the steep learning curve of the software remains a challenge. Unfortunately, there are currently no guides specifically tailored to the application of Blender in paleontology (Garwood & Dunlop, 2014).

3.2.3. ZBrush

ZBrush is a powerful software tool that focuses on digital sculpting and illustration and allows users to unleash their creativity and sculpt with intricate details. Moreover, ZBrush offers unique features that distinguish it from traditional 3D modeling programs, enabling closer integration with traditional drawing and sculpture techniques (Berroya Elosua et al., 2019). When feasible, digital sculpting can

incorporate CT data on particular morphological structures, whether from fossilized or extant materials, serving as a potent tool to increase the authenticity of the reconstruction. Digital sculpting enables the creation of intricate details at a resolution surpassing that of traditional clay sculpting, facilitating swift iterations and adjustments before reaching the final stage of digital sculpture (Eriksson et al., 2022).

Eriksson et al. (2022) performed an artistic reconstruction of the ichthyosaur that exhibits both strong esthetic value and scientific rigor, largely attributed to the powerful functionalities of ZBrush. ZBrush facilitates modeling, detailed texturing, and painting (Eriksson et al., 2022). In a separate investigation by Bicknell et al. (2023), the 3D reconstruction of Acutiramus, a colossal pterygotid sea scorpion, was accomplished using ZBrush. The process of model construction commenced with a sequence of basic shapes, which were manipulated to resemble the generalized morphology of Acutiramus and subsequently underwent more detailed sculpting through an additive and subtractive process. Furthermore, ZBrush is often used in the facial reconstruction of ancient humans, likely because of its significant advantages in portrait modeling. Lindsay et al. (2015) referenced a case report detailing the study and 3D facial approximation of an ancient Egyptian mummy head achieved through the utilization of medical imaging data and digital sculpting software. Similarly, Lee et al. conducted a study in which they utilized CT to reconstruct the face of a historical figure from 17th-century Korea based on mummified remains. In the final stage of their research, ZBrush was employed to visualize and reconstruct the complete appearance of the individual, including the skin texture, hairstyle, and clothing (Lee et al., 2014).

In their study, Béchard et al. (2014) employed the Wavefront OBJ file format to export data to ZBrush 4r4, facilitating modeling and reconstruction tasks. The Dynamesh tool played a crucial role in gap closure, mesh density reorganization, and simplification, while preserving the object detail during merging. Moreover, they used the Spotlight tool to enhance the grid with floating images in addition to utilizing a range of tools, including masks, grid projections, and sculpting brushes, during the subsequent reconstruction process.

3.2.4. Autodesk Maya

In the expansive array of 3D model reconstruction software options, Autodesk Maya is a popular choice within the paleontological community, albeit with limited uptake by a select number of researchers. Autodesk Maya offers a more user-friendly interface, which is regarded as an advantage. However, for novice users, the learning curve can still be steep (Garwood & Dunlop, 2014). The study conducted by Clark et al. (2023) illustrated that individual elements exported from raw data using 3D visualization or mesh editing software can be positioned for modeling or rigging in Maya.

Similar to Blender, Maya showcases its strengths in animation. Schmidt et al. (2021) used Autodesk Maya to develop a flexible endopod with movable articles. They outlined a workflow for reconstructing the mobility of a limb of the early Chengjiang arthropod, Ercaicunia multinodosa, from a renowned Chinese fossil site. Utilizing the X_ROMM add-on tool in Maya, they demonstrated, step-by-step, how to manipulate the articles of the limbs to swing inward toward each other. This kinematic approach provides a valuable and comprehensive guide for 3D animation and manipulation, facilitating mobility research in fossil arthropods based on μCT data.

3.2.5. Geomagic studio

Numerous references have detailed comparable workflows that entail data acquisition, segmentation, and reconstruction, with Geomagic serving as the primary tool for the reconstruction process. A more detailed description of the reconstruction procedure is provided below. Initially, the 3D fossil data undergo post-processing in Mimics or Avizo for splicing and preprocessing. The processed data are then exported as STL files. These files are imported into Geomagic Studio for meticulous refinement and comprehensive reconstruction of the complete biological structure (Clark et al., 2023; Lautenschlager & Rücklin, 2014; Pérez-Ramos & Figueirido, 2020; Sharp, 2014).

