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Introduction and History

Abstract: We define virtual palaeontology as the study of three-dimensional fossils through digital visualizations. This approach can be the only practical means of studying certain fossils, and also brings benefits of convenience, ease of dissemination, and amenability to dissection and mark-up. Associated techniques fundamentally divide into surface-based and tomographic; the latter is a more diverse category, sub-divided primarily into destructive and non-destructive approaches. The history of the techniques is outlined. A long history of physical-optical studies throughout the 20th century predates the true origin of virtual palaeontology in the 1980s. Subsequent development was driven primarily by advances in X-ray computed tomography and computational resources, but has also been supplemented by a range of other technologies.

1.1 Introduction

Virtual palaeontology is the study of fossils through interactive digital visualizations, or **virtual fossils**. This approach involves the use of cutting-edge imaging and computer technologies in order to gain new insights into fossils, thereby enhancing our understanding of the history of life. While virtual palaeontological techniques do exist for handling two-dimensional data (e.g. the virtual lighting approach of Hammer et al. 2002), for most palaeontologists the field is synonymous with the study of three-dimensionally preserved material, and the term is used in this context throughout this book. Note also that the manual construction of idealized virtual models of taxa (e.g. Haug et al. 2012, Fig. 11), while very much a worthwhile undertaking, is not included in the concept of virtual palaeontology followed herein.

The majority of fossils are three-dimensional objects. While compression of fossils onto a genuinely two-dimensional plane does of course occur (Figure 1.1a), it is the exception, and in most preservational scenarios at

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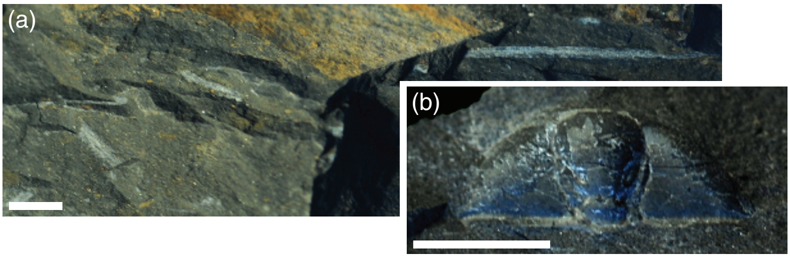

Figure 1.1 Dimensionality in fossils: (a) Completely two-dimensional graptolite fossils; genuinely two-dimensional fossils such as this are the exception. (b) A three-dimensionally preserved trilobite cephalon; most fossils exhibit at least partial three-dimensional preservation. Scale bars are 10 mm. Both specimens are from Lower Ordovician, Wales.

least an element of the original three-dimensionality is retained (Figure 1.1b). Three-dimensional preservation retains more morphological information than true two-dimensional modes, but typically this information is problematic to extract. Isolation methods, of which several exist, are one solution. Fossils may simply 'drop out' or be naturally washed out of rocks; wet-sieving of poorly consolidated sediments mimics this process. Specimens may also be extracted chemically, for example, by dissolving the matrix (e.g. Aldridge 1990). These approaches are effective where applicable, but are prone to losing associations between disarticulated or weakly connected parts of fossils, and to damaging delicate structures. Specimens can also be physically 'prepared' out using needles, drills or gas-jet powder abrasive tools (e.g. Whybrow and Lindsay 1990); while usually preserving associations, this approach may also damage delicate structures, scales poorly to small specimens, and cannot always expose all of a specimen. Finally, isolation of a fossil only provides access to its surface.

Correctly chosen, virtual palaeontological techniques can overcome many of the disadvantages of physical isolation methods, and bring many novel advantages too. Virtual specimens are typically more convenient to work with, requiring only a computer rather than expensive and lab-bound microscopes. They allow for virtual dissection and sectioning, where parts of the specimen can be isolated for clarity without fear of damage. They allow for mark-up, typically in the form of colour applied to discrete anatomical elements, which can greatly increase the ease of interpretation. They can be used as the basis for quantitative studies of functional morphology, such as finite-element analysis of stress and strain (e.g. Rayfield 2007), or hydrodynamic flow modelling (e.g. Shiino et al. 2009). Finally, as virtual specimens are simply computer files, they can be easily copied and disseminated to interested parties, facilitating collaborative analysis and publication.

