

# “Records of warfare...embalmed in the everlasting hills”: a History of Early Coprolite Research

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**Abstract:** Although ‘coprolite’ was introduced as a term for fossil faeces by William Buckland in 1829, specimens had been described and figured in earlier literature. John Woodward described specimens from the Chalk as fossil larch cones a century before Buckland’s work, an identity later confirmed by James Parkinson in 1804. Gideon Mantell described more Chalk specimens in 1822, whilst François-Xavier de Burtin described further spiral forms from the Brussels area as fossil nuts. Buckland first identified fossil hyaena faeces from the Ipswichian cave deposits of Kirkdale in Yorkshire, and then applied his experience to specimens from the Jurassic of Lyme Regis and the Rhaetic Bone Bed of the Severn estuary area. He developed a nomenclature for the specimens that he described, the first such attempt in ichnology. A rich network of domestic and foreign colleagues and correspondents either supplied him with information and further specimens, or applied his conclusions to their own material. Buckland’s coprolite research engendered good-natured ribaldry from his colleagues.

The first half of the nineteenth century was a time of radical change in thinking amongst the natural sciences in general, and in geology in particular. A cutting edge contributor to this rapid pace of conceptual change was William Buckland who worked tirelessly as a politician for science, gave many a helping hand to up and coming colleagues, developed a rich network of contacts and friends, and acted as a popular figurehead for geology. Among the many innovations for which he was at least partly responsible was the growing appreciation that the fossil record sampled a diversity of once living communities, rather than being the chaotic record of a universal deluge. It was Buckland who first recognized that in the same rocks that sported the panoply of body fossil such as shells, teeth and bones, there were also traces of the daily activities of once living organisms – footprints and faeces (Duffin, 2006). Coprolites were first identified by William Buckland, who also gave us the name, effectively making him a founder of palaeoichnology.

## Earliest Discoveries

John Woodward (1665-1728), was apprenticed to a draper at age 16, and worked in London (Fig. 1). He rose to become Professor of Physic at Gresham College in London, but had wide natural history and antiquarian interests. After collecting his first fossil from the London Clay in 1688, he developed a passion that involved a large and historically important collection, which he bequeathed to Cambridge University. He also endowed the famous Woodwardian professorship at what is now the Sedgwick Museum, partly so that his specimens could be cared for in the future.

Woodward set forth his views that the fossils which he had collected were once living creatures which had been destroyed by the Deluge in his *Essay toward a Natural History of the Earth* (1695), although the details of his thesis brought him much controversy and protracted acrimonious exchanges with other natural historians of the day. The handwritten manuscript cataloguing his collection was published posthumously

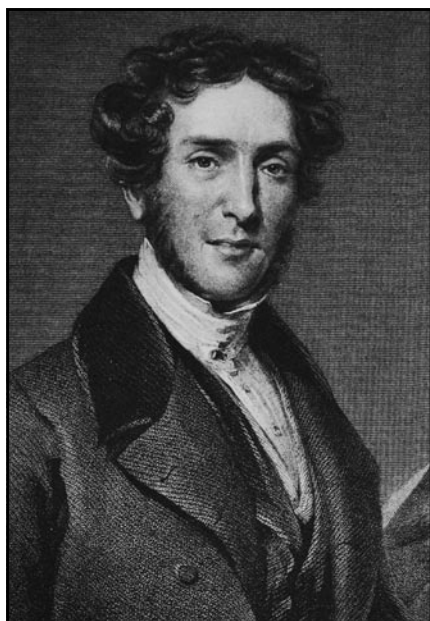
as *An Attempt towards a Natural History of England* (1728-9). Within his Classis II, Pars IV, “Nuts and other like fruits found in the earth”, he gives brief notice (1729 p22) of: *b. 72. Three cones seeming to be of the Larix. From Cherry-Hinton Chalk pits near Cambridge. These were not come to ripeness or maturity.*

Woodward was anxious to get as much information from these and similar specimens as possible. By comparing fossils in the preceding entry with extant larch cones, Woodward concluded that one of his specimens may have represented the growth stage normally reached in May.

Specimens from the same pits in the Middle Chalk at Cherry Hinton near Cambridge were later illustrated by James Parkinson (1755-1824), the physician famous for his treatise (1817) on the ‘Shaking Palsy’, later named ‘Parkinson’s Disease’ in his honour. He published *Organic Remains of the Former World* using an epistolary approach to his consideration of fossils in 1804. Letter XLVII considers various aspects of plant fossils, and Parkinson echoes Woodward’s comments