3.2.6. Other software

From the 48 articles, only Costa et al. (2014) employed Autodesk 3D Studio Max 5.0 (3DS Max) software, a professional software tool used for creating 3D animations, models, games, and images. It can manipulate a 3D scan model of the fossil specimens, reconstructing damaged components, identifying articulation points, and integrating the models into one overall reconstructed model. Cirilli et al. (2020) introduced a novel virtual reconstruction method called target deformation, which was designed to digitally restore severely deformed and partially incomplete cranial specimens. This approach uses target fossil remains from the same species to guide the reconstruction process. A proficient retrodeformation protocol was integrated into the R software environment as part of the Morpho R package. In the study by Cirilli et al. (2020), 12 digital scans acquired from two structured-light scanners were aligned and processed into meshes using Artec Studio 14 software.

3.3. Usability

Recent advancements in digital technology have revolutionized paleontology, offering unprecedented opportunities for data utilization in research and science communication. Creating, preparing, and dissecting a 'virtual' fossil involves segmentation, rendering, animation, stereo-anaglyphy, data storage, and dissemination (Abel et al., 2012). Therefore, certain scholars have directed their attention toward assessing the usability of 3D technologies for the reconstruction of fossils and the resulting reconstructed data. The creation of comprehensive databases containing fossil data has facilitated the efficient retrieval and sharing of information among researchers worldwide. These databases serve as valuable resources for digital reconstruction efforts, providing access to detailed anatomical data that are crucial for accurate 3D modeling. Furthermore, advancements in data-sharing platforms have enhanced collaboration within the paleontological community, enabling researchers to access and contribute to large-scale projects. This collaborative approach has been extended to 3D printing technologies, in which digitized fossil data can be transformed into physical replicas for educational and research purposes. In addition, digital reconstruction plays a crucial role in scientific communication by providing visually compelling representations of ancient life forms to the public. Through interactive exhibits, virtual tours, and educational materials, digital reconstructions engage audiences and promote a deeper understanding of paleontological research. Overall, the usability of data in digital reconstruction opens new avenues for advancing paleontology and fostering public interest in Earth's prehistoric past. In the following sections, we review the recent research on the usability of 3D technologies for paleontological reconstruction.

3.3.1. Publicly accessible databases

Owing to the recent technological revolution in digital acquisition, online databases now offer accessibility to 3D models, presenting opportunities to acquire or procure digital renditions of fossil specimens (Profico et al., 2019). Numerous online data repositories facilitate the deposition and retrieval of 3D imaging data encompassing μCT image datasets and 3D object files. Examples of such repositories include figshare (figshare.org), MorphoSource (morphosource.org), and Dryad (datadryad.org). Additionally, 3D object files can be archived simultaneously in open repositories, such as Makerbot's Thingiverse, which offers specific functionalities for 3D printing (thingiverse.com), and Sketchfab (sketchfab.com), which provides specialized features for crafting virtual and augmented reality experiences (Clark et al., 2023). Furthermore, the data act as digital records, allowing for wide dissemination and sharing between researchers and the general public. This accessibility has enabled researchers to study the internal and external features of rare and expensive specimens that were previously inaccessible (Racicot, 2016). Moreover, a growing number of vertebrate paleontologists and paleoartists have strongly advocated for more publicly accessible databases of basic research data (Uhen et al., 2013). Access to digital databases and open 3D datasets is becoming increasingly crucial for a globally connected scientific community (Racicot, 2016). Efforts are currently underway to facilitate the publication and sharing of authentic 3D data by developing online databases (Martone et al., 2002; Schmidt, 2013). Digitally accessible databases significantly accelerate research by enabling easy access to objects on the Internet.

Researchers can work virtually or with physical versions of virtual models using 3D printing (Bastir et al., 2019).

3.3.2. VR&ar

Digital techniques, particularly augmented reality (AR), significantly contribute to reconstructing and understanding paleontological data (Samuelson et al., 2024). Spatial augmented reality (SAR) is an emerging paradigm that integrates digital supplements into real-world environments, offering significant applications in paleontology (Bimber & Raskar, 2005). AR and virtual reality (VR) bridge the analog-digital divide, enabling researchers to interact with morphological data in ways not achievable through traditional methods (Cieri et al., 2021). Several key considerations for deploying AR in paleontology include barriers to app downloads, the aging novelty of AR, location-specific app usage, challenges in app maintenance, funding cycles, difficulties embedding educational content, conflicting priorities between users and event organizers, and the critical importance of animation quality (Bennett et al., 2022). Techniques such as transflective surfaces, Virtual Showcases, and Shader Lamps facilitate effective visualization of complex structures, addressing limitations in conventional AR displays (Bimber et al., 2000; Bimber & Raskar, 2003).

