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Finding the world's oldest mammals: sieving, dialectical materialism, and squabbles

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ABSTRACT

Mammals (or properly, mammaliaforms) originated in the Late Triassic and the first 50 Myr of their evolution through Late Triassic and Early Jurassic are best documented by rich faunas from numerous localities around Bristol in south-west England and in South Wales. The mode of preservation of the fossils, in sediment washed into karst features such as caves, is unusual but has led to a demand for specialized processing methods to extract the exquisitely preserved tiny teeth and bones from huge volumes of sediment. This rich documentation of the oldest mammals has made them especially important for mammalian palaeobiology on a global scale. The first specimens were found in the 1860s, and collection and study has been sporadic, with especially fruitful times in the 1860s, and then from 1938–1979. Throughout, the field collecting, processing, and interpretation of the fossils has been fraught, with heated debates between leading protagonists during the second half of the past century. Here, we track the substantial contributions made by Charles Moore, Walter Kühne, Rex Parrington, Kenneth Kermack, Pamela Robinson, and others, using published sources, unpublished letters and notebooks, and interviews, to establish some of the facts about the most heated public disputes.

Keywords: Late Triassic; Early Jurassic; fissure faunas; Bristol fissures; Glamorgan; Charles Moore; Walter Kühne; Francis Rex Parrington; Kenneth Kermack; Pamela Robinson

INTRODUCTION

Small things can be the subject of big arguments. In a discussion about the origin of mammals, Kühne (1973, p. 59) wrote, 'An unfortunate squabble over a nomenclatorial question has resulted that among the few authors writing on Rhaetic Mammalia one and the same thing is called by Crompton, Jenkins, Parrington and Hopson *Eozostrodon* Parrington, 1941 and by Kermack, Mussett, Mills and Kühne *Morganucodon* Kühne, 1949 … *Morganucodon* ought to be used, the name of *Eozostrodon* being used for sentimental reasons only or because of ignorance'.

These are strong words and go counter to normal taxonomic practice where the first-given name takes precedence: *Eozostrodon* was named by Parrington (1941) and *Morganucodon* was named by Kühne (1949a), both based on mammal teeth from the Latest Triassic or Earliest Jurassic, the former from Holwell Quarry, Somerset, the latter from Duchy Quarry, South Wales. In a detailed response and review, Clemens (1979) sought to calm the situation and declared that both *Eozostrodon* and *Morganucodon* are valid genera, and this is the generally accepted view (e.g. Kielan-Jaworowska *et al.* 2004, Kemp 2005, Butler and Sigogneau-Russell 2016).

Kühne (1973, p. 59) went on to say, 'It is my firm conviction that in order not to cloud the issue, it is advisable to let fall into oblivion the name *Eozostrodon*. It is obvious that I am not going to fight a legalistic battle on this issue'. This was part of a generally apocryphal struggle between Walter Kühne at the Free University in Berlin and Kenneth Kermack at University College London (UCL) on the one hand and Rex Parrington at the University of Cambridge on the other, which began in the 1940s and continued until the deaths of the principals in the 1980s and 1990s.

Disputes of this kind go on all the time, but this one was coupled with a remarkable episode in palaeontology, the discovery of a suite of extraordinary fossil sites in the south-west of the UK, commonly called the 'Bristol Channel fissures' (Evans and Kermack 1994), sites that richly document the small tetrapod fauna of some 200 Mya, including some of

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the oldest mammals. The story began in the 1860s and went through several phases, the most productive of which began with the work of Walter Kühne and Rex Parrington in the 1930s and 1940s and continue today to provide remarkable new information on early mammals, dinosaurs, and other reptiles (e.g. Gill *et al.* 2014, Whiteside *et al.* 2016, 2022, Jäger *et al.* 2019, Chambi-Trowell *et al.* 2020, Newham *et al.* 2020, Ballell *et al.* 2021).

Further, this was also a time of revolution in methods, methods that had been pioneered by Charles Moore in the 1850s and 1860s and were then seemingly forgotten until their application again by Walter Kühne in the 1930s and 1940s. There were two approaches to recovering tiny microvertebrate fossils, one being to walk (or crawl) over the ground, head down, searching for small bones and teeth, and the other to adopt more industrial methods of screen washing and processing large volumes of sediment. Indeed, Walter Kühne cast a discussion of alternative scientific approaches in light of political philosophy, and he argued in favour of the screen washing approach, because he believed it was more proletarian, based on his own support of the Marxist dialectic (Kühne 1979).

Finally, these debates and disputes received international attention because for a long time, the British Triassic-Jurassic fissure localities provided the richest sample of fossils of the first mammals, and so they laid the basis for understanding of how the mammals emerged, a core evolutionary transition. For example, Lillegraven *et al.* (1979), the first textbook on Mesozoic mammals and written by non-British authors, showed that most of the best materials came from England or Wales. They noted other Late Triassic and Early Jurassic mammal fossils from Germany, Switzerland, China, USA, South Africa, and India, but most were isolated specimens, often single teeth, and were generally described with reference to the core materials from the UK. Exceptions were the discoveries of *Sinoconodon rigneyi* (Patterson & Olson, 1961) and the skull of *Morganucodon oehleri* (Rigney, 1963) from the Early Jurassic of Yunnan, China. Still this century, in an updated version of the book (Kielan-Jaworowska *et al.* 2004), the Late Triassic and Early Jurassic British materials were core, but new and more complete materials are mentioned from Germany, France, Greenland, the USA, China, India, and South Africa. The important point is that all analyses of these specimens through the first 50 Myr of mammalian evolution hinged on the specimens Kühne, Parrington, and Kermack had described. The astounding new fossils of complete Mesozoic mammals from China, many even preserving their hair, are from the Late Middle Jurassic and Early Cretaceous (Meng 2014), so provide astonishing new detail but do not document the critical first 50 Myr.

The aim of this paper is to focus on the discovery of the tiny, but important vertebrate fossils around Bristol and in South Wales, and highlight the pioneering, but divisive, role of key figures, using published and unpublished archives, as well as interviews with witnesses. The wider context is that the Late Triassic and Early Jurassic fissures around Bristol and in South Wales have profoundly changed our understanding of the origin of mammals and of modern-style terrestrial ecosystems, and it is therefore significant to understand how this knowledge accumulated in the past 80 years.

Institutional abbreviations

BRLSI, Bath Royal Literary and Scientific Institution; BRSMG, Bristol City Museum and Art Gallery, Geology collections; BRSUG, University of Bristol Museum of Geology, School of Earth Sciences; CAMZM, University Museum of Zoology, Cambridge; NHMUK, Natural History Museum, London; NHMUK SFRAB, Natural History Museum, Section of Fossil Reptiles, Amphibians, and Birds, London; NMW, National Museum of Wales; UCL, University College London.

CHARLES MOORE IN THE 1860S

Much of the story, from the early days to Kühne revolves around Holwell Quarry, near Frome in Somerset. There are five or six distinct quarries beside the tiny village of Holwell, and Charles Moore (1815–1881) was the first to discover microvertebrate remains there in the 1850s (Fig. 1A). Moore was a self-taught, independent geologist who explored widely throughout his native Somerset, visiting quarries and cuttings on foot, always in search of new fossils. He found the fissures filled with Mesozoic sediment at Holwell in 1855 or 1856 (Savage 1993, Duffin 2019). Moore recognized that the Mesozoic sediments were preserved in fissures or caves within the clearly marine Carboniferous limestones (Fig. 1B), and hence termed these 'abnormal deposits' in three overview papers (Moore 1859, 1867, 1881).

