Deep questions about the nature of early-life signals: a commentary on Lister (1673) ‘A description of certain stones figured like plants’

Martin Brasier†

Department of Earth Sciences, University of Oxford, South Parks Road, Oxford OX1 3AN, UK

In 1673, Martin Lister explored the preservation of ‘St Cuthbert’s beads’ plus other fossil crinoid remains from approximately 350 Ma Carboniferous limestone in northern England. He used taphonomic evidence (transport, disarticulation, burial and cementation) to infer an origin as petrified plant remains, in contrast with his views expressed elsewhere that fossil mollusc shells could have formed abiogenically, by ‘plastic forces’ within rock. Lister also observed pentagonal symmetry, now seen as characteristic of living echinoderm skeletons. A postscript from John Ray supports Lister’s ‘taphonomic’ observations and accepts the biogenicity of these fossil ‘vegetables’. Ray then concluded with a prophecy, predicting the discovery of comparable living fossils in remote ocean waters. These early discussions compare with current debates about the character of candidate microfossils from the early Earth and Mars. Interesting biomorphs are now tested against the abiogenic null hypotheses, making use of features such as those pioneered by Lister, including evidence for geological context, rules for growth and taphonomy. Advanced techniques now allow us to extend this list of criteria to include the nanoscale mapping of biology-like behaviour patterns plus metabolic pathways. Whereas the science of palaeobiology once began with tests for biogenicity, the same is now true for geobiology and astrobiology. This commentary was written to celebrate the 350th anniversary of the journal Philosophical Transactions of the Royal Society.

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1. Introduction

In this earliest known journal article on the science of palaeontology [1], we observe a great
devatncnt centurv naturalist—Martin Lister—grappling with the nature of fossils. Are these the
remains of formerly living organisms (now extinct) or could they have been produced without the
need for biology? As explored below, Lister made some crucial and insightful observations about
this dilemma, relating to the fields we would now call ‘taphonomy’ and ‘biogenicity criteria’. His
observations therefore presage current debates about the earliest signs of life on Earth and Mars
[2–7].

Although Lister (figure 1a) is now revered as an early expert on both mollusc shells and
spiders [8,9], his historically important paper concerns what we would now recognize as the fossil
remains of crinoids (‘sea lilies’; figure 1c–g), a largely extinct class of the phylum Echinodermata
that also includes sea urchins and star fish. Interestingly, the animal fossils he puts before us
were, at the time of writing, among the oldest known, being some 320–350 Myr old (Lower
Carboniferous). None of this was known to Lister, of course, for that took another couple of
centuries to emerge.

The title of Lister’s paper clearly sets out a major paradox: ‘A description of certain stones
figured like plants, and by some observing men esteemed to be plants petrified’ (my italics). The
puzzle concerns the existence within limestone rock of surprisingly complex disc-shaped ‘fossils’,
called St Cuthbert’s beads (figure 1c–g). This name reflects not only the presence of a central
hole in each disc but also their occurrence around sacred Northumbrian sites. Using his printed
words alone, we can readily sketch out the complex morphology he describes. We could even
identify some of his fossils with precision. But palaeontology also requires graphic evidence,
which Lister provides with an abundance of anatomical drawings (figure 1), turned into copper-
plate engravings (figure 2) by ‘my very good friend, Mr William Lodge’ (see [10]). These detailed
illustrations were able to demonstrate, for the first time, the range of variation to be found within
a single fossil group. The puzzle, however, was to ascertain how they were formed.

2. The figured stones hypothesis

We need to remember that the word ‘fossil’ comes from the latin word fossa (a ditch, or hole).
‘Fossil’ was therefore available for any noteworthy object dug from the ground, meaning that
it could be mineral, antiquarian or biological in origin. More importantly, there were two
contrasting views about what we now call ‘fossils’ at this time [8–12]. The first was of growth
within the Earth as ‘stones figured like plants or animals’ (as stated in Lister’s title), produced
as the outcome of enigmatic ‘plastic forces’ (figure 3a). A second major perspective saw fossils as
relics of previously living forms left behind by major changes in sea level (figure 3b, c).

The concept of fossils as in-between beings—halfway between the living world and minerals—
is arguably very ancient, traceable back through the Neo-Platonists of ancient Greece, and perhaps
to the Stone Age. Following the establishment of the Christian church in the fourth century AD,
plastic forces were more likely to be seen as the work of God the creator, holy men (miracles) or
demons (spells). The popular name of ‘St Cuthbert’s beads’ for the fossils described by Lister
[1] likely reflects such a mode of thought, in which holy beads were transformed into rock.
We can still encounter similar concepts today, in religion (e.g. Holy Communion), literature
(e.g. Harry Potter) and computer games (e.g. Mortal Kombat). Expectations of ‘shape-shifting’ and
transformation seemingly lie deep within the human brain.

During the seventeenth century, the plasticity of boundaries was being seriously explored,
leading some to test whether ‘fool’s gold’ (pyrite, iron sulfide) could be turned into metallic gold
[12]. Interestingly, Martin Lister undertook experiments with pyrite [24] and was fascinated by
its role in the formation of fossils [8]. Importantly for our story, the boundaries between inert
minerals and living matter were also thought to be porous. Thus, when Conrad Gesner, the
Swiss naturalist and bibliographer, first illustrated fossil shells alongside modern shells in 1565, a
popular inference was that both kinds could generate spontaneously within water or within rock.
Figure 1. Martin Lister and his ‘plant’ fossils of 1673. (a) Portrait of Martin Lister. (b) Handwritten first page of Martin Lister’s letter, as read before the Royal Society on 13 November 1673. (c) Numbered sketches hand drawn by Lister, here showing two fossil ‘rock plants’ (crinoid stems) from the Carboniferous limestone of Yorkshire, UK, with the specimen on the left showing evidence for ‘joyns’ (ossicles) ‘slipped and out of order’. (d) Carboniferous limestone fossils showing similar features. (e) Numbered sketches by Lister showing lateral and basal views of a ‘radix’ or ‘root’ (actually a fossil crinoid calyx), showing the bases of arm-like features (brachia), rows of polygonal plates around the calyx and a portion of the stem with its central canal. (e,f) Comparable fossil specimens showing similar features. (h) Numbered sketches by Lister showing a ‘pentagonous’ plate (on the left) and another from Northamptonshire, UK, with sculpture resembling an cidariid echinoid interambulacrum (on the right). (i) A comparable Jurassic echinoid test, adoral view. (Sources: (b,c,e) Copyright The Royal Society; (d,f,g,i) Oxford University teaching collections.) Scale bar, 50 mm (d,f,g,i).