Recent studies highlight the effectiveness of marker-based web apps in enhancing accessibility and user engagement by allowing users to view 3D fossil models directly on mobile devices via QR codes and JavaScript implementations (Cieri et al., 2021; Samuelson et al., 2024). These apps eliminate the need for downloads and specialized software installations, thereby addressing common challenges such as app download barriers, maintenance issues, and location-specific usage limitations. Additionally, continuously updating AR content with interactive educational elements, such as quizzes and real-time data overlays, helps to sustain user interest and combat the aging novelty of AR (Bennett et al., 2022). The use of off-the-shelf software and open-source tools for AR development further alleviates maintenance challenges by ensuring compatibility with regular software updates. Collectively, these strategies improve user accessibility and support the long-term viability of AR technologies in paleontology.

3.3.3. 3D printing

Three-dimensional printing, also known as additive manufacturing or rapid prototyping, has become common in many academic institutions and engineering facilities. Additionally, 3D printers are becoming increasingly available to consumers. As the cost of digital printing technology continues to decrease, realistic 3D paleontological models will inevitably be made and printed into physical models. This type of model can include professional paleontology research, science teaching, museum displays, art collection, and other functions (Racicot, 2016). Rapid prototyping enables the conversion of digitally prepared specimens into physical models, facilitating the broader dissemination of copies of rare fossil specimens while preserving their intricate details (Lautenschlager & Rücklin, 2014). Bastir et al. (2019) also mentioned that in paleontology, direct manipulation of fossils, including tactile interaction, is restricted to select situations and individuals because of the scientific significance of these specimens. This limitation arises from the unique scientific value of precious fossils and historical casts, which are often considered rare. Nevertheless, insights gleaned from the physical interactions with these objects, along with the knowledge and expertise derived from such experiences, are vital for morphological research. In this context, 3D printing has emerged as a valuable tool for facilitating access to replicas that can be handled and studied more freely. Based on this background, Bastir et al. (2019) presented a series of tips and tricks for 3D printing that provided guidance for paleontology researchers (Bastir et al., 2019). Three-dimensional printing extends the curatorial, educational, and outreach possibilities of X-ray CT and its derivatives (Racicot, 2016).

4. Discussion

The 48 selected articles offer insights into the application of 3D digital technologies in paleontological reconstruction. First, we discuss digital technology by focusing on 3D scanning and imaging. We identify

Table 3. 3D technologies used in digital paleontology research and paleontological reconstruction.

Categorization	Function	Technologies & software	The number of identified articles mentioned specific related technologies
Visualization tools for data acquisition	Computer tomography	X-ray CT	23 (Abel et al., 2012; Bicknell et al., 2022; Cunningham et al., 2014; DeVries et al., 2022; Falkingham et al., 2018; Gaspard, 2013; Hoffmann et al., 2014; Hu et al., 2020; Kouraiss et al., 2019; Lautenschlager, 2017; Lautenschlager & Rücklin, 2014; Lee et al., 2014; Lindsay et al., 2015; Ogihara et al., 2015; Pérez-Ramos & Figueirido, 2020; Profico et al., 2019; Racicot, 2016; Schmidt, 2013; Sharp, 2014; Sutton et al., 2016; Uldin, 2017; Yan-Fang et al., 2019; Yu et al., 2022)
		Micro-CT	
	Scanning	3D surface scanner	9 (Bastir et al., 2019; Béchard et al., 2014; Cirilli et al., 2020; Costa et al., 2014; Das et al., 2017; Falkingham et al., 2018; Hoffmann et al., 2014; Lautenschlager, 2017; Reolid et al., 2021)
		Photogrammetry	3 (Bicknell et al., 2022; Fahlke & Autenrieth, 2016; Kouraiss et al., 2019)
	Photograph	Stereo Camera	1 (Olsen et al., 2015)
Fossil data pre-processing methods	Three-dimensional segmentation (labeling and segmentation of CT images)	Drishti paint	1 (Hu et al., 2020)
		VXelements	1 (Béchard et al., 2024)
		Mimics version	3 (Bicknell et al., 2022; Pérez-Ramos & Figueirido, 2020; Sharp, 2014)
		Avizo	4 (Clark et al., 2023; Lautenschlager & Rücklin, 2014; Pérez-Ramos & Figueirido, 2020; Sharp, 2014)
	mesh editing	Meshlab	3 (Clark et al., 2023; Lautenschlager & Rücklin, 2014; Pérez-Ramos & Figueirido, 2020)
		Polyworks	1 (Hoffmann et al., 2014)
	Format conversion	FreeForm modeling	1 (Lee et al., 2014)
3D modeling and reconstruction software		Blender	4 (DeVries et al., 2022; Garwood & Dunlop, 2014; Lautenschlager & Rücklin, 2014; Pérez-Ramos & Figueirido, 2020)
		Zbrush	5 (Bicknell et al., 2023; Eriksson et al 2022; Lindsay et al., 2015; Lee et al., 2014; Béchard et al., 2014)
		Autodesk 3D Studio Max (3DS MAX)	1 (Costa et al., 2014)
		Maya	3 (Clark et al., 2023; Pérez-Ramos & Figueirido, 2020; Schmidt et al., 2021)
		Geomagic Studio	3 (Bicknell et al., 2022; Pérez-Ramos & Figueirido, 2020; Sharp, 2014)