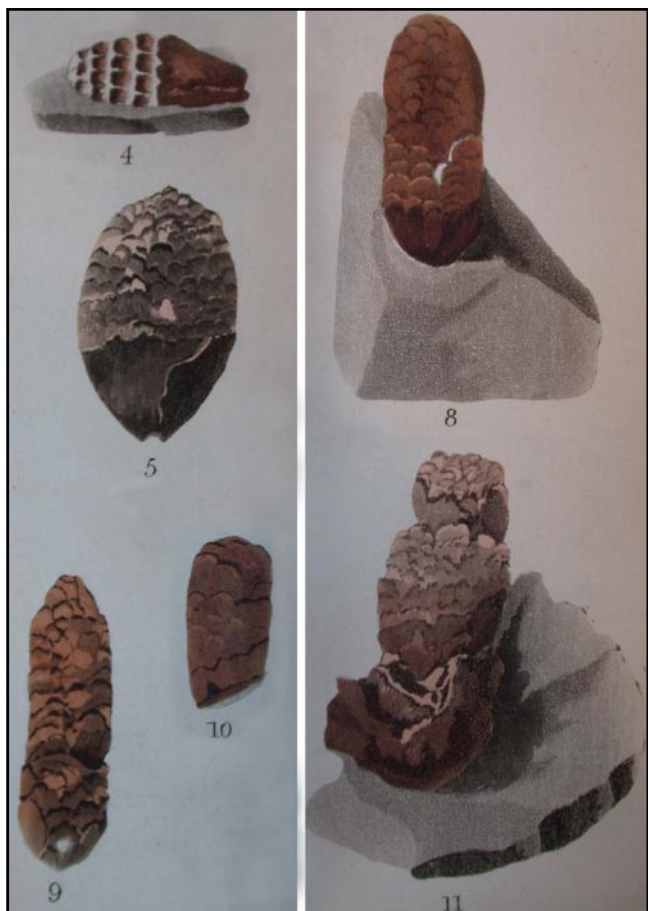


**Figure 1.** Portrait of John Woodward (1665-1728) (photo: David Ward; Sedgwick Museum).



**Figure 2.** Gideon Mantell's portrait, 1790-1852 (from Woodward, 1908).

that the Cretaceous specimens “approach very near in resemblance to the juli of the larch tree”. He adds the comment that a Dr Parsons considers them to be root structures rather than cones, but concludes that they are “either aments [catkins], or cones, of some tree not now known, at least to the European botanist” (Parkinson 1804, p456). The Dr Parsons in question is probably James Parsons (1705-1770; Chalmers 1815),



**Figure 3.** Coprolites from the Chalk at Hamsey (from Mantell, 1822).

physician and antiquary who had a passion for fossils and described fossil fruits from the London Clay of Sheppey. Parkinson did express concern that the Chalk specimens were not associated with any other plant remains (Parkinson, 1804 Plate VI, figs. 15, 17).

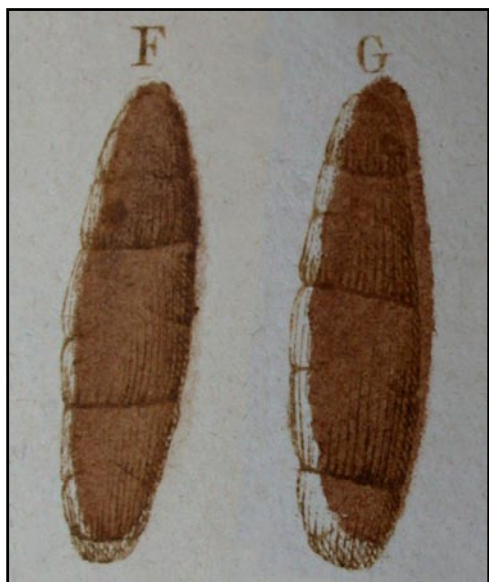
Gideon Mantell (1790-1852) described and illustrated specimens of similar morphology from the Chalk at Hamsey, near Lewes, his home town, in Sussex (Fig. 3). Commenting that “their nature is still involved in obscurity”, he remarks that they have “excited considerable attention”, and discussion centred around whether they were plant or animal in origin (Mantell, 1822). Correspondence with John Hailstone, Woodwardian Professor at Cambridge from 1788 to 1818, elicited the opinion that Woodward’s specimens had a “vegetable origin beyond all doubt” (Mantell, 1827), partly since he had described coniferous plant remains from the same quarries (Hailstone, 1816).

Mantell gives the most extensive description of these specimens, of which he claimed to have been given 50 or more by his brother, noting that they measure up to 5 cm long, have a scaly, corrugated surface, cylindrical shape and tapering obtusely to a point at one end. He makes the comment that they appear to have the same composition as associated vertebrate remains, and that some have fish scales attached to them. In comparing his specimens with larch cones, Mantell (1822) correctly indicates that the items from the Chalk have a spiral form, rather than possessing individual, imbricated scales. He goes on to describe and figure further specimens, also tentatively compared to larch cones, from the Chalk at Steyning, and repeating some of the elements of his discussion, eventually coming to the conclusion, “that they may hereafter prove to be parts of fishes”.

François-Xavier de Burtin (1743-1818) also postulated a botanical origin for local coprolites which he described and figured in his 1784 *Oryctographie de Bruxelles* (Fig. 4). Having spent some time discussing certain specimens which he concluded were comparable to coconuts, Burtin (1784) turned his attention to an elongate, spindle-shaped structure possessing 6 evenly-spaced spiral turns. He makes the interesting comment that he would have had no hesitation in classifying the specimen as an unknown coral (“polypières”), were it not for his earlier discussion on coconuts. In spite of the fact that he says he could find no evidence of internal cellular structure or points of attachment to twigs, he concludes that it must be an unknown fruit or kernel – at least it was very different from any other fruits or nuts that he either possessed or had seen elsewhere.

### Kirkdale Cave

William Buckland was born the eldest son of the Rev. Charles Buckland on 12th March 1784 at Axminster in Devon (Rupke, 1983; Duffin, 2006). In 1813, Buckland was appointed Reader in Mineralogy and then Reader in Geology in 1818.