Despite all these advantages, virtual palaeontology is not as widely used as it might be; one possible reason is that the techniques involved are perceived as 'difficult', and while there is no lack of technical detail available on individual techniques, no in-depth treatment and comparison of all available

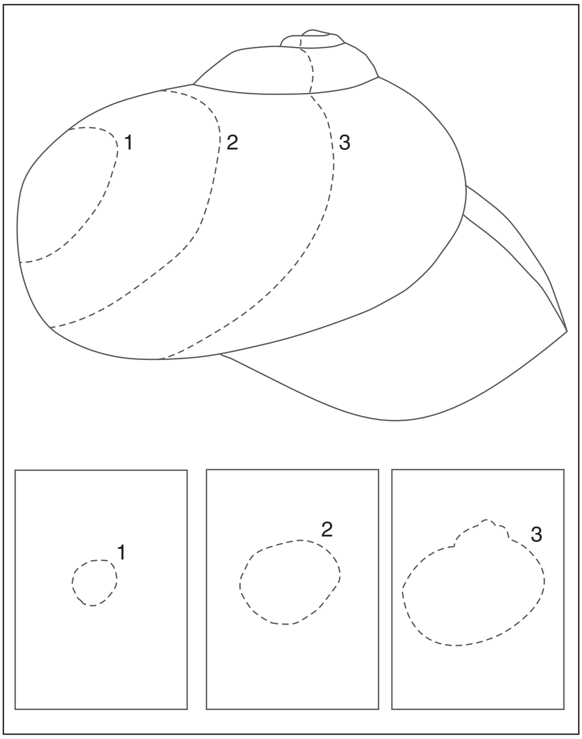

Figure 1.2 Tomography. Three parallel and evenly spaced serial tomograms (1–3) through an idealized gastropod fossil, and the resultant tomographic dataset. Modified from Sutton (2008, Fig. 1). Reproduced with permission of The Royal Society of London.

techniques exists, which can make the field intimidating to those entering it for the first time. This book aims to overcome this issue. It is intended to provide those interested in doing palaeontology through virtual methods, or in interpreting virtual data provided by other workers, with background theoretical knowledge and practical grounding. In particular, it aims to provide palaeontologists with the information they need to select an appropriate methodology for any particular study, to understand the pitfalls and limitations of each technique, and to provide suggestions for carrying out work with maximal efficiency. Theoretical concepts are covered with the intention of providing scientists with sufficient depth of understanding to develop and modify techniques, where appropriate.

Virtual palaeontological data-capture techniques can be divided most fundamentally into (a) tomographic (slice-based) approaches, and (b) surface-based approaches. **Tomography** is the study of three-dimensional structures through a series of two-dimensional parallel ‘slices’ through a specimen (Figure 1.2). In tomography, an individual slice-image is termed a **tomogram**, and a complete set of tomograms is (herein) termed a **tomographic dataset**. Any device capable of producing tomograms is a **tomograph**. Note that while the definition of tomography given above is the original one (derivation is from the Greek **tomos** – section, cut, slice and **graphein** – writing, imaging, study), in recent years this term has often been restricted to techniques where virtual tomograms are computed indirectly from projections, rather than imaged in a direct way. However, we consider our broader definition to be both more historically accurate and more useful, with all such techniques sharing much in common, especially with regards to reconstruction methodology. The term we prefer for tomographic techniques based on computation of virtual tomograms is **computed tomography**. Tomography can be divided into (a) destructive and (b) non-destructive (scanning) methodologies. The former include the long-established techniques of serial grinding, sawing, slicing, etc. (here grouped together as physical-optical tomography, Section 2.2), together with focused ion-beam tomography (Section 2.3). Non-destructive tomographic techniques are diverse, and include the many variants of X-ray computed tomography or CT (Section 3.2), neutron tomography (Section 3.3), magnetic resonance imaging (Section 3.4), and optical tomography (serial focusing – Section 3.5). Surface-based techniques are those where the geometry of an external surface is digitized in some fashion; they include laser-scanning (Section 4.2), photogrammetry (Section 4.3) and mechanical digitization (Section 4.4). This book concludes with an examination of the techniques and software available for specimen reconstruction and study (Chapter 5), a review of the applications of virtual models beyond simple visualization (Chapter 6), and a final overview and consideration of possible future developments (Chapter 7).