the capabilities of these technologies in capturing the intricate details of paleontological specimens and discuss their advantages over traditional methods. In contrast, the section on virtual reconstruction introduces digital modeling and reconstruction software, showcasing successful applications and their impact on scientific analysis and communication. Several articles discussed multiple technologies or methods; therefore, all papers related to a specific technology were summarized. We counted the number of mentions of each technology or method in the 48 articles, as shown in Table 3. Among these, 35 papers (12 of which focused on μCT) either introduced or employed CT in their case studies to visualize fossil data. Various technologies exist for the digitization of fossils. CT, including synchrotron, scanning is the most effective and precise method for morphological studies, enabling the examination of both external surfaces and internal structures. Depending on the overall imaging resolution, this method can reveal details that are inaccessible using other acquisition techniques (Lautenschlager, 2017; Profico et al., 2019). This underscores the significance of CT technology as a cornerstone of the digital paleontological reconstruction process and establishes it as the most dependable method for data acquisition.

The above analyses demonstrate that the integration of 3D modeling and reconstruction software in paleontology represents a crucial advancement in the field, offering researchers the tools needed to enhance their analyses, interpretations, and representations of fossil specimens. By leveraging the insights and methodologies presented in the aforementioned studies, paleontologists can continue to push the boundaries of knowledge and discovery into the realm of paleontological research. Among the software options, 3D Studio Max appears to be the least utilized (only one article mentioned it), lacking a significant advantage over other powerful modeling software. Maya offers robust functionality, albeit with a relatively complex interface and operation that require users to possess a certain level of software proficiency. However, Blender is easier to learn than the former options, although it is slightly less precise than ZBrush in digital sculpting. Considering the current trends in software usage, it is evident that Blender and ZBrush are poised to become mainstream tools for future paleontological reconstructions. The frequencies of several major 3D reconstruction software packages in the 48 articles are shown in Figure 3.

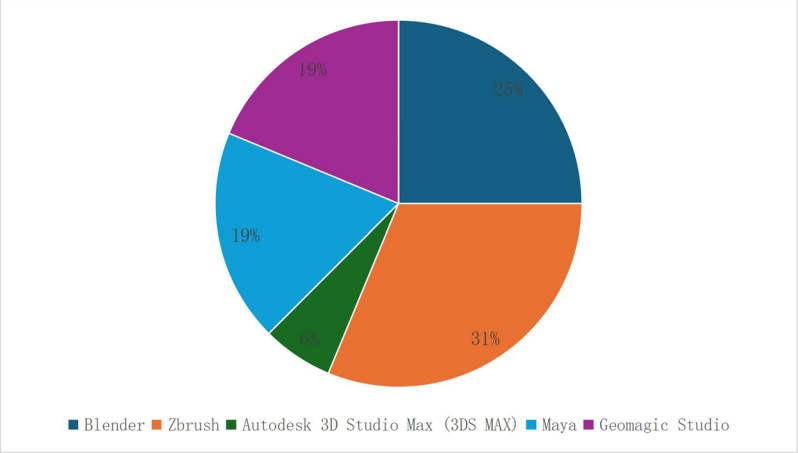

Figure 3. Utilization rate of various 3D reconstruction software packages.