Moore's key discovery, among thousands of other fossils (Moore 1859, 1867), were small numbers of mammal teeth he referred to *Microlestes* (Fig. 2A–C) The name *Microlestes* had been established by Plieninger (1847) for small mammal teeth with pointed cusps from the Rhaetian of Germany, and this was part of the evidence marshalled by Moore to show that equivalent-aged beds occurred in England. He noted that all the fish teeth were also of the same types reported by Plieninger and others from the German Rhät, marine units deposited during a major marine transgression at the very end of the Triassic. He also laid great store on placodont osteoderms found in bedded Rhaetian at the nearby Marston Road site, as well as remains of the two dinosaurs *Thecodontosaurus* and *Palaeosaurus* that he identified in the Holwell fissures, allowing direct comparison with the dinosaurs from the 'Dolomitic Conglomerate' at Durdham Down (Moore 1867, 1876, 1881).

Moore (1867, p. 39) referred to the *Microlestes* quarry at Holwell as the site 'from which I obtained so wonderful a harvest of Rhaetic remains'. He had earlier reported (Moore 1861) that he had processed three cubic yards (= 3 tonnes) of fissure sediment from which he recovered three mammal teeth by 1858, and 20 by 1860, when he gave his 1861 talk (Whiteside and Duffin 2021). He purchased these 3 tonnes of sediment from the quarrymen in about 1855 for 55 shillings (£2.75). Over 3 years, Moore (1867) reported that he had retrieved more than a million fossils from this sample, including '70,000 teeth of one kind of fish alone' (or 45 000; Duffin 2019), noted later as *Acrodus*, which we would now term *Lissodus*, the most abundant teeth of small sharks commonly found in Rhaetian bonebeds. We do not know the details of how he processed the fossiliferous sediments, but Duffin (2019, p. 148) suggests he followed advice from his friend Thomas Rupert Jones (1819–1911), Professor of Geology at the Royal Military College at Sandhurst, who recommended drying fossiliferous clays and then disaggregating them

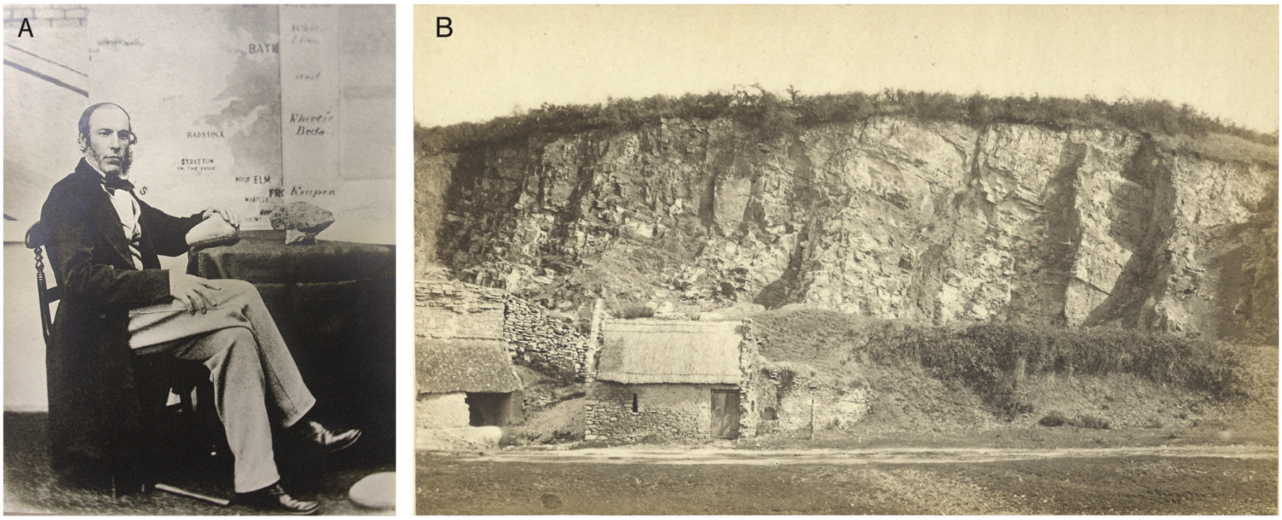

Figure 1. Charles Moore and the Holwell Quarry fissures. A, formal portrait of Charles Moore, sitting in front of a geological map of the Bath area, the local stratigraphic section, and some choice specimens on the table and floor, including his hammer. B, quarry wall at Holwell, the *Microlestes* quarry; the image bears an embossed message reading 'EXCURSIONS OF THE BRITISH ASSOCIATION. Photographed by J D Cogan & F York Bath 1864', so it was provided to conference delegates who attended Moore's field trip to the Mendips during the meeting of the British Association in bath in September 1864. Images courtesy of Matt Williams, Bath Royal Literary and Scientific Institution.

in boiling water, and for sands simply to wash them through to remove muddy debris. The resulting concentrates were then to be passed through sieves, perhaps even a stack of sieves with holes of decreasing sizes so that debris is trapped at each level. A magnifying glass was then used to examine the sieved residues, and Moore reported that it could take several days to work over such material.

Moore (1867) intended to describe his fossil finds from Holwell, but this never happened. Owen (1871) confirmed Moore's identification and the direct comparability of the teeth with those described by Plieninger (1847) from the German Rhaetian. Simpson (1928) revised the Natural History Museum collections of Mesozoic mammals described by Owen, plus others, and erected the new genus *Microcleptes* for some of Moore's specimens, and he identified three species: *Microlestes antiquus* Plieninger, 1847, *Microlestes moorei* Owen, 1871, and *Microcleptes fissurae* Simpson, 1928. Both names *Microlestes* and *Microcleptes* were found to be preoccupied, and the first was renamed *Thomasia* by Simpson (1928) and the second *Haramiya* by Simpson (1947). Later, Sigogneau-Russell (1989) concluded that the genus *Thomasia* is based on lower teeth and *Haramiya* on upper teeth from the same haramiyid dentition.

The monographs on the British (Simpson 1928) and North American (Simpson 1929) Mesozoic mammal materials mark a key point in their study worldwide. Simpson famously remarked at the time that the entire collection, representing all mammals of the Mesozoic known at the time worldwide, including numerous species, and housed in many museums, would fit in his hat. Indeed, much of what he studied in 1928 had been available to Owen in 1871, and not much more had come to light since then.

OTHER FISSURE FINDS

In fact, the first fissures to be identified (Table 1) were in the city of Bristol, in quarries in the Carboniferous limestone along the Worrall Road in Clifton, generally referred to as Durdham Down, where fossils were found in the 1830s. Indeed, these quarries had closed by about 1840, and all that was reported at the time was that the quarrymen had excavated various bones of the dinosaur *Thecodontosaurus*, and these were largely acquired by the Bristol Philosophical and Literary Society, forerunner of Bristol City Museum (Benton 2012). Almost nothing was said by geologists at the time about the nature of the deposits, presumably because they had not witnessed the discoveries or because the quarries were no longer functioning.

Charles Moore resolved the questions much later when he visited the Bristol quarries. He was able to consult the local, Bristol geologist, William Sanders (1799–1875), who had produced an important geological map of the Bristol coal fields in 1862, and had clear ideas about the 'dolomitic conglomerate', a Late Triassic wadi-fill breccia, and its relations to the fissure-filling. Sanders showed that the *Thecodontosaurus* bones occurred in a depression on top of the limestone, either a topographic dip or the floor of a collapsed cavern (doline) that had filled with brecciated Triassic red bed sediments. It is likely that Sanders had actually seen the bones *in situ* in the 1830s, so this evidence should be treated seriously. Robinson (1957a, p. 262) did not include this location in her review of fissure sites because she accepted it as a topographic depression, whereas Halstead and Nicoll (1971) recognized it as a collapsed cavern, a view we follow (Whiteside *et al.* 2016).