[11,25]. This view was also supported by the eminent naturalist Athanasius Kircher [13], who regarded corals (a group we now regard as simple animals) as transitional between vegetable and mineral because they resembled flowers in shape but had mineral skeletons.
Figure 2. These copper-plate engravings appeared in Lister (1673) as figs. 1–37 of his ‘Tab. 1’ [1]. They are reversed from his original drawings. Loosely translating his descriptions [1], to make palaeontological meanings clearer, these show the following: 1, a single ‘joynt’ with very fine and small rays; 2, ‘joynt’ with ‘pith’ [central canal] bored through in the manner of a cinquefoil; 3, single oval ‘joynt’ with scarcely visible rays, and a small point in place of the ‘pith’; 4, single ‘joynt’ with a very large ‘pith’; 5, a pack of dislocated ‘joynts’ kept in the correct order; 6, a very long column having many smooth ‘joynts’ with the branches broken off; 7, a column with smooth ‘joynts’ and without branches; 8, the biggest column, with stumps of branches; 9, a smooth column with very smooth and numerous ‘joynts’; 10, one of the widest and most deeply ‘joynted’ pieces of a column; 11, a column with numerous poorly ordered knot-like ornaments; 12, a column with only a single row of ‘knots’ in the centre of each ‘joynt’; 13, a column with three rows of ‘knots’ on each ‘joynt’; 14, a smooth column, with each ‘joynt’ bearing a single large ridge around the middle; 15, ‘joynts’ that are alternately raised and depressed; 16, a double facet on the edge of each ‘joynt’; 17, alternate ‘joynts’ bearing edged facets; 18–20, certain other differences noted in the paper, but unclear in the engravings; 21, a column bearing a distinct side branch; 22, a branch broken off from a column; 23, a column shaped like a fruit; 24, a ‘sastigium or summits’ [possible echinoid spine]; 25, a root-like ‘radix’ [crinoid calyx] in lateral view: A shows a ‘joynt’ remaining ‘whence an Entrochos [column] was broken off’; C, E, F, D, show four of the double ‘feet’ [brachia], the rest being hidden from view; 26, the same ‘radix’, seen in plan view: A shows the broken off column; C, B, D, E, F show the five double ‘feet’ [brachia]; note also the hexagonal plates with roughened ornament, ‘which incrustate the stone or cover it all over’; 27, a smaller ‘radix’ [calyx] with smooth plates and five single ‘feet’ [brachia]; H, the top stone; I, one of the five ‘feet’ [brachia]; K, one of the five angular plates which ‘incrustate the middle of the stone’; G, the base; also the same stone seen from the side; G, the same with the hollow bottom facing upwards. The following figures are of plates that are supposed to ‘incrustate divers roots’ [i.e. plates of the crinoid calyx]: 28, a ‘pentagonous’ plate knotted; 29, a thin-edged, smooth ‘pentagonous’ plate; 30, an indented ‘pentagonous’ plate; 31, the Northamptonshire ‘pentagonous plate’ [possible echinoid interambulacral plate from the Jurassic]; 32, a large ‘pentagonous’ smooth plate; 33, a ‘hexagonous’ plate sculpted with ‘angles’; 34, a ‘hexagonous’ plate ‘as deep as broad’; 35, 37, oddly shaped plates; 36, a quadrangular plate, ribbed and indented. (Copyright The Royal Society.)
Figure 3. Three alternative hypotheses available for the interpretation of fossils in 1673. (a) The figured stones hypothesis of Kircher [13]: fossils found in rocks grow under the influence of 'plastic forces,' perhaps including cosmic influences; living invertebrates and algae may also grow by spontaneous generation. This view was preferred by Lister for his fossil molluscs [14–16]. (b) The biogenetic hypothesis of Steno [17–19] and Hooke [20]: fossils found in stratified sediments are explicable as the remains of once living organisms; unfamiliar groups (e.g. ammonites, crinoids) may yet be discovered in remote areas or the deeper ocean. This view was hinted at by Lister [1] and explicitly suggested by Ray [21]. (c) The biogenic–extinction hypothesis is similar to (b), except that unfamiliar fossils may now be explained by their extinction [22]. This possibility was actually mentioned by Lister [16] for some of his fossil molluscs. The subsequent addition of evolution [23] then brought thinking towards its modern stance.

In 1665, an important new line of evidence was provided by microscopic analysis, highlighted by Robert Hooke [20] in Micrographia. But even here, Hooke felt free to speculate on the spontaneous generation of plant and animal life from inorganic matter within a water butt [20,26]. Indeed, it took centuries for the concept of spontaneous generation to retreat towards the origins of life alone.

3. Towards the biogenetic hypothesis

The biogenetic hypothesis has deep roots. Greek philosophers, including Strabo, had noted seashells far inland and inferred that such areas had once been covered by the sea [12,26]. A later shift towards biblical thinking encouraged their interpretation as doomed relics of a pre-Flood world (literally ‘antediluvian’) or as remains left behind by the Flood itself (‘diluvial’). The expectation of stories within rocks therefore became one of an act of Creation, followed by decline and decay [12].

These early hypotheses were seriously challenged by the Danish anatomist Nicolaus Steno in 1669, within his book De Solido [17]. An English translation was published soon after by the Royal Society [18]. Travelling across Europe, Steno had observed layers of rock containing fossil remains, allowing him to conclude that the history of the natural world could be read layer by layer, with the oldest rocks at the bottom and the youngest at the top (‘the law of superposition’). He argued that his rocks were once aquatic sediments and, most importantly, that many fossils were the remains of plants and animals (figure 3b). In so doing, Steno provided the first great challenge to the figured stones hypothesis, noting that fossils did not resemble simple crystals but took on more complex shapes. Those near to each other seemed to be broken like shells on a beach, and now seemed to be in the process of disintegration, not of formation. Most famously, he also examined tongue-shaped fossils (‘glossopetrae’) and compared them with the teeth of modern sharks [19]. He thereby showed that ‘comparative anatomy’ with living forms could help to infer a biological origin for fossil forms.