However, several limitations and challenges persist in paleontological reconstruction. First, the full potential of open-source software remains largely unrealized (Hu et al., 2020), despite its extensive application in noninvasive methods, particularly in cephalopod and other invertebrate research (Hoffmann et al., 2014). This discrepancy arises from the disparity between the advancement of tools for data generation and the lack of methods for visualizing 3D data. In addition, the cost and logistics associated with acquiring CT scans often restrict access to extremely large samples (Racicot, 2016). Second, the absence of a standardized file format or database for the 3D digital data obtained from CT scans poses a significant obstacle. Furthermore, the size of the original data and associated files makes them challenging to include as supplemental data (Racicot, 2016), highlighting the necessity of establishing a standard protocol for data recording, presentation, and archiving (Falkingham et al., 2018). Third, limitations persist in terms of the cloud data storage capacity and the ability to share data effectively with various users, including the public. This is compounded by the challenges in processing large datasets, given the considerable computational power and time required (Racicot, 2016). Finally, the impact of artistic paleontological reconstruction on science popularization and communication requires further exploration, as traditional publication methods hinder the dissemination of 3D information within the scientific literature (Lautenschlager & Rücklin, 2014).

4.1. Significance of paleontological reconstruction in education and popular science

Virtual paleontology has emerged as a valuable technique for investigating the history of life, offering substantial potential as a resource for public outreach and online data dissemination. This approach affords individuals the unique opportunity to actively interact with fossils beyond their reach, thereby greatly augmenting the ability of paleontologists to review the data of other researchers (Cunningham et al., 2014; Sutton et al., 2016). Each of these 3D technologies serves as a lasting digital record that can be shared with future researchers, museums, and the general public (Racicot, 2016). Abel et al. (2012) highlighted the significance of virtual processing delicate and uncommon specimens. The adoption of μCT and other 3D imaging techniques has progressively enhanced data sharing among scientists and supported educational and outreach endeavors. The retrieved 3D paleontological data offer a cost-effective and straightforward means of disseminating morphological data for both research and educational objectives (Racicot, 2016).

Kouraiss et al. (2019) highlighted 3D digital techniques that have emerged as dependable methods tailored to accentuate the potential of paleontological data stored in museums, facilitating the scientific dissemination of information. Moreover, an extensive array of accessible digital models is likely to be integrated into museum exhibitions, popular science publications, and outreach activities (Lautenschlager, 2017). Clark et al. (2023) provided a comprehensive guide on methods for constructing top-tier 3D digital models of both living and fossil organisms by leveraging freely accessible software aimed at students

and educators. Through case studies and accompanying tutorials, they offered step-by-step instructions to address the typical challenges encountered with 3D imaging data when reconstructing plants and animals. These methodologies are designed to enhance both scientific precision and computational efficacy and are applicable to a diverse spectrum of organisms.

From various dimensions, the digital restoration of paleontology has significant potential to influence science popularization. Bastir et al. (2019) proposed integrating contemporary digital technologies to establish a laboratory equipped for generating and replicating 3D anatomical models. This facility would support advances in research, education, and museum exhibition. Paleontological restoration bears great responsibility for science communication and public education, as it is crucial for people to understand the origins of modern biodiversity, the development of species, and the inspiration for the unique esthetic feeling of paleontology. Bimber and Raskar highlight the advantages of spatially augmented reality (SAR) over head-mounted displays, particularly its ergonomic benefits and ability to enhance user immersion, making it highly applicable for museum exhibits and educational settings (Bimber & Raskar, 2003). Similarly, Davis et al. (2022) underscore the importance of paleoart and augmented reality (AR) in producing visually accurate and engaging reconstructions, which serve both public outreach and scientific purposes. In the contemporary digital era, 3D paleontological models serve as vehicles for disseminating information. Therefore, it is imperative to explore their potential for public outreach. Eriksson and Horn (2017) emphasized the convergence of science and art through the creation of authentic, high-end sculptures depicting a notable Cambrian organism *Agnostus pisiformis*. These sculptures serve diverse functions, including research, scientific outreach, and educational purposes (Eriksson & Horn, 2017). Therefore, strategies for creating reconstructions that possess both esthetic appeal and scholarly rigor should be the focus of future research.