Moore (1881) reproduced Sanders' drawing (Fig. 3A) and used his knowledge from working on the *Microlestes* fissure at Holwell to identify the Bristol finds as relating also to ancient karst features, a mix of dolines and vertical fissures. He illustrated his paper with a largely imaginary cross section from east to west (Fig. 3A), showing a deep fissure at Quarry Steps, then a view of the north face of the row of quarries along the Worrall Road, and across Clifton to the Clifton Suspension Bridge. [He labels one spot as 'Bellevue', but he surely means Belgrave Terrace.] He continues west to the Avenue Quarry, located close to the air

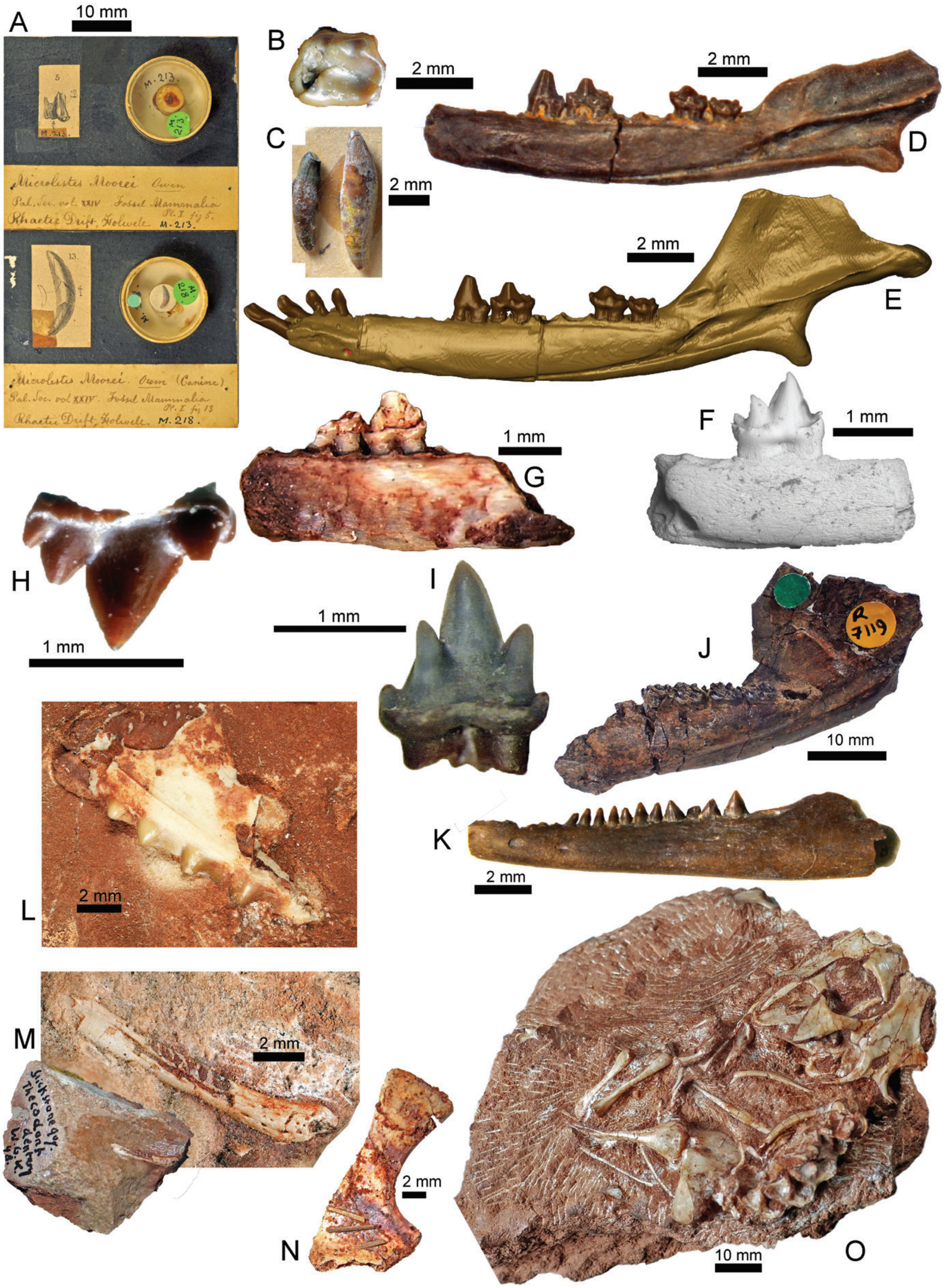

Figure 2. Historically important mammaliaform (A–J) and reptile (K–O) fossils from Bristol and South Wales Late Triassic/Early Jurassic fissures. A–C, Haramiyid mammaliaform fossils; Charles Moore's Holwell 1850s and 1860s collection, showing typical display boxes with BRLSI M213 and M218 (A), BRLSI M216, a molar of '*Microlestes moorei*', now *Thomasia moorei* (B), two examples (of four) of BRLSI M220, haramiyid anterior teeth (C). D, CAMZM Eo D45, from the Parrington collection in Cambridge, a *Morganucodon watsoni* right dentary, medial view; Pontalun 3. E, Jaw composite of *Morganucodon watsoni* (Gill *et al.* 2014), medial view comprising three scans, including CAMZM Eo D45; anterior is from Pontalun 3 specimen NHMUK PV M85507 with complete incisor row; prepared in Bristol in 2003 by Felix Marx. F, SEM medial image of *Morganucodon* sp., a UCL prepared left dentary fragment and molar (m1?) NHMUK PV M23035; from Pant 2,

vent tower for the Avonmouth Railway (at the north end of The Avenue), a quarry that has now been filled, but which showed another fissure containing iron-rich marl. Most of the fissures are narrow and more or less vertical. Continuing to the south-west, Moore (1881, pp. 75–76) noted several vertical fissures in sections of the Carboniferous limestone beside the roadway east of the Clifton Suspension Bridge and reported bedded Rhaetian level with the base of the eastern bridge abutment, but this can no longer be seen.

Moore (1881, p. 72) sampled a few kilogrammes of the mottled yellow and red fissure infilling from beside Quarry Steps and identified some bones, teeth, and other fossils. He also reported a mix of Pleistocene mammal teeth and Rhaetian-age fish teeth and bones from the mottled sediments of the Avenue Quarry. In a later study, Foffa *et al.* (2014) processed small rock samples from several of the original 1830s *Thecodontosaurus* blocks from Durdham Down, and identified a rich fauna of sphenodontians, archosauromorphs, and fishes.

After Moore's insights in 1881, no further fissures beyond Holwell and Durdham Down (Fig. 3B) were reported until the 1930s (Table 1; Supporting Information, Table S1). Swinton (1939) described a new rhynchocephalian, *Clevosaurus hudsoni*, based on numerous isolated specimens of toothed jaws and other fragments from 'fissures in the Carboniferous Limestone at Tortworth, near Thornbury, Gloucestershire'. These had been collected by Mr Frederick George Hudson (1883–1963), a farmer and President of the Cotteswold Field Club from 1938–1940. Hudson had worked earlier in Lancashire and lived in Gloucestershire through the late 1920s to mid-1940s, first as schoolmaster at Dursley until his resignation in 1931, and then as a chicken farmer at Stinchcombe, Dursley. He presented papers to the Field Club on a range of geological and archaeological topics around Gloucestershire but published little. The exact locality is Cromhall Quarry, near Tortworth, then sometimes called Slickstones Quarry, located 10 km south of Hudson's smallholding at The Elms, Stinchcombe. The type specimens of *Clevosaurus* were donated to the NHMUK and the remainder of Hudson's material to Professor W.F. Whittard (1902–1966) at the University of Bristol (e.g. Fig. 2L).

KÜHNE MEETS PARRINGTON

Despite the hard labours by Charles Moore in the 1860s, and his insights about the Durdham Down fissures in Bristol, nobody else seems to have thought about making a concerted hunt for other fissures around Bristol. Hudson's find before 1939 is notable but was not connected to other discoveries at the time, although after World War 2, others followed his lead to Cromhall (see below).

