

Virtual palaeontology and the Herefordshire lagerstätte

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General principles and methods

Animals are 3-dimensional (3-D) objects but many fossils are only 2-D and restoration to 3-D is not easy, resulting in many mistakes. The Burgess Shale fossil *Hallucigenia*, for example was initially reconstructed upside-down and what were thought to be spines were legs. 3-D fossils are preserved better with a higher information content and reconstruction of 3-D morphology should be easier. One problem is their rarity. While 3-D hard parts are common, 3-D soft parts are much rarer, though they do occur. They are also hard to work with. 2-D fossils are easily handled but 3-D fossils need to be extracted from the rock and it may still be hard to look inside and poorly attached bits may be lost.

Chemical extraction, eg by dissolving limestones, works well for phosphatic forms such as some brachiopods but causes breakage and loss of associations. Physical extraction is laborious, skilled work and can break fragile structures and we can still only look at one surface.

Virtual palaeontology is the study of 2-D fossils as virtual representations of 3-D structures. It represents a radical new approach to working with fossils, which can be examined in stereo, rotated, zoomed, dissected and sectioned at will. There are no issues with damage, movement of elements and loss of associations. They can be marked up to aid interpretation and can be copied and disseminated at will to collaborators and for teaching and publication.

Virtual palaeontology allows access to otherwise impossible material such as that in the Herefordshire lagerstätte. It can also be used as a basis for computational analysis, eg finite element analysis modelling stress transmission in skulls or computational fluid dynamics to model flow over trilobites.

Tomography is 3-D imaging using a set of parallel cross-sections. A number of physical-optical techniques involving serial spalling, shearing, grinding and peeling have been used for over 100 years. The technique was first used by Sollas but the best known application was by Stensiö in the 1920s working on the brains of fossil fish. Modern computers have fuelled a major development .



Stensiö *Cephalaspis* brain – wax model from serial grinding

The Herefordshire lagerstätte

This is a sequence of soft-bodied fossils from the Silurian Wenlock (425Ma) of the Welsh borderlands. They are contained in nodules in a volcanic ash layer on a subsiding patch reef in the deepest marine environment. Preservation is in 3-D so the fossils as found are random cross-sections.

For reconstruction, there is no simple way to extract the fossils and they are not amenable to non-destructive testing. Serial grinding has, therefore, been used with physical-optical tomography. There are now datasets of hundreds of tomograms with structures down to about 10µm or less resolved.

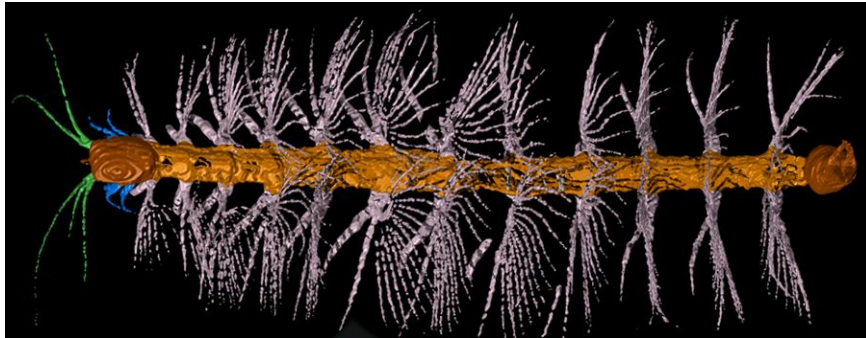
The fauna comprises 3,397 specimens, of which 25.7% were unknown. A broad range of taxa are represented, with sponges (157 species) being dominant, plus radiolarian, hydroids, molluscs, brachiopods and echinoderms. There is a very diverse, low-abundance tail, especially arthropods with 60-70 species in total. The fauna is dominated by benthos (mostly mobile benthos), though there are a reasonable number of swimmers, mostly nekitic-benthic with a few benthonic but no in-fauna.

Dibasterium durgae is a primitive horseshoe crab (?) with a typical carapace but the appendages are unexpected, the chelicerae being much bigger than in the modern group and multi-segmented. Other appendages appear to be biramous (2-branched). There are 7 pairs, so 14 in total, with walking legs like living forms but with new outer branches (exopods). These are the first convincing exopods in chelicerates and disprove the theory that exopods were restricted to crustacean and their relatives.



Dibasterium durgae

Enalikter aphson is a tailed brush-worm, which thinks it's an arthropod. Its primitive characteristics include a disc-like mouth, a simple 3-segmented head and a weakly sclerotised soft and flexible exoskeleton. Its advanced characteristics include biramous appendages, crustacean-like first antennae and a head capsule like some primitive crustacean. Its unique characteristics include pincers on the tail (for handling prey) and an anterior head=spine (possibly a sting). It is not a proper arthropod at all but is in one of the stem groups of megacheirans or 'Great Appendage Arthropods' which were around for most of the Palaeozoic. It extends their range with 3-D data from very near the base of true arthropods.