4.2. Development of a paleontological reconstruction workflow framework

The existence of domain-specific protocols, such as those proposed in ichnology (Falkingham et al., 2018), paleobotany (Contreras, 2018) and web technologies for the analysis and preservation of paleontological data (Valle Melón et al., 2019), represents a significant step toward standardizing 3D reconstruction workflows. However, their applicability remains confined to certain subfields. Based on the above review, a framework for a standardized workflow for paleontological reconstruction should be developed. This framework aims to standardize the reconstruction of fossils by providing guidelines and methodologies to researchers in the field. By synthesizing existing resources and incorporating technical advancements, this framework can enhance the efficiency and accuracy of paleontological reconstructions. Primarily, the framework should address tool selection and the advancement of raw fossil data visualization. Various techniques are available for characterizing 3D morphologies, including CT, μCT, and laser and optical scanning. However, each approach presents obstacles, particularly in terms of cost, time, and portability, when gathering data from multiple samples or under field conditions (Olsen & Westneat, 2015). Many studies have examined the advantages and disadvantages of various data collection methods, including their accuracy, efficiency, and reproducibility (Fahlke & Autenrieth, 2016; Hoffmann et al., 2014; Kouraiss et al., 2019).

Tomography has shown exciting potential for the internal investigation of fossils (Kouraiss et al., 2019). However, CT scanners vary in size and features, affecting scanning resolution, specimen size, duration, and cost. Medical CT scanners, which are available in diverse sizes, can handle large specimens, and are often accessible at no cost to certain hospitals. However, they may yield coarse resolutions for smaller fossils (Lautenschlager, 2017). Conversely, μCT scanners can provide higher resolution but have limitations in terms of specimen size, which is typically 20–30 cm. Their use may also involve additional expenses, either for scanning services or the acquisition of the scanner itself (Lautenschlager, 2017). Employing high-resolution scans enables the visualization of intricate external and internal structures, thereby facilitating the development of detailed 3D models of scanned entities (Hoffmann et al., 2014). CT scanning, including μCT, excels in reconstructing internal structures. Although it is feasible to derive external surfaces from CT scans, the process entails exceptionally long postprocessing durations, lacks photorealistic surface colors, and incurs high costs, rendering this approach less optimal for external 3D

surface generation than the alternative methods examined (Fahlke & Autenrieth, 2016). Surface scanning technologies such as laser or structured light scanners offer alternative options. However, these methods are limited to digitizing only the external surface (Lautenschlager, 2017). The comparison between microCT and conventional CT demonstrates the importance of context-specific tool selection in paleontological research. While microCT excels in resolving fine details in smaller fossils, conventional CT remains indispensable for larger specimens where resolution is less critical than the ability to scan the entire fossil. Future research should emphasize matching the scanning technology to the specific requirements of the specimen and study goals.

Access to the interior of fossils is not always necessary for paleontological studies. For fossils with straightforward morphologies such as non-cephalopod mollusc shells, typically only an external morphology is required. In such cases, alternative nondestructive 3D imaging methods can be utilized, such as surface scanning and photogrammetry techniques, which gather spatial and geometric data from a 3D surface at a distance. These methods are inexpensive and portable, with user-friendly equipment (Cunningham et al., 2014; Kouraiss et al., 2019). Manual photogrammetry exhibits a high level of reproducibility and is often preferred when the sole interest lies in the external surface of a specimen, particularly when operating within a limited budget. Although automated photogrammetry produces results similar to those obtained using manual photogrammetry, it often generates larger data volumes (Fahlke & Autenrieth, 2016). Furthermore, the price range for laser-scanning devices varies widely depending on the technical specifications. Structured light-based technologies offer good performance at low costs (Rocchini et al., 2001). Combining photogrammetry with laser scanning allows the capture of color information, resulting in highly realistic representations. Notably, photogrammetry can be performed using smartphones, achieving resolutions similar to those obtained through standard laser scanning. This accessible technique is promising for broad adoption (Falkingham, 2012). Stereo camera reconstruction is another useful method for surface data acquisition owing to its low cost, portability, and ease of operation. Image acquisition using this method is as simple as the photography of a specimen (Olsen & Westneat, 2015).

Considering the diverse applications, advantages, and constraints associated with raw fossil data acquisition tools, Falkingham et al. (2018) offered recommendations for standardizing the 3D data collection phase. They suggested ensuring the collection of 3D data for any pivotal traces essential was to the conclusions of a study and advocated high-resolution data acquisition to facilitate replication and further research by other scholars. Additionally, they advised against excessively fixating specific data acquisition methods, emphasizing the importance of prioritizing resolution and accuracy to meet the requirements for replicability and utility, regardless of the technique employed. Finally, they encouraged researchers to gather a significant amount of data to enrich their analyses and enhance scientific understanding (Falkingham et al., 2018).