So, when Walter Kühne (1911–1991), a German palaeontologist, and his wife Charlotte, emigrated to England, he took on this task. It may seem extraordinary that a German scientist would move to the UK in 1938, without employment and in the face of approaching war. This was not part of the Jewish diaspora but was forced upon Kühne by his support of communism. Kühne (Fig. 4) had had a troubled time in Germany (Krebs 1991, Schmitt 2013, p. 86): after school, he had studied for a few semesters at the University of Berlin but was expelled in 1933 because of his political engagement with the far left and was imprisoned for 9 months before trial. He married Charlotte Petsche in 1934, and for several years he earned a living in Germany as a freelance palaeontologist, selling fossil insects and doing other tasks; he 'worked as a library assistant, wrote popular science articles and collected documents for the Prussian curator-general for a directory of medieval church bells with thread reliefs' (Krebs 1991, p. 19).

Remarkably, Walter Kühne and his wife were saved by their move to Britain. At first, they survived by continuing to sell fossils. As an example, Cromie (2001) reports a reminiscence from A.W. ('Fuzz') Crompton at Harvard, that Kühne went to Francis Rex Parrington (1905–1981) at Cambridge University, known for his intense interest in the oldest mammals, and told him he knew where to collect specimens. Parrington, it is said, offered him the immense sum of £5 for every specimen he could find. Tom Kemp (interview, 15 March 2022) confirms this story, as he recalls hearing it from Parrington himself:

> Parrington's story was that before the war – 1938 – this character appeared knocking on his door in Cambridge, who announced that he was Walter Kühne and that he was a refugee from Nazi Germany because he was a communist, and he was a palaeontologist. I don't know whether Kühne specifically asked for work, but he said he had found Mesozoic mammal teeth. Of course, this was the time when Moore's Holwell haramiyids were pretty limited in numbers, and otherwise the earliest mammal teeth known were from the Stonesfield Slate, Middle Jurassic in age, so the idea that this guy had found mammal teeth in the Lower Jurassic or even Rhaetian, upper Triassic, was very exciting. And Kühne explained that the way he looked for fossils wasn't to go around with a hammer

which yielded a huge amount of material in 1955. G, NHMUK PV M27273, the only toothed specimen of a *Kuehneotherium* jaw in the UCL collection, prepared by David Pacey in 1973 for his PhD, under the supervision of K.A. Kermack; Pant 4. H, *Kuehneotherium praecursoris* tooth CAMZM Sy 87, buccal view; Pontalun 3. I, NHMUK M45079, mid-row left lower molar of *Kuehneotherium* sp., in lingual view; Pant 5, 1979, the last fissure collection made by the UCL team, in 1979–80. J, NHMUK R7119, right paratype dentary of *Oligokyphus*, antero-medial view, W.G. Kühne collection; Windsor Hill Quarry prepared either during his World war 2 internment on the Isle of Man or later; first of the fissure vertebrates to be reconstructed from isolated bones only. K, BRSUG 29383, mid and posterior part of left dentary of *Gephyrosaurus bridensis* in lateral view; Pontalun 3, prepared in Bristol by Maurice White, technician of R.J.G. Savage. L, NHMUK R9249, lateral view of left syntype maxilla of *Clevosaurus hudsoni*; collected in 1937–38 by F.G. Hudson, Cromhall Quarry. M, NHMUK R 6099, first archosaur fossil (a crocodylomorph) recorded from Cromhall; Kühne collection, 1948. N, BRSUG 1823, *Kuehneosaurus latus*, right scapula, medial view; Tom Fry collection, *c.* 1948. O, NHMUK R36832, a slightly disarticulated front skeleton of *Clevosaurus hudsoni*; P.L. Robinson collection (probably) 1954. Photo credits: Matt Williams and BRLSI (A–C), Andrew Conith (F), Ron Every (H), Mike Cawthorne (N); other photographs taken by the authors.

Table 1. A timeline of the fissure locality discoveries with the key researchers involved and the vertebrate, principally tetrapod, fauna recorded. Supporting Information, Table S1 provides further detail.

Year	Name of locality	Discoverer	Key fauna
1834	Durdham Down	Discovered by quarrymen; named by H. Riley and S. Stutchbury.	*Thecodontosaurus*, a phytosaur, possible coelophysoid, crocodylomorph, *Diphydontosaurus* and *Clevosaurus*. A few sharks' teeth.
1859	Holwell '*Microlestes*' Quarry	C. Moore	*Thomasia*, *Pseudotriconodon*. *Thecodontosaurus*, other archosauromorphs, *Diphydontosaurus*, *Penegephyrosaurus*, *Variodens*, possible *Gephyrosaurus*, unidentified lepidosaurs. *Pachystropheus* and a placodont. Also, coelacanth, many shark and osteichthyan teeth plus scales, gill rakers, and other fish fossils.
1938	Slickstones/ Cromhall	F.G. Hudson	*Clevosaurus hudsoni*
1939	Windsor Hill	W.G. Kühne	*Oligokyphus major*
1939	Holwell '1' and '2'	W.G. Kühne	*Eozostrodon*, *Microlestes*, *Clevosaurus*. Later, placodonts, possible *Oligokyphus* and crocodile.
1945	Ruthin	T.M. Thomas	Procolophonids, *Tricuspisaurus*
1946	Emborough	W.G. Kühne. Later, 1948, T. Fry. Later, 1985, Fraser and Walkden discover *Kuehneotherium* and *Planocephalosaurus*.	*Kuehneosaurus*, *Variodens*, archosaurs, *Pachystropheus*, lepidosaurs, including *Clevosaurus* and *Planocephalosaurus*. *Kuehneotherium*
1946	Batscombe	W.G. Kühne. Later, T. Fry 1948–1950.	A kuehneosaur *Kuehneosuchus*, other reptiles?
1947	Ruthin	W.G. Kühne	*Tricuspisaurus* and procolophonoids (cf. *Scoloparia*, *Haligonia*, a leptopleuronine, *Smilodonterpeton*), rhynchocephalians (cf. *Diphydontosaurus*, *Diphydontosaurus* sp., *Planocephalosaurus* sp.). Archosauromorphs including crocodylomorphs.
1947	Highcroft	W.G. Kühne	*Clevosaurus*, *Diphydontosaurus*
1947	Duchy	W.G. Kühne. Further material P. Robinson and F. Mussett (1952).	*Morganucodon*, *Kuehneotherium* (*Kuehneon*, Duchy no. 33) and *Gephyrosaurus*
1947	Pant (fissure 1)	W.G. Kühne	Bone fragments
1948	Slickstones	W.G. Kühne; also T. Fry	*Clevosaurus* and a 'thecodont'
1951	Slickstones	P.L. Robinson	Ten reptiles including *Clevosaurus*, *Planocephalosaurus*, *Diphydontosaurus*, other lepidosaurs and a procolophonid. Archosauromorphs e.g. cf. *Aenigmaspina*.
1952	Pant-y-ffynnon	P.L. Robinson, K.A. Kermack	*Pantydraco*. *Terrestrisuchus*, *Aenigmaspina*, *Pandraig*, *Clevosaurus cambrica*, *Diphydontosaurus* sp. Other sphenodontians.
1953	Cnap Twt	K.A. Kermack, F. Mussett, T.M. Harris	Lepidosaurs and rich plant remains.
1953–54	Pontalun (fissure 1)	K.A. Kermack, F. Mussett	*Kuehneotherium*, *Gephyrosaurus*, *Morganucodon*
1955–56 1959–60	Pant (fissure 2)	K.A. Kermack, F. Mussett	*Morganucodon*, *Gephyrosaurus*, *Kuehneotherium*
1957	Ewenny (fissure 2)	K.A. Kermack, F. Mussett	*Gephyrosaurus*, *Morganucodon*
1957–59	Pontalun (fissure 2)	K.A. Kermack, F. Mussett	*Morganucodon*, *Kuehneotherium*, *Gephyrosaurus*
1962–63	Pontalun (fissure 3)	L. Middleton (quarry manager), K.A. Kermack, F. Mussett, P. Lees	*Morganucodon*, *Gephyrosaurus*, *Kuehneotherium*. Occasional archosaur teeth.