**Figure 4.**  
*Coprolites*  
from near  
Brussels  
(from de  
Burtin,  
1784).

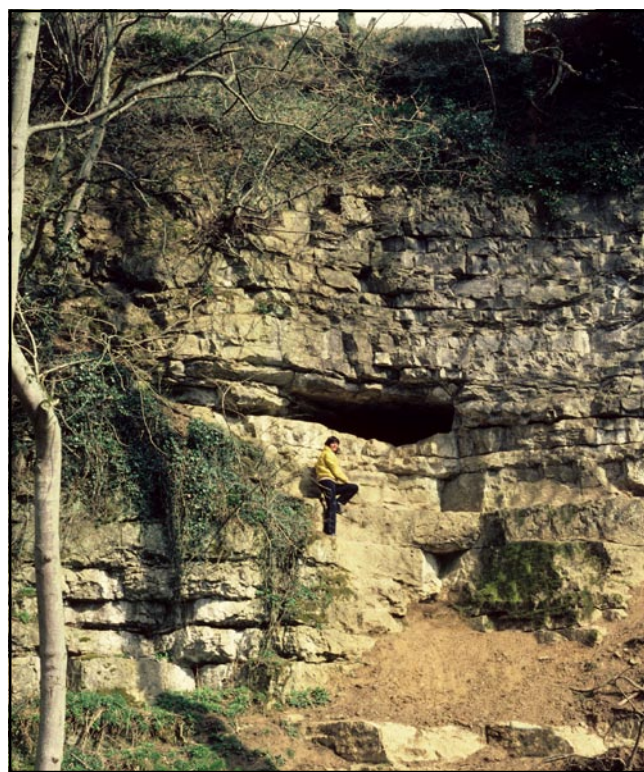
Quickly establishing himself as a popular lecturer, he illustrated his talks with the liberal use of specimens, maps and sections, holding the audience not only with the innovative approach and scientific content of his lectures, but also his rather theatrical style and sense of humour. Completing something of a ‘Grand Tour’ of European geology in the company of W.D. Conybeare and G.B. Greenough, he spent some time with August Goldfuss who was engaged with the careful excavation of the bone-bearing sediments in the cave floor at Gailenreuth near Muggendorf in German Franconia.

*“Little did the boy think, who stepped amongst the bushes, with which the mouth of the Cave was overgrown; or the woodman, when felling the oak; that he was walking on a spot, which in some future time, would interest the literary world, and draw many from the smoke of populous and polished cities and towns, and from the retired cloisters of colleges, to explore a Cavern, then unknown, and to visit a situation, which before had been comparatively unobserved! But unexpected circumstances every day unfold some mysteries, and give fresh stimulus to the energies of the human mind.”* (Eastmead, 1824 p4).

His experience in Germany was to hold Buckland in good stead when he later examined cave deposits at first hand in Yorkshire – deposits that would, indeed, “give fresh stimulus to the energies” of his mind! Quarrying of oolitic limestone was taking place near the small village of Kirkdale, a few miles away from Kirby Moorside in Yorkshire. During the summer of 1821, John Gibson (George, 1998), a manufacturing chemist, was visiting friends in the area. He noticed large blocks of limestone being used to repair the roads; scattered between them were various pieces of bone and tusk. Gibson traced the origin of the material to the small quarry by the side of Hodge Beck (SE678856), adjacent to Kirkdale Church. Believing the remains to have come from modern cattle which had either succumbed to the disease ‘murrain’ (probably Rinderpest), a highly infectious viral cattle plague, or had fallen into an open chasm, the quarrymen

had scattered them as aggregate on the local roads. The land owners (the Welburn Estate and a local solicitor) generously gave permission for the cave contents to be fully excavated, hoping that the bones and teeth would, “fall into the hands of such persons, who would deposit them in public institutions or otherwise take care of them, to preserve the interesting memorials of this wonderful cavern” (Eastmead, 1824 p7). Keen amateur geologists, collectors and enthusiasts were happy to oblige and gathered up some of the material; local surgeon, coroner and apothecary, Thomas Harrison also discovered the cave in the autumn of 1821 (*Gentleman’s Magazine*, February 1822), while George Young and his co-worker John Bird, and Rev. William Eastmead an independent minister in the village, all collected from the site. Retired colonel William Salmond reputedly funded and superintended the excavation, and executed the plan drawing of the cavern used in subsequent publications. On December 7th 1822 Salmond met with his colleagues Anthony Thorpe and James Atkinson, a retired surgeon, in an attempt to bring their various collections of Kirkdale fossils together in a suitable repository; hence the Yorkshire Philosophical Society was born. Gibson was credited with completing the bulk of the excavation and accumulating a huge collection which was shown, among others, to James Parkinson. Other material found its way into a wide range of personal collections and public institutions.

It was Edward Legge, Bishop of Oxford, who eventually informed Buckland about the discoveries at Kirkdale. Joseph Pentland was told of the finds. The Irishman was working in the laboratory of Georges



**Figure 5.** Entrance to Kirkdale Cave today.



**Figure 6.** Dabié Cave, Jordan (photo: Stephan Kempe).

Cuvier, Parisian father of comparative anatomy who, at that time, was engaged in writing the second edition of his *Recherches sur les ossements fossiles*. William Clift, curator of the John Hunter Collection at the Royal College of Surgeons, had also written to Cuvier, sending him some drawings of the better material from Kirkdale. Pentland wrote to Buckland on 26 November 1821, urging him to procure some specimens from Kirkdale for the French Professor. Buckland accordingly visited the cave in December 1821, and joined the team. At around 75m long, 4m high and up to 2m wide (Fig. 5), this cave was smaller and contained thinner deposits than those he had seen during his visit to Germany. Buckland's excited descriptions of the cave to his correspondents refer to a profusion of the comminuted, trampled bones and teeth of hyaenas, mixed together with a host of other species, including "Elephant, Rhinoceros, Hippopotamus, Horse, Ox, Deer, Fox and Water Rat", forming a sort of pavement over the cave floor. A full faunal list is given by Boylan (1981). Buckland went on to conclude that the assemblage represented a hyaena den, analysing breakage patterns of the bones to prove that they were from carcasses dragged into the cave and broken by feeding action. In doing so, he was the first person to conduct anything like a rigorous study of biostratinomy.