In the future, the field of paleontology will most likely embrace the fundamental tenets of this proposal, which endorse the digital documentation of fossil specimens, utilization of 3D data for both communication and analysis purposes, adherence to best practices to ensure the perpetual accessibility of files for other investigators, and inclusion of associated data alongside publications (Clark et al., 2023; Falkingham et al., 2018).

4.3. Data archiving standard protocol in preprocessing & reconstruction

Additionally, this framework facilitates collaboration and knowledge sharing among researchers in the field. Paleontological heritage belongs to all mankind; in the near future, global sharing of fossil data will be realized. To address this inevitable trend, paleontological data analysis requires a set of feasible workflows and guidelines encompassing the standardization of data formats and the exploration of the feasibility of digital paleontological restoration processes. This standardized workflow framework focuses on improving the utilization and enhancing the functionalities of various open-source software packages during the preprocessing of raw fossil data, as well as standardizing file formats and sizes.

Hu et al. (2020) emphasized that the extensive capabilities and functionalities of open-source software have not been fully explored. However, only a limited number of software systems are available for 3D image segmentation, such as ZIB-Amira or those provided by μCT manufacturers. These systems can handle large datasets and offer algorithms for geometric reconstruction of multi-component structures (Hoffmann et al., 2014). The protocol and workflow developed by Hu et al. (2020) can serve as a framework for segmenting CT and other forms of 3D volumetric data. This advancement will facilitate interdisciplinary collaborations using the 3D segmentation of CT data. Thus, the objective in constructing this framework is to assist paleontologists in making informed decisions regarding appropriate techniques for standard purposes. This decision-making process considers factors such as the accuracy, reproducibility, and efficiency of each technique (Fahlke & Autenrieth, 2016).

Beyond software usage concerns, this standardized workflow framework must also address file format and size challenges to ensure seamless opening and editing of fossil data across all software platforms. Falkingham et al. Falkingham et al. (2018) presented a new standard protocol for data collection, presentation, and dissemination. In terms of formatting, it is crucial that the data are open and not reliant on proprietary software. The most common open formats for processed 3D data are *.PLY and *.OBJ, both of which can be accessed using any 3D software. Color information can be stored either directly, linked to each vertex (as in XYZ or PLY formats), or as a separate texture file. The STL format, which describes triangular surfaces in a 3D Cartesian coordinate system, is feasible and can be imported into various 3D analyses, model cutting, printing, and related software. Formats that hinder easy manipulation or extraction of data, such as 3D PDFs, should not be used for data dissemination (Falkingham et al., 2018). Falkingham et al. (2018) suggested transforming raw data obtained in a proprietary format, such as LiDAR or similar laser-scanning methods, into a more accessible format. For instance, converting raw laser-scan data into ASCII text files with XYZ vertices, luminance, and color values ensures accessibility for all researchers and guards against the risk of the proprietary format becoming outdated.

Considering the ongoing increase in digital storage capacity, Falkingham et al. (2018) advised against downsampling data unless it is absolutely essential. Meshes exported from 3D image-processing software can sometimes be large and computationally demanding. To address this issue, Meshlab and Autodesk Fusion 360 offer various methods for reducing the total file size. These include tools for eliminating excess components and simplifying the mesh. Alternatively, if only a surface structure is required, the internal faces and vertices can be demarcated and removed. Although these tools can reduce file size, they may also compromise the quality of the 3D model. Therefore, the approach and degree of file reduction must align with the desired image quality (Clark et al., 2023). In the study of Lautenschlager and Rücklin (2014), the resulting surface model was subsampled to 100,000 elements using Avizo to decrease the final file size. This process was performed using a simplification editor employing an edge-collapse algorithm.