1.2 Historical Development

Virtual Palaeontology, in the sense used in this book, began in the early 1980s when the emerging medical technology of X-ray computed tomography was first applied to vertebrate fossils. The power of tomography to document and reconstruct three-dimensionally preserved material has, however, long been recognized, and modern techniques have a lengthy prehistory of physical-optical tomography (*sensu* Section 2.2), combined in some cases with non-computerized visualization techniques.

1.2.1 Physical-Optical Tomography in the 20th Century

Palaeontological tomography was introduced in the first years of the 20th century by the eccentric Oxford polymath William J. Sollas, who noted the utility of serial sectioning in biology and realized that serial grinding could provide similar datasets from palaeontological material. His method (Sollas 1903) utilized a custom-made serial-grinding tomograph capable of operating at 25 μm intervals, photography of exposed surfaces, and manual tracing from glass photographic plates. Sollas applied this approach with considerable zeal to a wide range of fossil material, and was able to demonstrate the fundamental utility and resolving power of tomography to a broad audience. He also described (Sollas 1903) a physical-model visualization technique in which tomograms were traced onto thin layers of beeswax which could then be cut to reproduce the original slice, stacked together and weakly heated to fuse them into a cohesive model. A quick-and-dirty approach to model-making, using glued cardboard slices rather than fused wax, was also in early use; while documentation is lacking, this appears also to be traceable back to Sollas.

Sollas was primarily a vertebrate palaeontologist, and it was in this field that his methods first became widely accepted, most notably in the seminal studies of Stensiö (1927) on the cranial anatomy of Devonian fish. From the mid-20th century, however, serial grinding became a well-established palaeontological technique, and was applied to a very wide range of fossil vertebrates, invertebrates, and plants. These applications are far too numerous to cite, but an excellent example of a group whose students embraced it with some degree of fervour is the Brachiopoda. Brachiopods are often preserved three-dimensionally and articulated with valves firmly closed, concealing taxonomically and palaeobiologically informative internal structures such as lophophore supports; following the pioneering work of Muir-Wood (1934), the use of manually traced serial sections to document these structures has become almost ubiquitous.

A range of serial-grinding tomographs, for the most part custom-built devices, have been used since Sollas's work (e.g. Simpson 1933; Croft 1950; Ager 1965; Sutton et al. 2001b); these have varied substantially in complexity, degree of automation, maximum specimen size and minimum grind-interval, although none have substantially improved on the original machine in the latter respect. Two major variants on the technique have also been important, both responses to the destructive nature of serial grinding. Firstly, acetate peels (Walton 1928, see Galtier and Phillips 1999 for a more modern treatment) have been widely adopted as a means of data capture, especially but not exclusively in palaeobotany. Peels provide a permanent record of mineralogy and can be combined with staining techniques to increase contrast between certain types of material; they have thus been viewed as superior to mere photography of surfaces. Peels do, however, bring a peculiar set of problems of their own (see Section 2.2.2.3), and their use has unfortunately rendered many historical datasets ill-suited to modern visualization methods. Secondly, serial sawing using fine annular or diamond-wire saws (Kermack 1970) became popular for larger fossils such as vertebrates in the latter quarter of the 20th century, as it allowed retention of original material (albeit at the cost of an increase in minimum tomogram spacing).