**Figure 7.** Painting by R. Ansdell R.A., from about 1843, of William Buckland dressed for fieldwork in a tailed topcoat over a dark waistcoat and white shirt, with a top hat, umbrella and black gloves, and brandishing a blue serge collecting bag.

Buckland was impressed by the fact that bone debris was strewn all over the cave floor, including the deepest recesses of the cavern, and that the walls and bone fragments had been polished by the passage of the predators through the cave. His ecological explanation of the fauna as a hyaena den was not universally accepted; there was some tension between Buckland and George Young, for example. Young preferred the notion that the accumulation of bones was part of a diluvial (flood) deposit and left the excavations as a result of the difference of views.

Many did embrace Buckland's view, however, and relished the idea of antediluvian hyaenas roaming the Yorkshire countryside in search of prey. Similar hyaena dens have been described much more recently from the volcanic plateau of Al-Shaam Harrat in Jordan (Kempe et al., 2006). The Dabié Cave (Fig. 6), with its almost unbroken covering of bone scatter, gives an impression of the sight, albeit partially obscured by marly sediment and stalagmite, that must have met Buckland's eyes as he entered and excavated Kirkdale cavern (Fig. 8).

Nestling between the bones and teeth, much as on the floor of Al-Fahda Cave (also in Jordan, Fig. 9), Buckland noticed some small balls of a white material. Intrigued as to their nature and origin, he wondered if they might be fossilised faeces deposited by the hyaena (Fig. 10). He referred to them both in his letters and in print as *Album Graecum*, an old apothecarial term pertaining to dog faeces which demonstrate the property of turning white on exposure to air. Rather frighteningly, *Album Graecum* (also known as *Stercus Canis Officinale*) was used as an ingredient, particularly in the 16th and 17th centuries, in the treatment of colic, dysentery, scrofula, ulcers (Wootton, 1910) and especially quinsy (a peritonsillar abscess that can form as a complication of acute tonsillitis), both as a component of a poultice or plaster and (possibly worse!) a gargle. The 'drug' was obtained by feeding otherwise half starved dogs with bone fragments; the protein inside was digested and absorbed from the bone, leaving an easily blanched



**Figure 8.** Caricature by W.D. Conybeare, of Buckland entering the Kirkdale hyaena den, only to find it occupied.



**Figure 9.** *Hyaena coprolite in situ in Al-Fahda Cave, Jordan (photo: Stephan Kempe).*

phosphate-rich faecal pellet which was collected with some eagerness (Burnett, 1833). The parallel drawn by Buckland between *Album Graecum* and hyaena coprolites thus becomes both appropriate and striking.

Buckland described the Kirkdale material (Buckland, 1824 p20) as having an external form that “*is that of a sphere, irregularly compressed, as in the faeces of sheep, and varying from half an inch to an inch and a half in diameter; its colour is yellowish white, its fracture is usually earthy and compact, resembling steatite, and sometimes granular; when compact, it is interspersed with small cellular cavities, and in some of the balls there are undigested minute fragments of the enamel of teeth.*” Anxious to confirm his suggested interpretation, he sent some of the material to William Hyde Wollaston, the chemist, physicist and mineralogist. Wollaston showed the specimens to the Menagerie Keeper at the Exeter Exchange, who immediately noted their similarity to the droppings produced by the Spotted Hyaena (*Crocuta crocuta*). The analysis conducted by Wollaston “finds it [the hyaena coprolite] to be composed of the ingredients that might be expected in faecal matter derived from bones” (Buckland, 1824 p22). In his reply to Buckland, Wollaston (24 June 1822; Buckland Papers, Royal Society) wrote that “though such matters may be instructive and therefore to a certain degree interesting, it may as well for you and me not to have the reputation of too frequently and too minutely examining faecal products.”

Buckland’s study of Kirkdale and its fauna was initially published in the *Philosophical Transactions of the Royal Society* in 1822, and then issued as the *Reliquiae Diluvianae*, published by John Murray in 1823. The importance of the work was recognised by the Royal Society, who awarded Buckland the prestigious Copley Medal for 1822, an honour reserved for “outstanding achievements in research in any branch of science”. Buckland’s was the 62nd in a long sequence whose pedigree included men such as Benjamin Franklin, William Herschel, Joseph Priestley,

James Cook and William Wollaston himself, and was the first such award for geology. The then President of the society, Humphrey Davey, commented, “I do not recollect a paper read at the Royal Society which has created so much interest as yours” (letter dated 18 March 1822; Buckland Papers, Royal Society).

Shortly afterwards (1827) Buckland published a note in the *Proceedings of the Geological Society of London* of his lecture of November 17 1826 entitled “*Observations on the bones of hyaenas and other animals on the cavern of Lunel near Montpellier, and in the adjacent strata of marine formation*”. Rather larger than Kirkdale, this cave contained a similar fauna to that of Yorkshire, but Buckland was astounded by the high incidence of hyaena faeces – “an extraordinary abundance of the balls of *album graecum* in the highest state of preservation”. He concluded that, at Kirkdale, “a large proportion of the faecal balls of the hyaenas appear to have been trod upon and crushed at the bottom of a wet and narrow cave, whilst at Lunel they have been preserved in consequence of the greater size and dryness of the chamber in which they were deposited.”