4.4. Future trends and recommendations in paleontological digital reconstruction

Over the past decade, digital visualization, analysis, and reconstruction techniques have significantly transformed paleontological research. Their usage will expand further as hardware and software become more accessible and affordable. A major development will likely involve automation of these processes. Certain reconstruction and recovery techniques are laborious and rely on user expertise. Implementing algorithms to expedite and automate reconstruction can streamline interpretation and facilitate extensive large-scale research initiatives. The continual advancement of new protocols and computational methods within the virtual realm will unlock new horizons for studying ancient realities throughout the history of life (Pérez-Ramos & Figueirido, 2020). There is a broad range of possible applications for noninvasive methods, and more noninvasive methods should be applied in cephalopod and other invertebrate studies (Hoffmann et al., 2014). Cunningham et al. (2014) emphasized that, in the future, the declining costs and broader availability of CT scanners will likely grant more paleontologists access to these techniques. Sutton et al. (2016) believed that although other tomographic methods would retain certain applications, X-ray CT is expected to remain the primary method in virtual paleontology. Collaboration between

models derived from CT scanning and emerging analytical tools such as R software is driving advancements in virtual anthropology with the introduction of faster or automated reconstruction methods (Profico et al., 2018, 2019; Veneziano et al., 2018). Similarly, Das et al. (2017) introduced a rapid and cost-effective technique utilizing Kinect scanning modules to perform 3D scanning and replicate large paleontological specimens. This study exemplifies the practical application of cutting-edge technology in the paleontological field, showcasing the potential of innovative software and hardware solutions. Therefore, with the development and upgrading of open-source software, the future potential of digital technologies for paleontological research is huge. An increasing amount of software and technology will be applied to paleontological restoration in the future.

However, paleontological reconstruction will likely also evolve beyond the realm of paleontologists, necessitating a multidisciplinary approach. Consequently, the development of shared databases and the sharing of fossil data are imperative. Data, encompassing images, measurements, counts, and models, form the cornerstone of vertebrate paleontology (Uhen et al., 2013). Therefore, making the scanning resources and data more accessible is crucial for the future scientific use of CT scans (Racicot, 2016). Falkingham et al. (2018) provided a compilation of publications accompanied by the corresponding DOI/links to accessible 3D data in their paper. Their intention was to formally correlate the data with publications, facilitating future discoverability (Falkingham et al., 2018). Finally, it is necessary to enhance the exchange of knowledge among disciplines such as paleoanthropology, paleontology, and archaeology (Uldin, 2017). Furthermore, a growing number of paleontologists and paleoartists have strongly advocated for more deposition of basic research data in publicly accessible databases (Uhen et al., 2013). Promoting an attitude that encourages data generation and sharing can only benefit individuals, paleoichnology, and the broader paleontological community (Falkingham et al., 2018).

5. Conclusions

This study performed a systematic literature review on digital paleontological reconstruction. With the progress in science and technology in the future, the application of digital technology in the field of paleontology research will become increasingly extensive. The 3D digitization of fossils has surged in popularity in recent years, with 3D models now extensively employed for research, exhibition, and archiving objectives. Several digitization methods are available, including X-ray CT (including μCT), laser scanning (both stationary and handheld), and photogrammetry, which are the most commonly utilized techniques in vertebrate paleontology. This array of options poses a challenge for researchers, who must carefully consider which method best suits their particular objectives (Fahlke & Autenrieth, 2016). Therefore, the development of a framework for a standardized paleontological digital reconstruction working process is suggested. We concur with the assertion of Falkingham et al. Falkingham et al. (2018) that establishing a standard protocol for paleontological reconstruction is essential to ensure that data are recorded, presented, and archived in a way that is beneficial to both current researchers and future generations. In the future, virtual paleontology will solidify its position as a well-established and readily accessible technique (Sutton et al., 2016). Combined with the research status and development trend of 'virtual paleontology,' paleontology data sharing, dissemination, science popularization, and education will be possible worldwide. The interactive nature of virtual fossils renders them potent instruments for engaging the public. From various dimensions, the digital restoration in paleontology has great potential to influence science popularization. Paleontological restoration is bound to develop with higher accuracy. Virtual paleontology can be combined with art, and how paleontological restoration can carry more popular science efficacy and esthetic value will become the focus of future research.

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conceived and designed the study. Lu Zheng collected and analyzed the data and drafted the manuscript. Rosalam Che Me and Rahmita Wirza O.K. Rahmat critically reviewed the draft for significant intellectual content. The final version of the manuscript was approved by Rosalam Che Me for publication. All authors have read and approved the final work.

Authors' contributions

CRediT: **Lu Zheng**: Writing – original draft; **Rosalam Che Me**: Writing – review & editing; **Rahmita Wirza O.K. Rahmat**: Writing – review & editing.

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Data availability statement

The data that support the findings of this study are available from the corresponding author, Rosalam Che Me, upon reasonable request.

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