Back in England, similar conclusions had already been reached by Robert Hooke in 1665, within the pages of Micrographia [20]. While much of Hooke’s work on fossils and fossilization...
was only published posthumously [27], *Micrographia* contains a very important comparison between the cellular fabric of living and fossil wood, and also makes plausible suggestions as to how they might have become petrified [20,26,28].

This article by Lister [1] therefore needs to be seen in the context of the ‘biogenic’ hypothesis of Hooke [20] and Steno [17–19]. Other ‘biogenic’ supporters within the Royal Society included Robert Boyle [29] and John Ray (21,30); see also [8,12]). Both Ray and Lister had collaborated with Steno while at Montpellier in France in 1668. But while Ray had become an advocate for the ‘biogenic’ origin of fossils, Lister is now seen as either a confirmed sceptic [12] or as sitting on the fence, arguing that ‘fossils were not always the remains of living creatures’ [8]. As explored below, Lister’s critical stance was arguably a prudent one for the time and remains so for modern debates about signals remote in time and space.

4. The crinoid paper by Martin Lister

We need to appreciate the huge list of unknowns for Lister and his colleagues in 1673. There was no accepted terminology for the chemical elements and minerals of which fossil remains were made. There was no agreement about the nature of sedimentary rocks, or the laws of stratigraphic succession. Nor was there a clear understanding about distinctions between plants and animals. No knowledge was available concerning the morphology of modern crinoids, and hence no appropriate terminology was available for use. And there was certainly no understanding about the phenomena of either extinction or evolution. Lister was therefore faced with trying to decode the remains of organisms (in this case, crinoids) wholly unknown to science as living organisms.

Despite these problems, the structure of Lister’s paper seems remarkably modern. The spellings, which can sometimes appear charming and idiosyncratic to modern eyes (e.g. ‘joynts’ for joints), belong to a time before those spellings were settled [31] and at least remain phonetic and recognizable. The paper might even pass today as the first draft of a research project written by a promising student. Using modern terminology, we can also divide Lister’s paper under the following headings: previous work; mineralogy and chemical composition; morphological terms used; localities visited; fossil size distribution; presence of natural fossil assemblages; evidence of growth, death and transport in fossils; species description and variation; numbered illustrations and figure descriptions. One might complain, a bit unfairly of course, that there is no geological map or stratigraphic column (the stratigraphic map was a later Lister invention [32]). It might also be criticized for being written in the first person, with an Almost random Scatter of capital Letters and italicized words, and then printed with elongated ‘f-like esses’. For a paper upon ‘fossils’, this can seem just a bit distracting, though all of this was completely normal for the time.

Fortunately, his descriptive features plus 37 illustrations (figure 2) clearly allow us to identify his fossils, gathered from the Craven district of Yorkshire, UK, as the calcitic remains of crinoid skeletons. He uses the term ‘Trochite’ for what we would now call a crinoid ossicle (figure 2, items 1–4), and the term ‘Entrochites’ or ‘Trochitae’ for collections of crinoid ossicles including what we would call columnals (from the stalk) and brachials (from the arms or brachia; see figure 2, items 5–21). Their calcareous composition he then demonstrates by their vigorous reaction to acetic acid (‘vinegar’; p. 6182, lines 1–5).

The bulk of the paper provides a detailed description of features (pp. 6184–6191) that were also illustrated (figure 2). Lister carefully assembles both his descriptions and images to show features of the curious, disc-shaped ‘joynts’ (ossicles) that characterized his fossils. Each had a central hole (‘hollows’ or ‘piths’), which in some was pentagonal (‘Cinquefoil’). They formed clusters, showing intervening sutures whose exterior profiles were smooth or ‘indented’. Adjacent ossicles could differ in size, shape and sculpture, forming complex alternating patterns, or be tapering from one end to the other. The outer surfaces of these ossicles could also be smooth, or sculpted by a single row of tubercles (‘knots in a circle’), or several rows of different sizes (‘this is huge pretty’), or be randomly placed. ‘Knots’ could also be replaced by a central ridge (‘joint rise’) or groove (‘double edge’) or a central swelling (‘swelled’). The ‘terminating’ junctions between ossicles were found to be smooth or sculpted by radiating ‘rayes’. While the bulk of these fossils
can be confidently identified as crinoids, a few appear to be echinoid fossils, including a cidariid spine (p. 6184, lines 34–38; see figure 2, item 24) plus an interambulacral plate provided with a sculpted boss (p. 6188, lines 11–20; see figures 1h,i and 2, item 31), both from the Jurassic of Northamptonshire, UK.

More complex fossils included ossicles (‘joynts’) arranged in columns that he found to ‘branch’ from a main ‘stemm’, with diameters getting progressively smaller as the branching proceeds (p. 6185, lines 1–13). By this stage in the paper, Lister was arguably thinking of a large and complex structure that seemingly had distinct rules for growth. Stranger still were his specimens of a crinoid calyx (figures 1e and 2, items 25–27), now known to house the main organs of the animal. Unlike Lister, we know that each calyx lies on top of the stalk and bears the branching brachials that caught the food. Lister describes his calices as having ‘the bigness of Walnuts’ and compares them with ‘a Pine Apple or Cone’. He correctly observes and clearly illustrates their construction from calcareous plates (figure 1e; cf. figure 1f,g), which encouraged him to infer that they were parts of a single ‘plant’—connected to the stalks and branches—though he incorrectly suggested they were ‘incrustations of roots’ that had become broken away (p. 6186).

It is especially interesting to observe Lister with respect to the rules for growth. He notes the ‘Cinquefoil’ pattern of the central canal in some stalk ossicles (fig. 2.2; p. 6186, lines 7–8). Some isolated pentameral plates he called ‘pentagonous’ (fig. 2.28–31; p. 6187, line 30 onward; p. 6188, line 1 onward.). He also noted a double row of five plates arranged around the calyx (figure 1e; fig. 2.26; p. 6186, lines 36–39), each plate being hexangular (p. 6187, line 1); and brachials in the form of ‘five single feet [arising] at equal distances’ around the calyx (p. 6186, lines 36–37). Although pentameral symmetry has since been regarded as a characteristic of the echinoderm phylum, it can also be found in plants. Together with the lily-like shape of crinoids, this may have encouraged him to refer to them as ‘plants’.