Table 1. Continued

Year	Name of locality	Discoverer	Key fauna
1968–73	Pant (fissure 4)	K.A. Kermack, F. Mussett, P. Lees	*Morganucodon, Kuehneotherium, Gephyrosaurus, Clevosaurus, Oligokyphus, Thomasia, Bridetherium, Paceyodon*, archosaur teeth.
1963–present	Holwell	R.J.G. Savage, M Waldman, C.J. Duffin, C.J.T. Copp	Tritylodont *incertae sedis*. Placodonts, *Thecodontosaurus*, lepidosaurs including *Diphydontosaurus*.
1974	Tywn-yr-Odin (or Odyn)	K.A. Kermack, F. Mussett, M. Howgate	*Legnonotus* (fish)
1975–present	Tytherington	M.C. Curtis, T. Ralph. Later (1976–1984), D.I. Whiteside discovers another 16 fissures.	*Thecodontosaurus*, cf. *Terrestrisuchus*, a phytosaur, a coelophysoid, other archosauromorphs e.g. a drepanosaur. *Diphydontosaurus, Clevosaurus* sp. *Pelecymala, Sigmala*, other rhynchocephalians, and a procolophonid. Also shark teeth and other fish fossils e.g. *Pholidophorus*.
1979–present	Cromhall (formerly Slickstones)	N.C. Fraser, G.M. Walkden. D.I. Whiteside and M.C. Curtis discover the 'cover' sequence at Cromhall in 1984.	See Slickstones 1951 and other archosauromorphs e.g. *Agnosphytis*, a drepanosaur. *Diphydontosaurus, Clevosaurus minor, Fraserophenodon, Pelecymala, Sigmala*, other rhynchocephalians, and two procolophonids. Early squamate *Cryptovaranoides*. Also shark teeth and other fish fossils e.g. *Pholidophorus*.
1979–80	Pant (fissure 5)	K.A. Kermack, F. Mussett, P. Lees	*Kuehneotherium, Morganucodon*, larger morganucodontid, a tritylodont, *Gephyrosaurus, Clevosaurus* cf. *convallis, Thomasia*, archosaur teeth.
1989	Woodleaze (Tytherington, south quarry)	C. Alabaster	*Clevosaurus sectumsemper. Diphydontosaurus*
2007	Pant (fissure 6)	P. Gill, M. Pound	Research on taxa currently underway.

> in the traditional way, but to start with the geological maps. He clearly had an awareness of the idea of fissure fills. So, you could go to fissure-forming places particularly in the Carboniferous; in there you could find underground channels which were choked up with junk from the surrounding territory.
>
> Kühne brought some haramiyids, *Microcleptes*, and Parrington said he would pay him £5 each for every tooth, and that was a kindness to Kühne. So, in 1938 or 1939, along comes Kühne with a handful of about 20 haramiyids, and these two amazing teeth with three cusps in a row and little trace of a cingulum, and these got Parrington's heart beating so fast… it was the earliest possible mammal, the ancestor of all mammals. Parrington used these in his 1941 paper, saying it was so important the world ought to know. Then this was followed by his 1947 paper. In 1941 he named *Eozostrodon*… and in 1947, he compared them with specimens that had already been found by Peyer in Switzerland. He thought the name *Eozostrodon* was suitable, meaning the 'dawn of the ring', referring to the cingulum.

The exact story and eventual home of the Kühne specimens was later disputed. Parrington (1978, p. 189) wrote, rather testily perhaps:

> Contrary to what stands in print (Parrington 1947), Kermack *et al.* (1973, p. 105) say of Kühne's collection, 'The whole collection was sold to Parrington who named the two teeth in question *Eozostrodon parvus* and *E. problematicus*'. This statement is both erroneous and irrelevant. If they had read Parrington's (1947) account of Kühne's material, they would have learned that the tooth with the field number H 3 was sold to Bristol University while the tooth numbered H 11 was sold to the Bristol Museum and lost in the air attack on that city during the 1939–45 war. Nine of Moore's specimens have been lost (Simpson 1928) and it is not desirable that the Curators of the Cambridge University Museum of Zoology should some day be held to have lost two specimens which were never in their possession except for description (H 3).

Here, Parrington is talking about two collections—but conflates the two into one argument—he references Moore's quite different specimens, and he appears to have added the missing Moore teeth for effect, even though they are unconnected with Kühne's collections.

In the late 1930s, Parrington (Fig. 5A) was the most obviously well-established palaeontologist for Kühne to approach. Parrington had been at Cambridge since 1927, starting as Assistant to the Director of the Museum of Zoology, and was then promoted to the Directorship and a Lectureship in Zoology in 1938 (Charig 1990). By then, he had had experience in field work in Africa, and had published several papers on Triassic cynodonts through the 1930s. He was shifting attention to the origin of mammals, and Kühne's finds provided the first of many papers on Mesozoic mammals (Parrington 1941), in which he named the first mammals from the Triassic, two species *Eozostrodon parvus* and *Eozostrodon problematicus*, each based on a single tooth (Fig. 5B, C). Subsequently Parrington (1971) designated *E. problematicus* as a junior synonym of *E. parvus*.