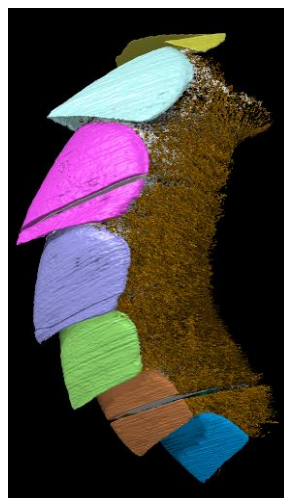


Enalikter aphson

There are 3 groups of molluscs:

- Polyplacophora – chitons;
- Aplousobranchia – shell-less molluscan worms; and
- Conchifera – common shelled molluscs.

There is no apparent fossil record for Aplousobranchians but chiton-like valves found in the Upper Cambrian were long assumed to be from chiton-like animals. Some recent fossil finds hint that not all were. *Acaenoplaxhyae* is an armoured molluscan worm with 7 chiton-like plates on its back and soft tissue serial repetition. It also has Aplousobranchian characteristics including a tubular body with no foot and a posterior respiratory chamber. It is suggestive of an Aplousobranchian/chiton link. *Phthipodochiton*, another worm-like and chiton-like animal from Girvan in Scotland has a spicule coating, which is probably complete ventrally so it has no foot. *Kulindroplax perissokomos* is a new chiton from the Herefordshire lagerstätte, which has shells on its back and spicules all the way around. It is unambiguously what was called a chiton in the Palaeozoic but its body is equally worm-like.



Kulindroplax perissokomos

There are 2 competing hypotheses for molluscan evolution. The first is that Aplacophorans are primitive and ancestral molluscs has no shell. The alternative is to find the split at the base is from Conchifera and Aplacophora (Acuifera) and Aplacophorans evolved from shelled molluscs. Aplacophorans now are shell-less remnants of a major Palaeozoic group. Support for Acuifera comes from using new fossil data and has implications for the placement of molluscs in the grand tree of life.

Methods in virtual palaeontology

Serial sawing	Physical-optical	Destructive	Tomography		
Serial grinding					
Serial slicing					
Focused ion beam (FIB) tomography	Optical	Non-destructive			
Confocal laser scanning microscopy (CLSM)					
Serial focusing with light microscopes					
Magnetic resonance imaging (MRI)	Rotational radiation transmission scanning	Non-destructive			
Neutron tomography				X-Ray (CT)	
Nano-CT					Attenuation-based
Micro-CT (XMT/ μ CT)					
Medical & industrial CT					
Synchrotron CT (SRXTM)					Phase-based
Synchrotron phase-contrast CT					
Lab-source phase-contrast CT					
Triangulation-based laser scanning	Active	Non-contact	Surface-based		
Time-of-flight laser scanning					
Phase shift laser scanning					
Photogrammetry					
Mechanical digitization					

Techniques for Virtual Palaeontology

Physical-optical tomography can be high resolution, has numbers of historical datasets, and can be the only predictive method. However, data reconstruction is difficult and time-consuming and the technique is destructive.

X-ray CT uses rotational transmission radiographs from a laboratory-based micro-scale to an engineering macro-scale. It is the most widely used technique, being relatively fast and cheap at a wide range of scales and producing relatively clean datasets. The results depend on X-ray contrast and there are some issues with the shape of the block, which needs to be equi-dimensional.

SXRMT uses a synchrotron source to produce very high resolution with usually less noise. Phase contrast enables imaging of low-contrast material but it is not widely available.

Optical tomography uses serial focussing with a microscope. It can be very high resolution ($<0.1\mu\text{m}$) and is fairly easy but it requires translucence and cannot go deep into the specimen.

MRI and Neutron tomography are readily available give a quick scan and potentially indicate chemical composition but they are difficult to use with geological materials. Neutron tomography is good with organic materials but is relatively low resolution and uses a radioactive source. Both of these are niche techniques.

Surface methods include laser scanning and photogrammetry. They are portable, have a large scale range, capture surface colour and are cheap. However, they capture the fossil surface only and there are some data quality issues.

There is now a toolkit of materials with lots of different techniques available. Almost all 3-D specimens can be digitised by at least one method and they are already changing the way we do palaeontology.

Publication of fossil descriptions is conventionally illustrated with photos or drawings, which are convenient to use but do not capture the full morphology. For 3-D models, publication has mostly followed the same approach. We could publish the underlying datasets alongside papers. This makes palaeontology more repeatable and makes studies of new material much easier. This would be analogous to the Genbank in genetics. The reasons it does not yet happen include:

- Cultural issues – “Why should I release data when others won’t?” This could be overcome by united data release research groups instead of data being issued by publishers;
- Technical issues relating to data type and data format and there is no perfect data format or agreement; and
- The lack of a single central repository.

Conclusions

The Herefordshire lagerstätte is a palaeobiological treasure trove which is a showcase for virtual palaeontology, which is now a mature set of technologies and techniques. It is already revolutionising the subject but there is still a lot of untapped potential.