5. Lister’s biogenic dilemma

Lister [1] never mentions the work of Nicolaus Steno [17–19] nor does he mention the biogenic hypothesis directly here. This is curious, given that Lister is usually seen as a critic who questioned Steno elsewhere [9,12]. Throughout the paper, indeed, we gain rather the opposite impression—that Lister is pointing towards evidence for life, death, transport and burial. If this is a correct interpretation, then it could be argued that Lister was contemplating the significance of death and burial processes in the fossil record—the discipline called ‘taphonomy’ (e.g. [33]). For example, when reviewing the size and arrangement of ossicles, he makes observations that suggest they have been broken apart long ago:

They are all broken bodies; some shorter Pieces some longer, and some of them, indeed, Trochites, that is, but single joints…. And as they are all broken bodies, so are they found dejected and lying confusedly in the Rock, which in some places, where they are to be had, is as hard as Marble…. (p. 6182, lines 31–38, his italics)

Turning over a page, we see Lister making use of words that suggest he conceived of the fossils as having once been growing, provided with a living posture, then suffering injury and being transported and dislocated at the place of burial:

As to the injuries they have received in the removal from the natural posture, if not place of their growth, and formation, they are manifest. For, besides their being all broken bodies, we find many of them depressed and crushed… Again these stones…are many of them strangely dislocated; sometimes two, three, or more of the joynts in a Piece are slipped and out of order or rank, and sometimes a whole series of joynts, as when as pack of Crown pieces leans obliquely upon a Table. (p. 6183, lines 6–16; see also fig. 2.5)

To this he then adds a picture of the structures becoming twisted and suffering ‘injuries’:

Further, others I have that are twisted like a Cord, if this possibly may be reckoned amongst the injuries. (p. 6183, lines 16–18)
And later, he even gives us a tantalizing picture of life posture, death and transport:

Some...sare yet visible in their natural place and posture in the described stones: But I find
the greatest part of them broken up and heaped together in great confusion in the Rocks.
(p. 6187, lines 21–24)

Then, there come seminal observations suggesting that these fossils may have been buried in
sediment, and then cemented like a layer of bricks or by sparry calcite:

Lastly, some have their joynts [ossicles], indeed, even in file [columnals], but are yet stuffed
with a forrain [foreign] matter, as when bricks are layed in morter. (p. 6183, lines 18–20)
...the substance that covers them (if not the Stones themselves) is Sparr.... (p. 6186, lines
17–18)

An important conclusion here is that these could be different ‘species’ of plants:

there are many other differences to be noted.... Very probably because they are Parts or
Pieces of different Species of rock-Plants. (p. 6184, lines 2–4, his italics)

One interesting conclusion, therefore, is that Martin Lister thought of these as fossilized plants
(which, for him, may have included simple animals like corals) which had once lived on the
rocks. There is an alternative view, however: that by ‘rock-Plant’, he actually meant a fantastic
kind of plant that could grow within the rocks by a process of spontaneous generation [8]. While
he leaves it moot, Lister was clearly faced with a dilemma. Of the five-rayed central canal seen in
some ossicles, for example, he reveals his puzzlement:

This is most surprising and I know not of any Vegetable, whose Pith is perforate in such a
manner. (p. 6186, lines 10–12)

6. John Ray and living fossils

The deeper meaning of these fossils was further hinted at in a short postscript by John Ray
[21]. This naturalist had collected similar fossil remains from Lindisfarne, and he may well
have encouraged Lister to prepare a personal report [8]. Here, Ray recalls his earlier travels
to Malta (in the steps of Steno), where he saw branched and stick-like fossils that resembled
rock plants (possibly *Thalassinoides* crustacean burrows from the Miocene). Ray then points out
the need to understand the rules for growth within living (and, by implication, fossil) plants,
through the analysis of both branching and taper. Importantly, he reinforces Lister’s taphonomic
model, with evidence for breakage, stating that ‘Those Roots [calices and brachials], that you
have observed, are a good argument, that these Stones were originally pieces of Vegetables’ [21].
Equally prophetic was his final section, in which he wonders whether such organisms might be
found living attached to rocks on the seafloor today, predicting that they might yet be trawled up
by fisherman [21].

Ray was therefore speculating about what we would now call ‘living fossils’ (figure 3b). Final
confirmation of stalked crinoids—living fossils—in deep waters had to wait for almost another
century [34].

7. Towards biogenicity criteria

Piecing together the observations and interpretations made by Martin Lister [1] and John Ray [21],
we can now highlight four basic rules for the biogenicity of candidate fossils which date right back
to the very start of the discipline. Such tests still remain important for calibration of the fossil
record. They are especially required at the start of a palaeontological field, when the rules can otherwise seem unclear, as in the search for life’s origins in the early rock record (e.g. [3,4,26,35]). Much hangs on this, because fossils tend to become increasingly scarce as we dig ever deeper into the past. A single reliable fossil from deep time can therefore wholly transform our understanding of biosphere history.

(a) An appropriate null hypothesis

This rule comes first because it allows palaeobiologists to set up a hypothesis which will prevail until proved false (loosely adapting the framework of Karl Popper; see [36]). Any newsworthy, and culturally challenging, interpretation must therefore be tested against a less exciting interpretation. This ‘null hypothesis’ is usually regarded as the ‘most boring explanation’. It is boring precisely because it is thought to have a higher probability of being correct. As the Royal Society motto still says: ‘take nobody’s word for it’.

For Martin Lister in 1673, the null hypothesis was that his fossils formed by abiogenic, plastic forces within rock [8], as caricatured in figure 3a. This was also the view of Kircher [13] and it prevailed for some decades afterwards, following the ideas of Oxford ‘chymist’ Robert Plot [8,37]. While Lister’s choice of words shows that he was willing to play with the concept of petrified plants, he also found it much harder to accept the idea of fossilized animals. Elsewhere, Lister [38] noted that the character and mineralogy of fossil shells differed from living forms, and also reflected the character of individual quarries, both correct observations in themselves. Suspecting plastic forces at work, he tried growing mollusc shells within beakers of mineral solution mixed with the body juices of molluscs [8,12]. His preferred conclusion about fossil molluscs, therefore, was that variations in size and state of preservation were the product of different stages of formation inside the rocks [12,14,15]. Rather tellingly, though, he also wrote that ‘Either these [molluscs] were terriginous [i.e. formed by plastic forces], or, if otherwise, the animals they so exactly represent have become extinct’ [16]. It seems that his mind was therefore open to the hypothesis shown in figure 3c.