## Coprolites

Buckland returned to his musings on faecal products in 1829. A friend of the famous “fossilist”, Mary Anning (1799-1847), Buckland often collected with her from the Lias cliffs and foreshore of the Lyme Regis and adjacent successions. The dark grey structures, up to 10 cm long, resembling “elongate pebbles, or kidney-potatoes” and occurring in the Lias, were called “Bezoar stones” by the locals, referring to their supposed superficial similarity to the concretions developed in the stomach of the oriental Bezoar Goat (*Capra aegagrus*), used extensively in medicine as a universal antidote to poisons, particularly during the 16th and 17th centuries. He later wrote that “these Coprolites are so abundant that they lie in some parts



**Figure 10.** *Hyaena coprolites, Album Graecum, from Kirkdale, on display in Oxford University Museum (OUM).*

of the lias like potatoes scattered in the ground” (Buckland, 1836 p188). Buckland concluded that these were fossilized faeces from the ichthyosaurs, based upon their co-occurrence with those marine reptiles, and their contents - undigested bones and scales of fishes such as *Dapedium politum*, as well as the bones of small ichthyosaurs (Fig. 11). He noted the spiral form of some of the specimens, their presence in the pelvic region of the body cavity in certain ichthyosaur specimens, and the chemical analyses showing a composition similar to that of the *Album Graecum* he had described from Kirkdale (Buckland, 1829a). A later comment in the same volume described “the bony rings of the suckers of cuttle-fish ... frequently mixt with the scales of various fish, and the bones of fish, and of small Ichthyosauri in the bezoar-shaped faeces from the Lias at Lyme Regis” (Buckland, 1829b p142) (Fig. 12). This time, William Prout, the physician and chemist, was let loose on performing the chemical analyses; he concluded that the black colouring was of the same chemical composition as material in fossil teuthoid ink sacs, and that they were therefore amongst the prey on which ichthyosaurs fed (Buckland, 1829b).

Similar specimens were noted from the Late Triassic Rhaetic Bone Bed (then called the “Lias bone bed”) and the basal Carboniferous Limestone of the Bristol District. Beginning to develop a taxonomic nomenclature (probably the first in ichnology), Buckland proposed that these black fossil faeces should be called “Nigrum graecum” on the basis of their colour (Buckland, 1829b p142; a name he later [1835] credited to a Mr Dillwyn), and that specimens of demonstrably piscine origin (found within the body cavity) should be called Ichthyo-coprus; ichthyosaur faeces would be Sauro-coprus, and the term *Album Graecum* should be replaced with Hyaino-coprus. Referring obliquely to the earlier descriptions by Woodward, Parkinson and Mantell, he noted that the spiral faecal structures were very similar to the “Iuli” or fossil fir cones of the chalk, and that these Cretaceous specimens were therefore also faecal in origin, and should be referred to as *Copros iuloides*. His final proposition was that



**Figure 12.** Coprolite 76 mm long from Lyme Regis, described by Buckland as containing “bony rings of the suckers of cuttle-fish” but which are actually fish teeth (photo: OUM).

he would “include them all under the generic name of Coprolite” (Greek, copros = dung, lithos = stone).

This lecture formed the basis of a fuller treatment of the subject (Buckland, 1835). Here, Buckland freely admitted that he and W.D. Conybeare had been confused over the identities of the objects now identified as fossil faeces earlier in their careers, originally believing them to be particularly dense masses of heavily rolled bone or palatal teeth. This, together with Buckland’s new conclusions, must have struck a chord with the broader scientific community; colleagues rooted out a plethora of items that fitted Buckland’s descriptions very closely. Mr J.S. Miller furnished specimens from the Rhaetic Bone Bed and Carboniferous Limestone of the Bristol district. Mr Jelly (probably Rev. Henry Jelly of Bath) provided specimens from the Kimmeridge Clay of the Oxford district, and Reverend Benjamin Richardson of Farleigh Hungerford near Bath provided specimens from the Wiltshire Greensand. Gideon Mantell and the Philpott sisters of Lyme Regis also made material available to Buckland.

John Josias Conybeare was, like his brother, W.D. Conybeare, a keen geologist. He conducted fieldwork with Buckland in Devon and Cornwall during the summer of 1813. In 1808, as Vicar of Bath Easton he had retrieved specimens of the Rhaetic Bone Bed (“lias breccia”) from a trial borehole sunk in an attempt to find coal; the coprolites were turned over to Buckland.

Robert Anstice of Bridgewater, rather appropriately to this topic, was appointed Commissioner of Sewers and charged with overseeing various projects to drain the Somerset Levels (Dance, 2003). Anstice started collecting for his own personal museum just before the close of the 18th century and was a regular correspondent of Buckland’s in the 1820s. He wrote to Buckland on 13 April 1829, enclosing some specimens of Rhaetic Bone Bed from Blue Anchor Point on the north Somerset Coast, as well as water colour sketches of two specimens, both containing numerous coprolites, in one case associated with a fin spine of *Nemacanthus monilifer*, and in the other with a jaw fragment of *Severnichthys acuminata* (Figs. 13). He apologised for being unable to prepare the coprolites out of the bed, writing “You are well aware of the difficulty of extricating from their matrix any of the subjects contained in this very impracticable stone”, but lauding Buckland’s efforts with the comment that “No fossil subject ever presented a greater difficulty of explanation to me than these Pupae shaped bodies have”, but that “I have no doubt but that you have cleared up the mystery” (OUM Coprolite File). It was another 150 years before coprolites from the Rhaetic Bone Bed received further serious attention (Duffin, 1979; Swift & Duffin, 1999).