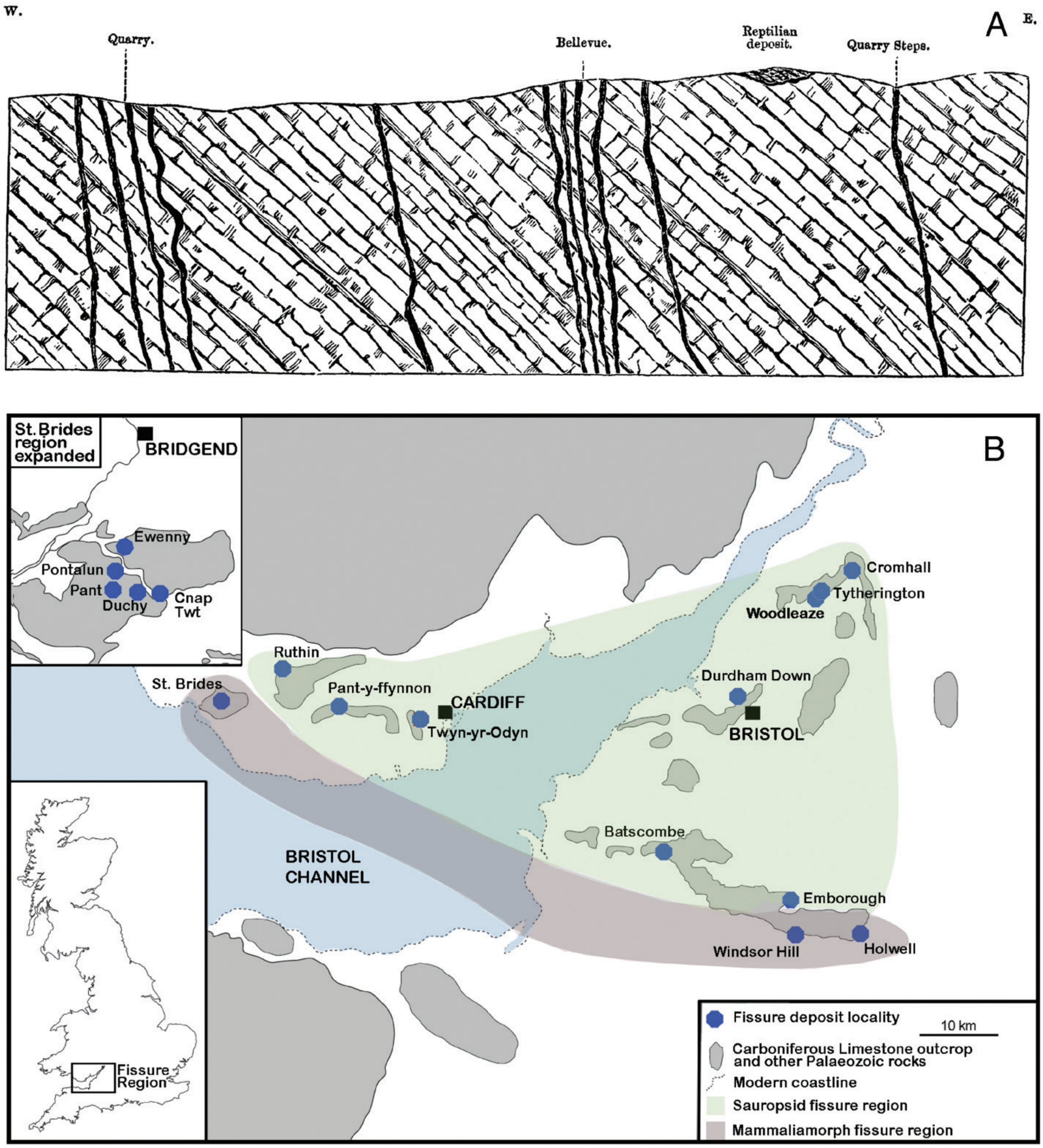

Figure 3. The Bristol fissures. A, Section of the edge of Durdham Down, showing Charles Moore's rendition of a drawing by William Sanders of Bristol, confirming that there were numerous semi-vertical fissures of Triassic age penetrating the uplifted and steeply dipping Lower Carboniferous limestones in and around Bristol. B, Map of the Severn Estuary and Bristol Channel showing the main fissure sites around Bristol and in South Wales, distributed on islands of Carboniferous limestone that stood above the shallow Rhaetian-to-Jurassic-aged seas. A, from Moore (1881, fig. 1). B, modified from Whiteside *et al.* (2016); fauna from these localities is shown in Table 1.

Walter Kühne had somehow re-located the fissure where Moore found his *Microlestes*, checking its exact location and lithology as closely as he could, using Moore's written descriptions. Kühne worked at Holwell from January to July 1939. In explorations around the area, and using his newly established knowledge of what the fossiliferous fissures looked like, he found a rich source at Windsor Hill (Fig. 3B) in September 1939; he identified the source as a tectonic fissure fill of 'Charmouthian' (= Pliensbachian) age, and he first named it 'Mendip 14'. According to the journals of Tom Fry (see below), he also discovered reptile bones in Batscombe Quarry near Cheddar, but Robinson (1957a, table 1) asserts that the Batscombe fissure discovery was in 1946.

THE SECOND WORLD WAR, AND AFTER

The outbreak of World War 2 in September 1939 had a huge impact on most scientists, particularly those in the nations involved

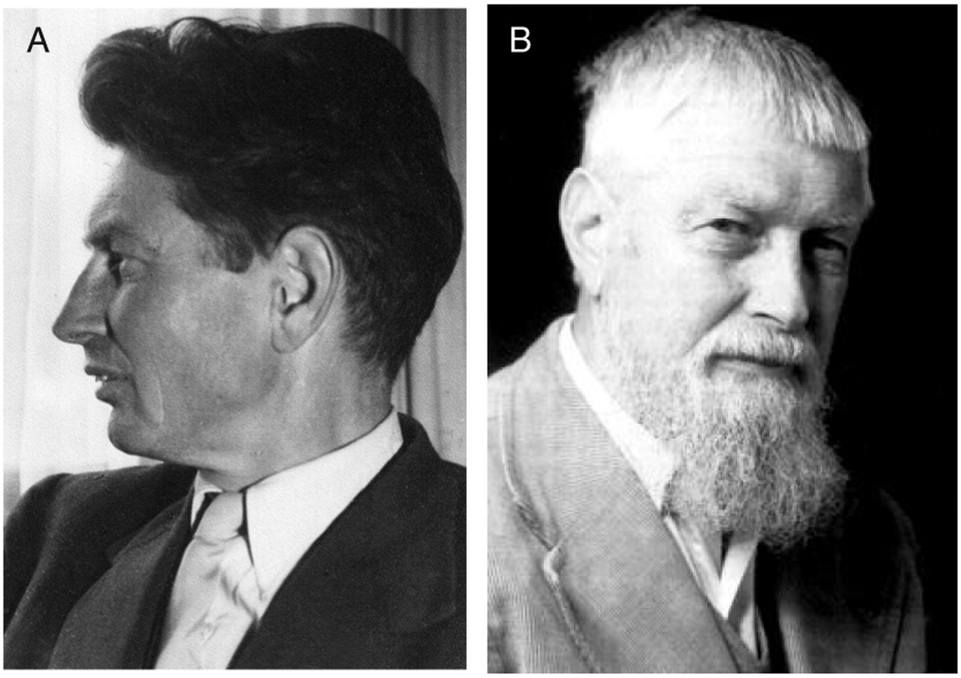

Figure 4. Walter Kühne (1911–1991), as a young man about 1950 (A), and as an older more patrician-looking professor, about 1980 (B). Both images, Wikimedia.

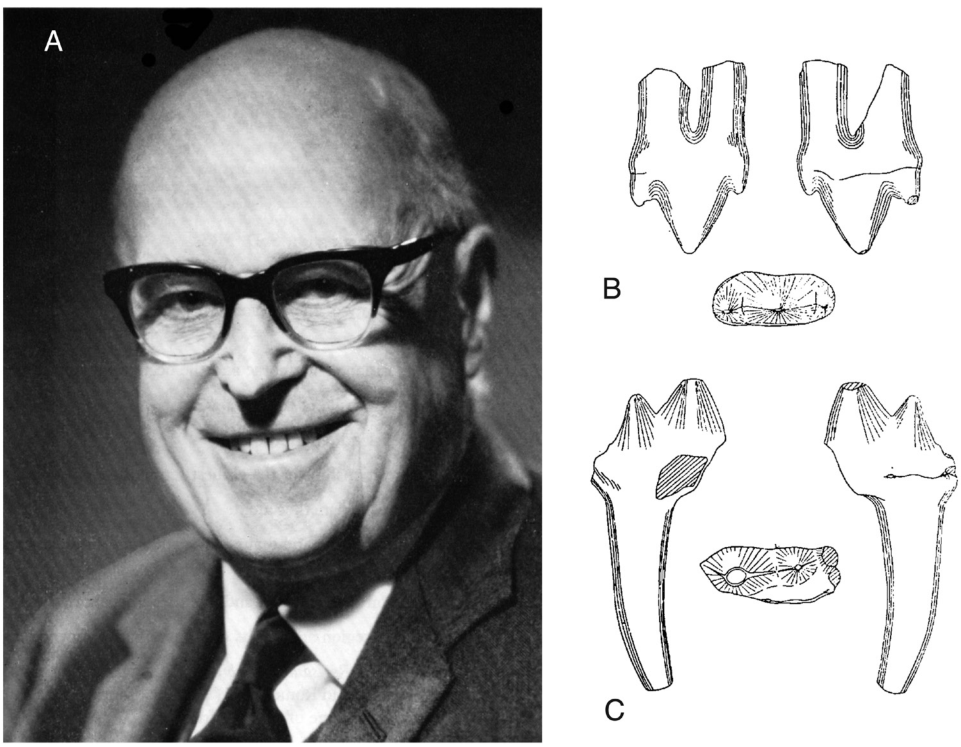

Figure 5. Francis Rex Parrington (1905–1981), shown in the 1960s (A), and his two prize Mesozoic mammal teeth, the type specimens of *Eozostrodon parvus* (B) and *Eozostrodon problematicus* (C), both found by Walter Kühne at Holwell, Somerset.

in the war. Parrington had visited Germany in 1936, and was convinced war was inevitable, so he signed up for military service 2 days after war was declared (Charig 1990, pp. 365–366). Parrington served in the Royal Artillery during the entire war, and only returned to Cambridge in the autumn of 1945, when he resumed his work on the early mammals.