While physical-optical tomography was commonplace in the 20th century, physical model-making noticeably fell out of favour, considered perhaps to be too laborious and of doubtful scientific utility. Students of particular groups (e.g. brachiopods) became sufficiently familiar with tomograms to be able to integrate them into mentally conceived three-dimensional representations, and the potential benefits of being able to directly communicate these visualizations beyond the *cognoscenti* were arguably overlooked. Reconstructions from tomographic data, where published, typically took the form of idealized pictorial or diagrammatic representations from such mentally assembled models; while aesthetically pleasing and often gratifyingly simplified (for an example from palaeobotany see the cupule reconstructions of Long 1960), this form of reconstruction lacked objectivity. That said, physical models were undoubtedly difficult to assemble, fragile, difficult to transport and hard to work with; while some workers continued to use them (e.g. Jefferies and Lewis 1978), truly effective visualization was not eventually achieved until the advent of interactive virtual fossils at the start of the 21st century.

1.2.2 The CT Revolution

Tomography in palaeontology has seen an enormous rise in uptake in recent years – Figure 1.3 provides a graphical representation of the use of the term 'tomography' in the palaeontological literature. It shows a fairly steady rise for the 30 years between 1975 and 2005 (the drop in 1996 is probably a methodological artefact of the way the literature was indexed), followed by an upswing that is, to say the least, eye-catching. This phenomenon is, for the most part, a result of the increasing availability and popularity of X-ray CT, and we refer to it herein as the **CT revolution**. X-ray computed axial tomography (CT or CAT scanning) is a technology that arose as an advanced form of medical radiography in the early 1970s, taking advantage of the increasing availability of computing power together with technical and algorithmic advances. CT, its history and its derivatives are described in more detail in

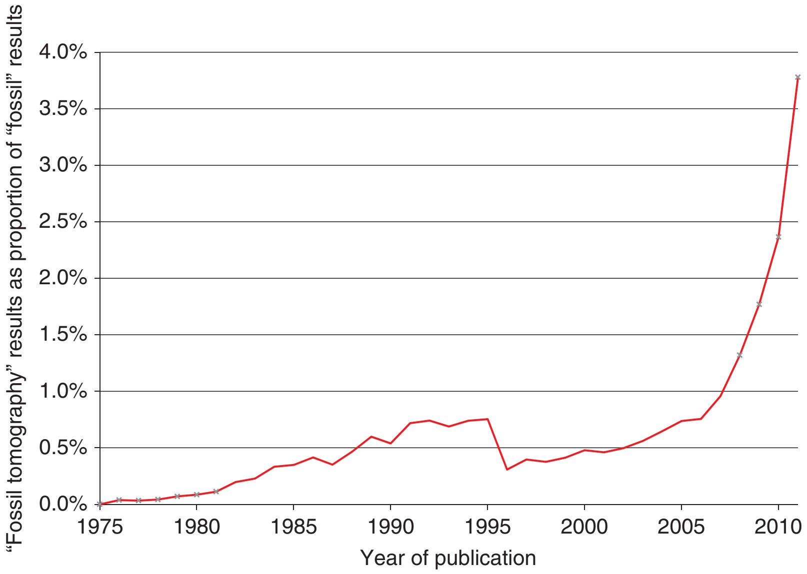

Figure 1.3 Relative increase in the importance of tomography in palaeontology from 1975 to 2011, as calculated by the ratio of publications including 'fossil' and 'tomography' to those only including 'fossil'. Data from Google Scholar (scholar.google.co.uk), July 2012. While these data inevitably include biases, they give a clear indication of trends. Note that the step down in 1996 is best interpreted as an artefact of the search engine.