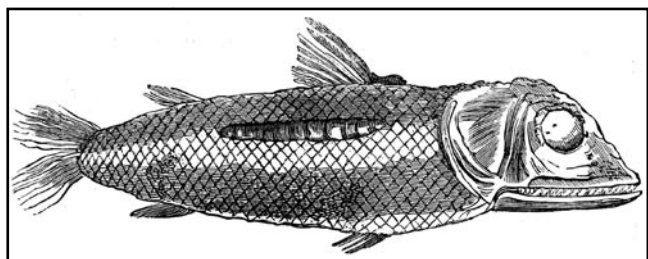
As the list of formations from which coprolites were identified grew, Buckland tinkered a little with his nomenclatural scheme, referring now to “Iulo-eido-coprolites” from the Chalk, and “Amiacoprus” a



**Figure 13.** Water colour sketches by Robert Anstice of (above) *Nemaacanthus monilifer* fin spine and coprolites and (below) jaw fragment of *Severnichthys acuminatus* and accompanying coprolites, both from the Rhaetic Bone Bed of Blue Anchor Point, north Somerset (photos: OUM, Buckland papers, Coprolite File).

specific type of ichthyocopus located within the body cavity of a Cretaceous specimen (Fig. 14) described as *Amia lewesiensis* by Mantell (1833). He reserved the name *Ornithocopus* for the recently described guano deposits of Peru (Buckland, 1835).

Some of the specimens described by Buckland are illustrated in the accompanying paper by Ford and O'Connor (this *Mercian Geologist*). Buckland found that coprolites from Lyme Regis showed considerable diversity. Their colour varied from ash-grey through to black; they ranged in size up to around 10 cm; some were amorphous, while others showed spiral marking,



**Figure 14.** The Cretaceous *Amia lewesiensis* that contained "*Amiacopus*" a specific type of ichthyocopus within its body cavity (from Mantell, 1833).



**Figure 15.** Spiral coprolite 122 mm long, from Lyme Regis, figured by Buckland (1835) (photo: OUM).

the number and distribution of which also showed some diversity (three to six full convolutions); their contents varied considerably with fish scales and ichthyosaur bones; supposed suckers of cephalopods are actually the tooth-bearing bones of small bony fishes such as *Eomesodon* (Fig. 12).

Buckland found spiral coprolites (Fig. 15) particularly interesting. He had some specimens cut and polished to show their internal structure (Fig. 16), and he dissected several extant rays and scyliorhinid sharks (dogfishes) in order to study the spiral valves of their intestinal tracts. Anxious to see if such a structure would confer spiral structure on faecal material passing through it, he set out to test the hypothesis with a typically innovative technique. He injected the intestines with Roman cement. Despite its name, this was a highly successful, quick setting (5 to 15 minutes) hydraulic cement developed by James Parker in the 1780s but patented only in 1796, and made by burning and then grinding down clay-rich septarian nodules. He found that he could produce "artificial coprolites that in form are exactly similar to many of our fossil specimens" (Buckland, 1835 p234). A similar experiment was performed over a century and a quarter later by Zangerl and Richardson (1963). Buckland visualised the process of spiral coprolite formation as follows (Buckland, 1836 p194) : *The form is nearly that which would be assumed by a piece of riband, forced continually forward into a cylindrical tube, through a long aperture in its side. In this case, the riband moving onwards, would form a succession of involuted cones, coiling one round the other, and after*



**Figure 16.** Sectioned and polished spiral coprolite 60 mm long, from Lyme Regis, figured by Buckland (1835) (photo: OUM).

a certain number of turns within the cylinder, (the apex moving continually downwards,) these cones would emerge from the end of the tube in a form resembling that of the Coprolites . . . In the same manner, a lamina of coprolitic matter would be coiled up spirally into a series of successive cones, in the act of passing from a small spiral vessel into the adjacent large intestine. Coprolites thus formed fell into soft mud, whilst it was accumulating at the bottom of the sea, and together with this mud, (which has subsequently been indurated into shale and stone,) they have undergone so complete a process of petrification, that in hardness, and beauty of the polish of which they are susceptible they rival the qualities of ornamental marble. Closer inspection of the spiral coprolites from Lyme Regis revealed “a series of vascular impressions and corrugations on the surface of the coprolite, which it could only have received during its passage through the windings of this flat tube [the spiral valve]” (Buckland, 1836 p153).

In his later volume for the *Bridgewater Treatise* series (Buckland, 1836 p188), Buckland was able to incorporate even more examples of Formations yielding coprolites, from information and material sent to him from home and abroad in response to his earlier papers. Georg Friedrich Jaeger wrote to him from the Eberhard-Ludwigs-Gymnasium in Stuttgart where he was Professor of Natural History and Chemistry (Warth 1992), sending specimens, drawings and descriptions of spiral coprolites from the Alaunschiefer (Lettenkeuper, Ladinian, Middle Triassic) of Gaildorf in Baden Württemberg, Germany, probably the famous Alum mine (Buckland, 1836 p149; letter 2 April 1833, OUM Coprolite File). Similarly, James Ellsworth DeKay, later of the Geological Survey of New York State, sent him a coprolite cast from New Jersey (Folk, 1965).