By the eighteenth century, plastic forces were giving way to biblical narratives [12], and the remains of Noah’s Flood were therefore being pursued by leading ‘diluvial’ geologists, such as William Buckland, well into the nineteenth century [11,12]. The ever-growing demand for mineral resources during the industrial revolution, however, led towards the discovery of an increasingly thick pile of ancient sediments, punctuated by more changes in sea level than expected from the diluvial theory [22].

There then followed a succession of fashionable null hypotheses for the earliest signs of life. The laying of Atlantic cables from 1856 onward led towards an obsession with deep sea life and hence with the antiquity of foraminiferid protozoans [35]. Such a hypothesis was seemingly confirmed by reports of complex, foram-like structures called *Eozoon* from the Precambrian of Canada. Although *Eozoon* was hailed by Darwin [23] as an early fossil, it was later shown to be abiogenic, formed by self-organization during metamorphic mineral growth [26]. Lister’s dilemma had returned.

A cyanobacteria-centred hypothesis followed later, including the global search for Precambrian stromatolites, and cyanobacteria-like microfossils (figure 4b) [26,40,47,48]. The search for life on Mars during the Viking expeditions of 1976 (e.g. [6]) was arguably influenced by such a ‘cyanosphere’ perspective.

There then came a major twist, following high-profile debates about bacteria-like signals and ‘Martian microfossils’ within meteorite ALH 84001 (figure 4a) [2,3]. A major concern of the critics was that bacteria-like mineral growths can also be generated abiogenically, within populations of complex self-organizing physico-chemical systems [5,49,50]. It has further emerged that complex stromatolite fabrics can likewise result from physical processes [48,51]. More crucially, some of the earliest candidate microfossils—once compared with cyanobacteria [3,47]—are now interpreted as abiogenic mineral growths [4,5,52–54]. Finally, it has been found that cyanobacteria are not
Figure 4. A conceptual framework for the critical testing of early fossil claims may follow this ‘cone of contention’ structure, as suggested elsewhere [39]. Fossils expand in abundance as the fossil record proceeds and as more complex forms emerge. The favoured null hypothesis may likewise shift with time, with (a–e) illustrating some ‘controversial’ fossil candidates of progressively younger age. (a) Approximately 4.0 Ga prokaryote-like structures from Mars (ALH 84001) [2] that were challenged by an abiogenic null hypothesis (e.g. [3]); (b) 3.46 Ga Archaeoscillatoriopsis disciformis from the Apex chert, at first compared with prokaryotes [3] that were later challenged by an abiogenic null hypothesis [4]; (c) 1.88 Ga complex microfossil Eosphaera from the Gunflint chert, usually regarded as of problematic affinity [40] but sometimes suggested to be a eukaryote cell colony [41]; (d) approximately 600 Ma complex microfossil Megaspheara from the Doushantuo Formation, whose stem-group metazoan (animal) embryo interpretation [42] has been challenged by a prokaryote hypothesis [43] and a protistan eukaryote hypothesis [44]; (e) 560 Ma complex megafossil Charnia, long regarded as cnidarian but whose animal affinities have been questioned [45,46]; (f) the Carboniferous crinoid whose biogenicity was at first considered moot by Lister [1] but is now interpreted as the remains of an extinct echinoderm. Scale bar is 1 μm (a), 40 μm (b), 10 μm (c,d), 30 mm (e).

a basal eubacterial group at all, but are relatively young and derived [55]. This ‘cyanosphere’ perspective is therefore extinct.

Early life science has now turned full circle, to embrace again the abiogenic null hypothesis. For biomorphs older than 3.0 Ga, it seems prudent not to accept them as biogenic until plausible abiogenic origins have been tested and falsified [4,5]. Comparable abiogenic tests likewise remain important for many younger Precambrian fossils [56,57]. Where biogenicity of early fossils is less in question, the chosen null hypothesis may then move upwards along a conceptual ‘cone of contention’ (see figure 4, adapted from [39]). Such a framework requires the rejection of prokaryote (e.g. bacterial) affinities in the first place, and then of simple eukaryote (e.g. protozoan and algal) affinities, before moving towards acceptance of the much sought-after but highly controversial category of early metazoan. Examples of current debates along these lines (figure 4b–d) [41–46] are here illustrated alongside Lister’s drawing of a problematic fossil (figure 4e). Lister’s dilemma is therefore back in favour.
(b) A fully mapped context

The ability to tell biogenic from abiogenic structures is greatly aided by ‘geological intelligence’: the geological and mineralogical context of a candidate fossil, mapped at scales from kilometres to nanometres. Only in this way can a reliable narrative be constructed that passes along a time-line trajectory that broadly runs: 1, sediment deposition; 2, burial; 3, folding and metamorphism; 4, uplift and weathering. Fossils should, of course, be indigenous (initiated during phase 1) and may well show signs of modification that are distinct for each of phases 2, 3 and 4.

For Lister in 1673, the importance of context was only just emerging, and few clues were available. Although he made references to fossil localities that now allow us to place them on modern geological maps, they were rather scant. Other writings of Lister [14] more clearly highlight the finding of distinct fossils at different quarries. And while we now tend to think of William Smith as the father of stratigraphy in 1815 [58], Lister had the sagacity to promote this line of thinking [15,22,32], suggesting that distinctive stratigraphic units could be mapped to reveal their continuity across a country: ‘if it were noted how far these (Chaulk, Flint, Pyrites, Sandstone, Turf, Coal, etc.) extended, and the limits of each Soil appeared upon a Map, something more might be comprehended from the whole…than I can possibly foresee, which would make such a labour very well worth the pains’ [15].

Geological context is now fundamental for testing for all early fossil claims. It not only allows candidate fossils to be placed on a time line but also tests whether the conditions of formation were likely to have been conducive to life. Recent examples of this approach include geological mapping at the kilometre scale of the ‘questionable microfossils’ from the 3.46 Ga Apex chert [4,52–54,62] as well as new candidate fossils from the 3.43 Ga Strelley Pool arenite [61,63], accompanied by petrographic and geochemical mapping of fabrics down to the nanometre scale. Without such evidence for a viable context plus an indigenous origin, the abiogenic null hypothesis cannot be falsified convincingly.