Section 3.2. Many types of fossil material have long been known to be amenable to X-ray analysis (i.e. to have high contrast between fossil and matrix in terms of X-ray attenuation), and this form of non-destructive tomography thus clearly had palaeontological potential. Early machines were limited in availability and resolution, however, so it was not until 1982 that CT was first applied to vertebrate fossil material (Tate and Cann 1982, see also Conroy and Vannier 1984). Medical development of CT was accompanied by parallel development of visualization tools, and thus by the time these early studies were undertaken three-dimensional digital models, albeit in a somewhat limited form, could be reconstructed from the data. Arguably, the first high-profile palaeontological use of the technology was in a restudy of *Archaeopteryx* (Haubitz et al. 1988), and since the 1990s the technology has become increasingly commonplace for the study of the relatively large specimens typical of vertebrate palaeontology, many of which are suited for the range of scales handled by the readily available medical scanners. Serious study of invertebrate and other smaller fossils using CT did not begin until the 21st century (although see Hamada et al. 1991), with the advent of X-ray microtomography (XMT). Developed initially by Elliot and Dover (1982), XMT systems work on smaller scales, typically with resolutions down to a few microns. The palaeontological pioneers of XMT worked in the University of Texas High-Resolution X-ray Computed Tomography Facility (see e.g. Rowe et al. 2001 and www.digimorph.org), but the increasing availability of relatively low-cost laboratory or even desktop-scale scanners in recent years has resulted in a profusion of studies using XMT. Finally, the advent of X-ray tomography beamlines at third-generation synchrotrons (see e.g. Donoghue et al. 2006; Tafforeau et al. 2006) has provided facilities for extremely high-resolution and high-fidelity tomographic study of palaeontological material. Particularly in combination with methodological advances such as phase-contrast imaging, these facilities have enabled the study of otherwise intractable material in an unparalleled level of detail.

1.2.3 Modern Physical-Optical Tomography

Although the CT revolution has hugely increased usage of tomographic methods, it has not entirely swept away traditional physical-optical methods; rather, these have enjoyed a limited resurgence. Despite their destructive nature they remain, for some material, the most cost-efficient or even the only practical means of data recovery. The study of the invertebrate fossils of the Silurian Herefordshire Lagerstätte (Briggs et al. 2008) has provided the best example of this resurgence, demonstrating in a series of publications the power of serial-grinding tomography married to modern digital photography; Watters and Grotzinger (2001) provide a contemporaneous example of similar techniques applied to different material. The nature of existing physical-optical datasets, typically relatively sparse in terms of tomogram spacing, drove early experimentation with vector-based digital visualization (e.g. Chapman 1989; Herbert 1999), where manually or automatically traced structures were surfaced to produce reconstructions which were crude but low in polygon count and hence easily rendered on available hardware. Other ingenious but somewhat idiosyncratic approaches to visualization were also tried (e.g. Hammer 1999), but it was only with the application of the more medically mainstream approach of isosurface generation and rendering (see Chapter 5) to Herefordshire data by Sutton et al. (2001a, b) that genuinely high-fidelity virtual models from physical-optical data began to appear, the key ingredient simply being the collection of a large number of closely spaced tomograms. The isosurface approach has been the primary visualization tool used for all palaeontological tomographic datasets since that study, although direct volume rendering (e.g. Hagardorn et al. 2006) and vector surfacing (e.g. Kamenz et al. 2008) have found occasional applications.

1.2.4 Other Modern Tomographic Techniques

Other approaches to palaeontological tomography exist, of course, and are detailed in this book (see Section 1.1); they include magnetic resonance imaging (MRI), neutron tomography, optical tomography, and focused ion beam (FIB) tomography. All could fairly be described as niche techniques, and their history of application is, in each case, short. MRI is a medical scanning technology that was initially developed during the 1970s; while MRI tomograms are typically lower resolution than those generated by CT, radiation doses are lower, and for medical samples data acquisition can be faster and tissue differentiation better. None of these advantages are especially relevant to palaeontological material, however, and MRI often performs poorly on solid materials. Applications have hence been rare and primarily experimental in nature (Mietchen et al. 2008, although see Gingras et al. 2002; Clark et al. 2004 for practical applications). Neutron tomography utilizes neutron beams to perform tomography in a manner analogous to CT. Some studies have demonstrated limited utility, particularly in fossils preserving organic compounds (Schwarz et al. 2005; Winkler 2006), and the relatively weak absorption of neutrons by metal-rich rocks theoretically allows large and dense specimens, opaque to X-ray beams, to be studied. However, the relatively low resolution of the technique together with the limited number of facilities at which it can be undertaken have militated against a broad uptake. Optical tomography or serial focusing, typically but not exclusively using confocal microscopy, provides a very high-resolution non-destructive approach to tomographic data capture, albeit only for translucent samples and only on small scales. The optical techniques concerned have a long history, confocal microscopy originating in the late 1980s and less precise serial-focusing methods having existed long before; however, while confocal microscopy was first applied to fossils in the 1990s (e.g. Scott and Hemsley 1991; O'Connor 1996), applications of any optical tomography techniques to palaeontological material since have been sporadic (e.g. Ascaso et al. 2003; Schopf et al. 2006, Kamenz et al. 2008). Finally, focused ion beam (FIB) microscopes were developed primarily for use in material science in the late 1970s (see e.g. Phaneuf 1999); while they were originally used for imaging, the ion beam can also mill material, and hence they can be employed, somewhat laboriously, to perform nano-scale tomography. Although a smattering of studies has been published in recent years (e.g. Schiffbauer and Xiao 2009; Wacey et al. 2012), this approach has yet to see widespread application to fossil material.