Other members of the British geological fraternity also responded. Samuel Hibbert, the Mancunian who trained as a physician in Edinburgh, but foreswore medicine for antiquarianism and geology, is probably best known for describing and mapping the rocks of Shetland (Ware, 1882). He noted that coprolites were abundant in the lacustrine Burdiehouse Limestone of the Dinantian Oil Shale Group near Edinburgh. Buckland’s former student, Sir Philip de Malpas Grey Egerton, then Member of Parliament for Chester, located similar specimens in the Coal Measures of Newcastle-under-Lyme, Staffordshire. Sir Walter Calverley Trevelyan, a diligent collector of all manner of natural history specimens, recognized coprolites in the Coal Measures around the fishing village of Newhaven near Leith, on the Firth of Forth in Scotland. Buckland visited the section in September 1834 with Trevelyan and Lord Greenock (Charles Murray Cathcart, 2nd Earl Cathcart), discoverer of the rare mineral form of CdS, which was subsequently named after him (greenockite). The party found a series of clay ironstone nodules with coprolite nuclei “strewed so thickly upon the shore, that a few minutes sufficed to collect more specimens than I could carry” (Buckland, 1836 p199). Buckland

also notes that, “These nodules take a beautiful polish and have been applied by the lapidaries of Edinburgh to make tables, letter presses, and ladies’ ornaments, under the name of Beetle stones, from their supposed insect origin.” It may be these nodules that were cut, polished and fashioned into the famous coprolite table, now housed in the Philpott Museum in Lyme Regis.

Buckland was renowned for his rather earthy sense of humour. Indeed, Charles Darwin wrote of him in his *Autobiography*, “though very good-humoured and good-natured, [Buckland] seemed to me a vulgar and almost coarse man. He was incited more by a craving for notoriety, which sometimes made him act like a buffoon, than by a love of science”. He was certainly not averse to a joke at his own expense and revelled in the cartoons and doggerel which flowed from the fertile minds and pens of some of his friends. Coprolites were, of course, grist to the mill for this type of ribaldry.

Philip Bury Duncan, a stalwart of the Bath Royal Literary and Scientific Institution (Chairman 1834-1859), for example, wrote to Buckland with some oft-quoted verses :

*Approach, approach ingenuous Youth  
And learn this fundamental truth  
The noble science of Geology  
Is bottomed firmly on Coprology  
For ever be Hyaena’s blest  
Who left us the convincing test  
I claim a rich Coronam Auri  
For these Thesauri of the Sauri*

The couplet at the end links the golden crown with the ‘treasures’ (thesauri) of the extinct saurians, these treasures being their faeces. Duncan also delivers some lines of Latin :

*Avia Pieridum peragro loca nullius ante  
Trita solo, coecas iuvat explorare ferarum  
Speluncas, iuvat et merdas exquirere priscas  
Saurorum duro et vestigia quaerere saxo*

These lines are modeled on Lucretius’ *De Rerum Natura* 1, lines 925-927. An English translation of the classical original reads as follows :

*I wander through the pathless places of the Muses,  
Previously trodden by the foot of none.  
I am glad to approach the virgin springs,  
And drink; glad, too, to pluck new flowers*

Duncan’s modified version can be translated as :

*I wander through the pathless places of the Muses,  
Previously trodden by the foot of none.  
I am glad to explore the hidden caves of wild beasts,  
glad, too, to search out ancient turds of lizards,  
And to look for traces in the hard rock.*

On a fold of the envelope he wrote : “Tear off the other side for Mrs B for she must know nothing of the *Bona Dea Coprologia - Cloacina Oceaningae*”. Even here, he is playing a coprolitic theme. The Good Goddess Coprologia is linked with the Cloacina Oceaningae or oceanic sewer, in the oblique reference to



Rome's sewage system, the Cloaca Maxima, which ran into the River Tiber and thence to the sea. In a parallel with the Roman sewage system, Duncan refers to the oceanic sewer – the Lower Jurassic sea that became the repository for the coprolites produced by the living community of reptiles and fishes within it.

This theme was taken up pictorially by Thomas Henry de la Beche, the founder of the Geological Survey who lived much of his early life in Lyme Regis, in the execution of his famous watercolour (1830) "*Duria antiquior – a more ancient Dorsetshire*" – the first attempt at reconstructing an ancient ecosystem (Fig. 17). This 'cartoon' was copied by George Scharf, artist to the Geological Society as a lithograph that was then sold, mostly to Fellows of the Society, for two pounds and ten shillings each, to assist the Anning family, who were then suffering hardship. De la Beche's depiction of the Lower Lias sea scene shows a virtual rain of coprolites to the sea bed as many of the subjects, particularly the marine reptiles in his sketch go about their daily business of eating and being eaten. The sea floor is similarly littered with coprolitic debris.