Meanwhile, Walter Kühne had a productive time during the war and was able to continue his palaeontological work unhindered. He and his wife were interned on the Isle of Man as enemy aliens; indeed, Kühne was arrested while engaged in field work just a few days after Britain had declared war on Germany. As Tom Kemp recollected (interview, 15 March 2022):

> Kühne was an alien, as a German, and he was allowed to stay but had to report every day or every week at the police station, and he then disappeared. They finally found him wandering around Somerset with six-inch-to-the mile maps, making strange marks on them. That wasn't a smart move in 1939. So, he was interned on the Isle of Man. Meanwhile he was in with the UCL lot, and D.M.S. Watson arranged for all the *Oligokyphus* stuff from Windsor Hill to go with him. So, Kühne had a wonderful war, writing his monograph, while the bombs were falling.

This is confirmed by Kielan-Jaworowska (2013, pp. 74–75) who reported how Walter and Charlotte Kühne had large volumes of material to process during their internment. Even on release back to Bristol, Kühne did not escape controversy. 'He spotted an interesting fossil in the wall at Temple Meads Station and produced a geological hammer to dig it out. The railway police arrested him, and Professor D.M.S. Watson had to come down from London to rescue him' (Pat Ferguson, letter, 11 April 2023).

After the war, Kühne (1947) described his method: the Holwell fissure rock was stored on site, and he washed it, 1 hundredweight (= 51 kg) at a time, in a large barrel in which the sediment was mixed with water. He goes on to say:

> After a day or two, the clay in the barrel was violently agitated with a digging fork, until the clay was converted into a sludge. The sludge was put upon two attached sieves, 2 ft. by 2 ft., the upper sieve having holes of 2.5 mm diameter and the lower holes of 1 mm. The two sieves were put on a wheelbarrow and the sludge poured on to the upper sieve; the thick slime accumulating below in the wheelbarrow, was discarded into the brook. The gritty material resting on the 1 mm sieve was collected and thoroughly washed, first in a tank and later in the brook, and dried. Another sifting of the dry concentrate, disposed of those particles below 1 mm which were still in it. The concentrate was then hand-picked without optical aid. About 40 gr. were heaped upon a sheet of Bristol board and 10 to 15 particles were moved at a time towards the collector and scrutinised. All fossils and all other objects attracting the eye were picked out and the remainder discarded.

Kühne reduced 2250 kg of clay to 121 kg of concentrate from which 19 mammalian teeth or fragments were extracted. Kühne (1949a, p. 350) emphasized 'the desirability of strict surveillance of all quarries in the Carboniferous Limestone of Somerset and South Glamorgan. As quarrying continues, new fissures may be revealed at any time …'.

Impressed with his promise, and through the influence of Watson, Kühne secured a post as Assistant Lecturer at UCL in 1944, and he held it until 1951 (Schlüter 1981, Kielan-Jaworowska 2013, p. 75, Schmitt 2013, p. 86, Şengör 2021). During this time, he wrote his doctoral dissertation on the tritylodont *Oligokyphus*, of which he had extracted over 2000 bones and teeth from half a ton of fossiliferous sediment from Windsor Hill and submitted it to the University of Bonn in 1949. His doctoral work on *Oligokyphus* (Fig. 2J) was published by the Natural History Museum London as a lavishly produced monograph (Kühne 1956). In his review of the monograph, Simpson (1957) wrote, 'In 1938 a young German student, Walter Kühne, went to England … In the course of the next ten years, some of them spent in an internment camp, he proved his point. With almost superhuman patience and with, it is pleasant to add, the wholehearted help of nominally enemy British scientists, he accumulated more than 2000 specimens of the early Jurassic tritylodontid genus *Oligokyphus* …'.

KÜHNE FINDS MORE FISSURES

Walter Kühne continued his search for bone-bearing fissures during his tenure at UCL and found two Triassic sites rich in tiny reptile bones, one in 1946 at Emborough Quarry, and the other at Batscombe Quarry, as well as a single reptilian bone from a fissure at Highcroft Quarry, all in the Mendips (Fig. 3B; Robinson 1957a, p. 261). The Emborough fissure was excavated by Kühne in 1947, with financial support from the Gloyne Fund of the Geological Society of London, and he reported his new finds to the Society (Kühne 1949b). He also discovered the poorly known Highcroft Quarry fissure fauna in 1947, selling two specimens he identified as either *Palacrodon* or *Clevosaurus* to the NHMUK in 1948; in a letter to Pamela Robinson dated 7th November 1952 (copy in NHMUK SFRAB archive) he stated 'Highcroft is a pig' because of the difficulties of finding fossils and of freeing them from the quartzite fissure matrix.

In 1947 too, Kühne began exploring the Carboniferous limestones of South Wales (Fig. 3B; Table 1; Supporting Information, Table S1), realising that bone-bearing fissures should be present based on geological similarities to the Mendips area; this is an example of his brilliance as a field observer and fossil finder. He had recognized (Kühne 1949a) that the grey limestone matrix was unlike typical Late Triassic red sediment and was likely to be younger ('Lower Lias or older'). Kühne took a few handfuls of matrix he had collected in summer 1947 from a fissure in Duchy Quarry, near Bridgend, Glamorgan, back to London, and he reported (Kühne 1949a), 'on re-examining one of the lumps of rock under the binocular microscope, my eye fell upon the stumps of two broken roots of a tooth, and it was possible to extract a complete posterior mammalian cheek tooth'. This specimen (NHMUK PV M16536) was a new mammal that he named *Morganucodon watsoni*, from Morganuc = South Glamorgan in the Domesday Book and in honour of D.M.S Watson (Kühne 1949a). This he identified as a triconodont mammal. Thus began one of the most fruitful field campaigns to recover rich resources on some of the world's earliest mammals, but this also began the long-lasting dispute over nomenclature noted above, whether *Eozostrodon* named by Parrington (1941) and *Morganucodon* named by Kühne (1947) were distinct taxa or one and the same.

Kühne (1950) noted a further discovery in Duchy quarry of 'about 50 teeth or fragments of teeth'. Frances Mussett (unpublished UCL field guide; NHMUK SFRAB archive) provides a further first-hand account of the Duchy quarry finds and the importance of her visit with Robinson: 'This quarry is where Kühne made the first discovery of *Morganucodon* in 1947. He picked up lumps of grey fissure material from the floor of the quarry - he never found the fissure from whence it came. Dr Robinson and I visited the quarry in 1952 and picked up more lumps of the grey matrix. We sent this material to Kühne in Berlin, and it formed the basis for his second definitive paper on *Morganucodon*'.

Kühne (1958) confirmed that these specimens were found in fissure sediment left behind after the fissure itself had been quarried away, and they were used to reconstruct a provisional postcanine dentition. Kühne (1958, fig. 27C, D) also figures *Morganucodon* dentaries, the first probably from Duchy, and the second from Kermack (1956). This Kermack paper described an exhibition of new Mesozoic mammals at the Geological Society, but did not figure specimens, so presumably Kühne made his drawings from the specimens at UCL. Kermack (1956) described the successful results of field work at the Pant and Pontalun (now known as Lithalun) quarries. In fact, Kühne also discovered a fissure at Pant Quarry in 1947 (Fig. 3B, 13C), but it yielded only scraps of bone, and was always named 'Kühne's fissure' in the Kermack field notes (NHMUK SFRAB archive).

Morganucodon was not the only mammal found at Duchy Quarry by Kühne, and in 1950 he described a 'symmetrodont tooth', adding the personal note that 'my wife found a fragment of matrix, and on inspecting it, I detected a mammalian tooth'. He noted this was very different from *Morganucodon* and had triangulated cusps. This specimen was given the number Duchy 33, and subsequently named *Kuehneon duchyense* by Kretzoi (1960). The specimen has been lost and is designated a *nomem vanum* (Kermack *et al.* 1968) or *nomen dubium* (Kielan Jaworowska *et al.* 2004).