(c) A well-defined morphospace

Biological structures tend to occur in populations that show distinct and measurable rules for growth. These can be mapped, quantified, mathematically modelled and then placed onto a theoretical morphospace diagram. Such analysis will typically show that biological groups occupy distinct portions of a given morphospace.

Interestingly, the rules of growth for both living and fossil echinoderms were being observed and pondered by both Lister and Ray [1,21], including the presence of calcitic skeletons and pentameral symmetry. Lister also pioneered the study of mollusc shell geometry [14,15]. Such work ultimately led to the computation of a ‘Raupian’ morphospace in which bivalve, gastropod and cephalopod molluscs can now be seen to occupy distinct domains [64].

Morphospace analysis has latterly become a valuable tool for the testing of problematic relationships in very ancient fossil groups, such as Ediacaran fronds [45]. There currently remains, however, a pressing need to better characterize the nature of abiogenic morphospace and to contrast this with living examples. Over recent decades, for example, it has become clear that complex biology-like structures can be generated by wholly abiotic processes, including self-organizing systems (SOSs) involving mineral growth [49]. Such abiogenic SOSs include bacteria-like filaments [50], stromatolites and wrinkle-mats [51], microscopic trace fossils [65] and sponge-like spicules [57]. One interesting conclusion, therefore, is that Martin Lister was conceptually correct. Complexity alone is not a reliable biogenic signal.

(d) Evidence for taphonomic behaviour

Both Lister [1] and Ray [21] clearly appreciated that fossils must often be reconstructed from separated components. This means that populations, not single specimens, are often required
for the reconstruction of long-extinct organisms. Lister also realized that truly biogenic remains should show something like the following taphonomic trajectory: life posture—growth—death—transport—breakage—burial—decomposition—mineral replacement and infilling. For his fossil crinoid remains (figures 1 and 2), this trajectory was easy to read. Fossil molluscs and brachiopods are less inclined to breakage, however, making their taphonomic trajectory harder to decipher. That could explain, in part, why Lister was more inclined towards an abiogenic hypothesis for his fossil molluscs.

Evidence for a taphonomic trajectory is an important criterion for current early biosphere studies. We might expect such evidence to be incomplete or lacking within structures formed abiogenically within rocks, either by plastic forces (as Lister confronted [1]) or by mineral growth, including crystals (as we still confront [59,65]). The absence of a taphonomic trajectory within controversial biomorphs from the 3.46 Ga Apex chert [5] may therefore be significant. It contrasts with clear evidence for taphonomic patterns now being found between different microfossil taxa within the 1.88 Ga Gunflint chert [60,66].

8. Future developments

Biosignatures are now fundamental tools for reconstructing the ways in which our habitable planet was built (‘geobiology’), and they are increasingly being explored as signals beyond the Earth (‘astrobiology’) [6,7]. Criteria for testing the biogenicity of such signals are therefore becoming ever more urgent and more rigorous, the latter made possible by significant advances in the use of high-resolution techniques (e.g. laser Raman; nano-secondary ion mass spectrometry or nanoSIMS; focused ion beam-transmission electron microscopy or FIB-TEM; time-of-flight secondary ion mass spectrometry or ToF-SIMS; synchrotron) [56]. Such techniques currently allow the mapping of morphology, ultrastructure, geochemistry and isotopes at the nanometre scale [60]. The quality and density of information about ancient life, and of possible distant life, now seems destined to grow at an exponential rate.

Technical advances (including those on robotic missions) are therefore allowing us to test for an ever wider range of biological and taphonomic features within candidate ‘biomorphs’. Hence, old and new search criteria can be usefully brought together to form a structured and practical checklist, of the kind now being used by geobiologists. Of these criteria, rules 1–4 relate to issues anticipated within Lister [1] and Ray [21], while rules 5 and 6 look towards advances in nanotechnology and imaging. Adherence to criteria of this kind will hopefully help to stimulate high-resolution analysis of biology-like behaviour and of biology-like metabolic pathways in early and remote fossil candidates (e.g. [60,67]).

9. Conclusion

In 1673, the biological nature of fossils was a highly controversial matter. Kircher [13] had argued that they formed by means of abiogenic ‘plastic forces’ within the rock. Hooke [20] and Steno [17] suggested that they were the remains of living organisms. Martin Lister [1] was seemingly the first to explore the ways in which direct observation could help to show whether fossil remains (in this case, Carboniferous crinoids) had grown abiogenically within the limestone or whether they had once formed part of a formerly living biological population. Prophetically, he achieved this by using the earliest known example of taphonomic reasoning in a scientific paper: that fossils of biological origin should show various lines of evidence, including those for life posture, growth, death, transport, breakage, burial, decomposition and subsequent mineral replacement and infilling.

Interestingly, abiogenicity has recently returned as a core null hypothesis. Falsification of abiogenicity now lies at the very heart of scientific debates about early life and the fossil record [5]. Taphonomic observations, such as those inferred by Lister, therefore continue to inform studies
of the earliest signs of life on Earth [60]. In future, should biomorph-like signals ever be obtained from the surface of Mars, or from the icy moons of Titan, Europa and Enceladus (e.g. [6,7]), then science will have good cause to reflect again upon Martin Lister and his great dilemma of 1673.

Author profile

Martin Brasier passed away on 16 December 2014, shortly after this article was accepted. He was Professor of Palaeobiology at the University of Oxford where he was also a Fellow of St Edmund Hall. His research aimed at decoding the early history of life by trying to understand big transitions in the fossil record, which involved comparing recent and ancient ecosystems using innovative high resolution techniques. He worked on the earliest well-preserved fossils of cells, mapping the earliest life on land, and the development and evolution of Ediacaran to early Cambrian organisms.