## Later work

The response to Buckland's work was immediate and enthusiastic. His close friend, Louis Agassiz, who was in the midst of a massive, fundamentally important five-volume work on fossil fishes (Duffin, 2007), was called upon to identify isolated scales enclosed in Carboniferous and Lower Jurassic coprolites; the fact that he could do so immediately was a source of some wonder to Buckland (1836). At the same time, Agassiz shared some conclusions over ribbon-like fossils from the Solnhofen Plattenkalk (Tithonian, Late Jurassic) described as annelid worms by Goldfuss, and accordingly named *Lumbricaria*. Agassiz believed

these structures to be fossilised fish intestines, referring to them as Cololites (Buckland, 1836). In defence of his suggestion, Agassiz made close observations of the decomposition sequence shown by dead fish in the lakes of his native Switzerland, anticipating similar work by Wilhelm Schafer (1972) by over a hundred years. Carcasses, re-floated belly upward by the accumulation of gaseous products of putrefaction, eventually burst open through the abdomen. The intestines are able to exit the body through the rent, become detached from the remainder of the carcass, and float away in a coherent mass, eventually being stranded on the shore. This interpretation of *Lumbricaria* is still accepted today (Frickhinger, 1994). Georg Graf zu Münster (1830) was quick to identify coprolites from the same locality and other stratigraphical levels in Germany. Robert (1832-3) was the first to record coprolites from France (Oligocene), but was followed by Robertson (1834) who may have been the first to describe a dinosaur coprolite from the French Cretaceous (Lambrecht, 1933). A number of papers followed, mostly reiterating previous work or citing new records of coprolites from different localities, and filling gaps in their stratigraphical distribution (including Girard, 1843).

In 1844, Georges Louis Duvernoy, professor of Natural History at the Collège de France in Paris and former co-worker of Cuvier, suggested that some fossils with a spiral form might be "urolites" ("fécès urinaires") rather than coprolites ("fécès alimentaires"). This stemmed from his work on the Chameleon, whose faeces possess a simple cylindrical morphology, but whose solid urine has a spiral structure. The producers of such fossil urolites would be limited to lizards and snakes (lacertilians and ophidians).

The earliest reference on invertebrate coprolites is that of Christian Erich Hermann von Meyer (1852),



**Figure 17.**  
"*Duria antiquior – a more ancient Dorsetshire*", the water colour sketch by Thomas Henry de la Beche (photo: National Museum of Wales).

the doyen of German palaeontology and founder of the journal *Palaeontographica*, who discussed the possibility of faeces from insect larvae in lignitic deposits at Salzhausen.

With the idea of fossil faeces (coprolites), fossil intestines (cololites) and fossil urine (urolites) established in a gradually expanding literature, there was little controversy as publications described new finds, often with chemical analyses. However, Fritsch (1895) and Neumayer (1904) concluded that coprolites with a spiral form were actually fossilised valvular intestines. As such, it could be argued that they fell within Agassiz's definition of cololites, but Fritsch proposed the name 'enterospirae' for them (Duffin, 1979). Neumayer (1904) distinguished two morphologies of spiral coprolite: heteropolar coprolites are spindle-like with relatively closely spaced turns concentrated at the more obtuse or 'anterior' end of the specimens; amphipolar forms possess more widely spaced spiral turns more evenly spaced along most of the length of the relatively blunt-ended coprolites. The debate over the coprolitic versus cololitic origin of spiral forms resurged with descriptions of heteropolar coprolites from the Permian of Kansas by Williams (1972). Thin sections of these revealed bifurcating mucosal folds arising from the whorl interfaces, showing a strong similarity to spiral valve structure and leading Williams to conclude that they are true enterospirae. Further specimens with similar histology from the Niobrara Formation (Late Cretaceous, USA) added weight to this hypothesis (Stewart, 1978). However, McAllister (1985) showed that the spiral valve of extant *Scyliorhinus canicula* is able to extrude faecal material into the colon, and then expel it from the body while retaining its undistorted spiral riband form; sections of hardened examples of these modern coprolites showed similar mucosal fold histology to that described for the Permian forms. At the current state of knowledge, it is likely that spiral faecal structures could be fossilised spiral valvular intestines (enterospirae), fossil colon contents (cololites *sensu lato*) and true coprolites.

A recent review by Hunt *et al.* (2007) made the comment that "coprolites are the least studied and most under-sampled vertebrate trace fossils". Building on earlier work (Hunt *et al.*, 1998), the need to produce a taxonomic framework led to the definition of a number of coprolite ichnotaxa, partly embracing Buckland's original specimens described some 170 years earlier. *Saurocoprus*, a name introduced by Buckland (1835) is formally defined as one of six coprolite ichnotaxa, and *Saurocoprus bucklandi* is applied to heteropolar coprolites from the Lyme Regis Lower Jurassic – a fitting tribute to the father of coprolite research, whose fundamental work and innovative insight laid the foundation for a rich topic of geological enquiry. By 1968, at least 376 publications on coprolites were known (Hantzschel *et al.*, 1968), and research has continued unabated since on an ichnological group that is known from Ordovician times onward; some

surprising results include the description of possible coprophagous arthropods (Duffin, 1978), dermestid beetle debris stripping embryos inside dinosaur eggs (Cohen *et al.*, 1995), and even a new Oligocene snake named, aptly, *Coprophis* (Parris & Holman, 1978).

Mundane they might be, and a source of humour and fascination they certainly are, but who would have thought that in the excited conclusion to a careful piece of analysis by William Buckland they could also take on an air of romanticism: "*In all these various formations our Coprolites form records of warfare, waged by successive generations of inhabitants of our planet on one another: the imperishable phosphate of lime, derived from their digested skeletons, has become embalmed in the substance and foundations of the everlasting hills; and the general law of Nature which bids all to eat and be eaten in their turn, is shown to have been co-extensive with animal existence upon our globe; the Carnivora in each period of the world's history fulfilling their destined office,—to check excess in the progress of life, and maintain the balance of creation.*" (Buckland, 1835 p235)

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