1.2.5 Surface-Based Techniques

Surface-based digitization techniques represent an entirely different approach to virtual palaeontology (see Section 1.1); rather than relying on tomograms, these approaches digitize the topography of the surface of a specimen, and can also capture surface colour. While obviously inappropriate for looking inside physical objects, they represent a powerful set of techniques for performing virtual palaeontology on fossils where the surface morphology represents all or most of the preserved information. While a substantial portion of this book is devoted to these methods, their history of usage in palaeontology is brief.

Contact or mechanical digitization involves the use of a robotic arm equipped with sensors that can record the position of a tip in three-dimensional space; an operator can use this device to collect surface points over an object. Developed in the 1990s for a variety of digitization applications, this approach has been sporadically applied in palaeontology in the 21st century (Wilhite 2003; Mallison et al. 2009), although only to vertebrate fossils.

The majority of surface-based digitization has instead made use of laser scanning, a set of techniques where the reflection of a scanned laser-beam from a surface is used to record surface topography at distance. The technology was first commercialized in the 1980s for capturing human faces and later entire bodies for the animation industry, and the first relatively portable devices capable of rapid and precise scanning became available in the late 1990s; since then they have become increasingly cheaper and better specified. The first palaeontological application was by Lyons et al. (2000) in a study of part of a dinosaur skull; subsequently, a flurry of studies have used this approach on a range of fossils including vertebrates (Bates et al. 2009), footprints (Bates et al. 2008) and Ediacaran problematica (see e.g. Antcliffe and Brasier 2011). The technique is also in curatorial use for major museum-based digitization initiatives such as the **GB/3D type fossils online** project (Howe 2012), which, at the time of writing, is undertaking laser-scan digitization of a substantial proportion of all UK-held-type fossil specimens.

The other important surface-based approach to digitization is photogrammetry, in which three-dimensional models are assembled from a series of two-dimensional photographs of an object. Digital photogrammetry has a long pre-history that can be traced back to the origins of photography, and analogue photogrammetry has long been important, in cartography in particular (see e.g. Kraus 2007). The widespread use of stereo-pair images in palaeontology to provide a form of three-dimensional model can also be seen as a forerunner of true photogrammetry-based virtual palaeontology. As techniques have matured and digital photogrammetry has become available, in which models are automatically constructed direct from digitally captured images, a rapid expansion of applications has taken place; photogrammetry is now widely used in forensics and archaeology, for example. Palaeontological applications have hitherto been few, and predominantly concerned with dinosaur tracks (e.g. Breithaupt and Matthews 2001; Bates et al. 2009). However, recent developments in photogrammetric software (see Falkingham 2012) suggest that photogrammetry can be at least as effective as laser scanning in some palaeontological contexts, and the method can be expected to become increasingly important in the near future.

1.2.6 Historical Summary

The history of virtual palaeontology is relatively short when considered in its narrowest form. However, when considered with its precursors and related methods, it shows a long-standing appreciation in the palaeontological community of the value of three-dimensional data and models, despite the difficulties in actually obtaining them using older methods. The last decade has seen a remarkable rise both in the number of studies using virtual palaeontological techniques and in the breadth of techniques employed; this outpouring represents not simply the exploitation of newly available opportunities, but also the satisfaction of a long-present hunger amongst palaeontologists. Virtual palaeontology enables us to work with three-dimensional fossils not so much in a ‘way that we never knew we could’, more a ‘way that we always thought we should, but didn’t know how to’.

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