References

1. Lister M. 1673 A description of certain stones figured like plants, and by some observing men esteemed to be plants petrified. Phil. Trans. 8, 6181–619. (doi:10.1098/rstl.1673.0061)
2. McKay DS, Gibson Jr EK, Thomas-Keprta KL, Vali H, Romanek CS, Clemett SJ, Chilier XDF, Maechling CR, Zare RN. 1996 Search for past life on Mars: possible relic biogenetic activity in Martian meteorite ALH84001. Science 273, 924–930. (doi:10.1126/science.273.5277.924)
3. Schopf JW. 1999 Cradle of life. The discovery of Earth’s earliest fossils. Princeton, NJ: Princeton University Press.
4. Brasier MD, Green OR, Jephcoat AP, Kleppe AK, Van Kranendonk MJ, Lindsay JF, Steele A, Grassineau NV. 2002 Questioning the evidence for Earth’s oldest fossils. Nature 416 76–81. (doi:10.1038/416076a)
5. Brasier MD, McLoughlin N, Green O, Wacey D. 2006 A fresh look at the fossil evidence for early Archaean cellular life. Phil. Trans. R. Soc. B 361, 887–902. (doi:10.1098/rstb.2006.1835)
6. Gilmour I, Sephton M (eds). 2004 An introduction to astrobiology. Cambridge, UK: Cambridge University Press.
7. Hazen R. 2005 Genesis. The scientific quest for life’s origin. Washington, DC: Joseph Henry Press.
8. Roos AM. 2011 Salient theories in the fossil debate in the early Royal Society. The influence of Johan Van Helmont. In Controversies within the scientific revolution (eds M Dascal, VD Boantza), pp. 151–170. Amsterdam, The Netherlands: John Benjamins Publishing Company.
9. Roos AM. 2011 Web of Nature: Martin Lister (1639–1712), the first arachnologist. Leiden, The Netherlands: Brill.
10. Unwin RW. 1995 A provincial man of science at work: Martin Lister, FRS and his illustrators 1670–1683. Notes Rec. R. Soc. Lond. 49, 209–230. (doi:10.1098/rsnr.1995.0024)
11. Rudwick MJ. 1976 The meaning of fossils: episodes in the history of palaeontology. Chicago, IL: University of Chicago Press.
12. Cutler A. 2003 The seashell on the mountaintop. London, UK: Arrow Books.
13. Kircher A. 1665 Mundus Subterraneus in XII Libros Digestus; quo Divinus Subterrestris Mundi Opificium. Amsterdam, The Netherlands: Joannem Janssonium.
14. Lister M. 1678 Historia Animalium Angliae tres Tractaus. Unus de Araneis. Alter de Cochleis tum terristribus tum fluviatilibus. Tertius de Cochleis marinis. Quibus adjectus est Quartus de Lapidibus eiusdem insula ad Cochlearum quandum imaginem figuratis. Memoriae et Rationi. London, UK: John Martyn.
15. Lister M. 1684 An ingenious proposal for a new sort of Maps of Countrys, together with Tables of Sands and Clays, such chiefly as found in the North parts of England, drawn up about 10 years since, and delivered to the Royal Society, Mar. 12 1683 by the Learned Martin Lister M.D. Phil. Trans. 14, 739–746. (doi:10.1098/rstl.1684.0067)
16. Lister M. 1685–92 Historia Conchyliorum. London, UK.
17. Steno N (Stenonis N). 1669 De Solido intra Solidum naturaliter Contento Dissertationis Prodromus. Florence, Italy: Jacobum Moukee.
18. Steno N (Stenonis N, translated by Henry Oldenberg). 1671 The Prodromus to a Dissertation Concerning Solids Naturally Contained within Solids. Laying a Foundation for the Rendering a Rational Account both of the Frame and the several Changes of the Masse of the Earth, as also of the various Productions in the same. London, UK: Royal Society.
19. Steno N (Stenonis N). 1667 Elementorum Mologiae Specimen, seu Musculi description Geometrica, cui accedit Canis Carchariae dissectum Caput, et Dissectus Piscis ex Canum genere. Florence, Italy.
20. Hooke R. 1665 Micrographia, or some physiological descriptions of minute bodies made by magnifying glasses, with observations and inquiries thereupon. London, UK: Royal Society.
21. Ray J. 1673 Untitled extract of letter, as postscript to Lister (1673). Phil. Trans. 8, 6190–6191.
22. Lyell C. 1850 Principles of geology. London, UK: John Murray.
23. Darwin C. 1872 On the origin of species, 6th edn. London, UK: John Murray.
24. Roos AM. 2004 Martin Lister (1639–1712) and fools’ gold. Ambix 51, 23–41. (doi:10.1179/amb.2004.51.1.23)
25. Palmer D. 2003 Fossil revolution: the finds that changed our view of the past. London, UK: Collins.
26. Brasier MD. 2012 Secret chambers: the inside story of cells and complex life. Oxford, UK: Oxford University Press.
27. Waller R. 1705 The posthumous works of Robert Hooke MD, FRS, Geom. Prof. Gresh. Etc. Containing his Cutlerian Lectures and other discourses read at the meetings of the illustrious Royal Society. London, UK.
28. Jardine L. 2004 The curious life of Robert Hooke: the man who measured London. London, UK: Harper Perennial.
29. Boyle R. 1673 Essays of the strange subtlety determinate nature great efficacy of effluviums. Also an essay, about the Origine and Virtue of Gems. To which is added the prodromus to a dissertation concerning solids naturally contained within solids giving an account of the earth and its productions. By Nicholaus Steno. English’d by H.O. London, UK.
30. Ray J. 1673 Observations topographical, moral and physiological, made in a journey through parts of the Low Countries, Germany, Italy and France; with a catalogue of plants not native to England. London, UK.
31. Howard-Hill TH. 2006 Early modern printers and standardization of English spelling. Mod. Lang. Rev. 101, 16–29.
32. Hunter M. 1995 Science and the shape of orthodoxy: intellectual change in late seventeenth-century Britain. Woodbridge, UK: Boydell and Brewer.
33. Behrensmeyer AK, Kidwell SM, Gastaldo RA. 2000 Taphonomy and paleobiology. Paleobiology 26, 103–147. (doi:10.1666/0094-8373(2000)26[103:TAP]2.0.CO;2)
34. Amezniane N, Roux M. 1997 Biodiversity and historical biogeography of stalked crinoids (Echinodermata) in the deep sea. Biodivers. Conserv. 6, 1557–1570. (doi:10.1023/A:1018370620870)
35. Brasier MD. 2009 Darwin’s lost world: the hidden history of animal life. Oxford, UK: Oxford University Press.
36. Okasha S. 2002 Philosophy of science. A very short introduction. Oxford, UK: Oxford University Press.
37. Plot R. 1676 The natural history of Oxfordshire. Oxford, UK: The Theatre Press.
38. Lister M. 1671 A letter confirming the observations in no 74 about Musk scented Insects; adding some notes upon D. Swannerdam’s book of Insects and on that of M. Steno concerning Petrify’d Shells. Phil. Trans. 6, 2281–2284. (doi:10.1098/rstl.1671.0050)
39. Antcliff J, McLoughlin N. 2009 Deciphering fossil evidence for the origin of life and the origin of animals; common challenges in different worlds. In From fossils to astrobiology (eds J Seckbach, M Walsh), pp. 211–232. Dordrecht, The Netherlands: Springer.
40. Barghoorn ES, Tyler SA. 1965 Microorganisms from the Gunflint Chert. Science 147, 563–577. (doi:10.1126/science.147.3658.563)
41. Kazmiersczak J. 1979 The eukaryotic nature of Eosphaera-like ferriferous structures from the Precambrian Gunflint Iron Formation, Canada: a comparative study. Precambrian Res. 9, 1–22. (doi:10.1016/0301-9268(79)90048-2)
42. Xiao S, Zhang Y, Knoll AH. 1998 Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite. Nature 391, 553–558. (doi:10.1038/35318)
43. Bailey JV, Joye SB, Kalanetra KM, Flood BE, Corsetti FA. 2007 Evidence of giant sulphur bacteria in Neoproterozoic phosphorites. Nature 445, 198–201. (doi:10.1038/nature05457)

44. Bengtson S, Cunningham JA, Yin C, Donoghue PCJ. 2012 A merciful death for the ‘earliest bilaterian’ Veranimalcula. Evol. Dev. 14, 421–427. (doi:10.1111/j.1525-142X.2012.00562.x)

45. Antcliffe JB, Brasier MD. 2007 Charnia and seapens are poles apart. J. Geol. Soc. Lond. 164, 49–52. (doi:10.1144/0016-76492006-080)

46. Antcliffe J, Hancy A. 2013 Critical questions about early character acquisition—comment on Retallack 2012: ‘Some Ediacaran fossils lived on land’. Evol. Dev. 15, 225–227. (doi:10.1111/ede.12040)

47. Schopf JW. 1993 Microfossils of the Early Archean Apex Chert—new evidence of the antiquity of life. Science 260, 640–646. (doi:10.1126/science.260.5108.640)

48. Brasier MD. 2010 Towards a null hypothesis for stromatolites. In Earliest life on Earth. Habitats, environments and methods of detection (eds SD Golding, M Glikson), pp. 115–125. Dordrecht, The Netherlands: Springer.

49. Ball P. 1999 The self made tapestry. Pattern forming in nature. Oxford, UK: Oxford University Press.

50. Garcia-Ruiz JM, Hyde ST, Carnerup AM, Christy AG, Van Kranendonk MJ, Welham NJ. 2003 Self assembled silica-carbonate structures and detection of ancient microfossils. Science 302, 1194–1197. (doi:10.1126/science.1090163)

51. McLoughlin N, Wilson LA, Brasier MD. 2008 Growth of synthetic stromatolites and wrinkle structures in the absence of microbes: implications for the early fossil record. Geobiology 6, 95–105. (doi:10.1111/j.1472-4669.2007.00141.x)

52. Brasier M, Green O, Lindsay J, Steele A. 2004 Earth’s oldest (c. 3.5Ga) fossils and the ‘Early Eden Hypothesis’: questioning the evidence. Orig. Life Evol. Biosph. 34, 257–260. (doi:10.1023/B:ORIG.0000009845.62244.d3)

53. Brasier MD, Green OR, McLoughlin N. 2004 Characterization and critical testing of potential microfossils from the early Earth: the Apex ‘microfossil debate’ and its lessons for Mars sample return. Int. J. Astrobiol. 1, 1–12.

54. Brasier MD, Green OR, Lindsay JF, Stoakes C. 2005 Critical testing of Earth’s oldest putative fossil assemblage from the ∼3.5 Ga Apex chert, Chinaman Creek, Western Australia. Precambrian Res. 140, 55–102, 22 plates. (doi:10.1016/j.precamres.2005.06.008)

55. Blank CE, Sanchez-Barracaldo P. 2010 Timing of morphological and ecological innovations in the cyanobacteria—a key to understanding the rise in atmospheric oxygen. Geobiology 8, 1–23. (doi:10.1111/j.1472-4669.2009.00220.x)

56. Wacey D. 2009 Early life on Earth: a practical guide. Dordrecht, The Netherlands: Springer.

57. Antcliffe JB, Callow RHT, Brasier MD. 2014 Giving the early fossil record of sponges a squeeze. Biol. Rev. 89, 972–1004. (doi:10.1111/brv.12090)

58. Winchester S. 2002 The map that changed the world: William Smith and the birth of modern geology. New York, NY: Harper Collins.

59. Wacey D, Kilburn M, Saunders M, Cliff J, Brasier MD. 2011 Microfossils of sulphur-metabolizing cells in 3.4-billion-year-old rocks of Western Australia. Nat. Geosci. 4, 698–702. (doi:10.1038/NGEO1238)

60. Brasier MD, Green OR, Lindsay JF, Stoakes C, Brasier AT, Wacey D. 2011 Geology and Putative Microfossil Assemblage of the 3460Ma ‘Apex Chert’, Western Australia—a Field and Petrographic Guide. Record 2011/7. Perth, Australia: Geological Survey of Western Australia.

61. Wacey D, McLoughlin N, Stoakes CA, Kilburn MR, Green OR, Brasier MD. 2010 The 3426–3350 Ma Strelley Pool Formation in the East Strelley Greenstone Belt—A Field and Petrographic Guide. Perth, Australia: Record of the Geological Survey of Western Australia.
65. Grosch E, McLoughlin N. 2014 Reassessing the biogenicity of Earth’s oldest trace fossil with implications for biosignatures in the search for early life. Proc. Natl Acad. Sci. USA 111, 8380–8385. (doi:10.1073/pnas.1402565111)

66. Wacey D, Menon S, Green L, Gerstmann D, Kong C, McLoughlin N, Saunders M, Brasier MD. 2012 Taphonomy of very ancient microfossils from the ∼3400 Ma StrelleyPool Formation and ∼1900 Ma Gunflint Formation: new insights using a focused ion beam. Precambrian Res. 220–221, 234–250. (doi:10.1016/j.precamres.2012.08.005)

67. Brasier MD, Wacey D. 2012 Fossils and astrobiology: new protocols for cell evolution in deep time. Int. J. Astrobiol. 11, 217–228. (doi:10.1017/S1473550412000298)