At first, Kühne was unaware that Trevor Thomas and his brother had found fossiliferous fissures at Ruthin Quarry in 1945 (Kermack *et al.* 1973, p. 99), later described by Thomas (1952) as a collapsed Triassic 'cave'. Kühne excavated the Ruthin deposit in 1949 and his collection is held in the NHMUK; some of his original collection of rocks was prepared in Bristol University in 2019 (Skinner *et al.* 2020). In the letter to Pamela Robinson on 7th November 1952, Kühne gave a report on Ruthin and mentioned the jaw of an animal 'probably related to' *Trilophosaurus* that corresponds with his invoice for sale of the specimen (plus two others of the same animal) to the NHMUK dated 9th September 1948 (copy in digital documents, NHMUK SFRAB). This invoice states that Kühne must have found the fossils in 1947 or 1948. Robinson (1957b) described the trilophosaur-like specimens from Ruthin as *Tricuspisaurus thomasii* and another trilophosaur from Emborough Quarry as *Variodens inoppinatus*; she does not mention Kühne's suggestion that *Tricuspisaurus* is a trilophosaur. The species name *T. thomasii* is a reference to Trevor M. Thomas who Robinson (1957b) stated made the 'original discovery of this reptile'. Robinson notes that she worked on the NHMUK specimens collected by Kühne, and in fact these formed the basis of her description of *Tricuspisaurus*.

In the same 1948 NHMUK invoice for the Ruthin fossils, Kühne sold *Clevosaurus* bones and teeth and jaw fossils of a 'thecodont' (NHMUK R 6099; Fig. 2M) from Slickstones (= Cromhall) Quarry; this is the first mention of archosauromorphs from that quarry. The invoice, totalling £59.50, further details the sale of bones from Emborough (probably *Kuehneosaurus*), Batscombe (kuehneosaur), and Windsor Hill (*Oligokyphus*). Therefore, the discovery of the highly fossiliferous Somerset localities of Emborough, Batscombe, and Windsor Hill, as well as Ruthin and Duchy in South Wales, can be assigned to Kühne; the 'thecodont' fossils in Slickstones (= Cromhall) Quarry, increased its known biodiversity. As he said in the 7th November 1952 letter to Pamela Robinson 'I had a completely untouched field of near 200 quarries'. There is a later invoice for £52.50 from Kühne to the NHMUK where he details finds of placodont and *Oligokyphus* teeth from Holwell, 'thecodont' bones from Emborough, and bones from Batscombe. This sum is equivalent to nearly £1500 at 2023 prices.

However, in 1952, after his research on *Oligokyphus* was essentially complete, but before his monograph was ready for the printer, Walter Kühne and his wife returned to Germany, and he remained in Berlin for the rest of his life. Krebs (1991, p. 19) comments: 'in 1952 Walter Georg Kühne returned to Berlin, presumably in the hope that, as a former fighter for the communist idea, he would be welcomed with open arms by the Humboldt University in East Berlin. Nothing like that happened. Kühne still had to keep afloat selling fossils. At that time, the graptolites, which he prepared completely freely, were his main source of income'. Kühne was first supported by a stipend from the Deutsche Forschungsgemeinschaft to continue his work on English fossil mammals (Şengör 2021), and became Dozent at the Freie Universität Berlin in 1955 and qualified as professor in 1958 thanks to his Habilitation on early mammals and their relatives that he had excavated in the UK. Meanwhile, he and his wife Charlotte divorced in 1956, and he re-married in 1963, to Ursula Kühne, a distant relative. He was promoted to Assistant Professor in 1963 and Full Professor in 1966, and retired in 1976 (Schmitt 2013, pp. 86–87, Şengör 2021).

After retirement, Kühne (Fig. 4B) continued active academic work, and frequently attended the annual meetings of the Society of Vertebrate Palaeontology and Comparative Anatomy in the UK. His obituarists, Kohring and Schluter (1991) wrote that Walter Kühne was 'a rebel who spoke his mind, right or wrong', and many would regard him 'as an inspiring and thoughtful palaeontologist'. Interestingly, he was an ardent, and perhaps the only German, supporter of Willi Hennig's (1913–1976) ideas of cladistics for many years, and some would say that this support might have aligned with his Marxism (Schmitt 2013, pp. 86–90). Schlüter (1981) noted that Kühne never received any medals or academy fellowships, and as Şengör (2021, p. 760) notes, 'All of this, plus his difficulty in suffering fools gladly, goes a long way in explaining why his chest remained bereft of decorations'.

KÜHNE'S 'PALÄONTOLOGIE UND DIALEKTISCHER MATERIALISMUS'

Kühne's strangest publication provides a strong link from Charles Moore to Kühne himself and the later studies of the Late Triassic and Early Jurassic fissures in South Wales and around Bristol. Kühne (1979) is a short book titled 'Paläontologie und dialektischer Materialismus' (Fig. 6), published by the distinguished German publishing house Gustav Fischer, based in Jena, which by chance fell in East Germany after the War, even though it had long published palaeontological journals and books coming from the Prussian scientific establishment and Germany as a whole. The book was noted occasionally, but very little referenced by other scientists, until Şengör (2021) wrote about it as a historical curiosity. He noted that the book is more about how to study geology and palaeontology in a practical sense, and indeed the 'Marxist tirades' form only a small part of the book, and the overall approach and philosophy does not differ much from what Karl Popper (1902–1994) said, even though

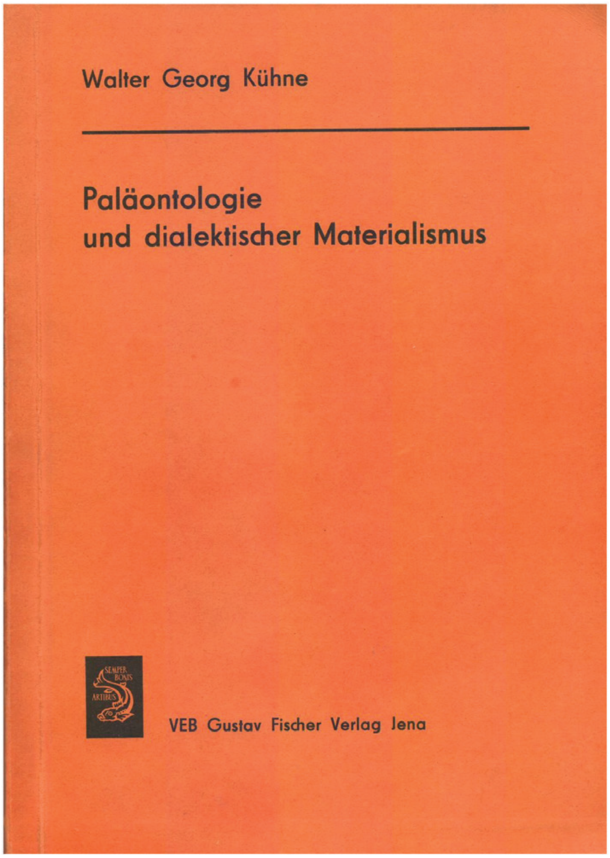

Figure 6. Kühne's 'Paläontologie und dialektischer Materialismus', published in 1979, showing the characteristic orange card cover of the Gustav Fischer publishing house.

Popper detested Marxism. In fact, Şengör (2021, p. 765) notes that when he was Kühne's student in Berlin, he saw 'absolutely no indication that he was a Marxist'.

In the last year of his life, Kühne (1990) published an English translation of the book, with additional notes. One of the authors (M.J.B.) had some small role in the production of this work, because Walter Kühne asked him to read his translation and improve the English, which was done, but the published work includes none of the small corrections. Here, as Şengör (2021) outlines, Kühne seeks to apply a Marxist dialectic approach to palaeontology, using his own work as an example. He argues that key to his success in discovering so many fossiliferous fissures in and around Bristol and Cardiff was his application of what he called the 'building of relations', whereby he looked at the occurrence of Charles Moore's fossiliferous deposits in cave deposits at Holwell, and predicted where more such finds might be made, and indeed he went on to discover the fossils at Windsor Hill, as well as numerous other fossiliferous fissures in the Mendips and in South Wales. Kühne (1979, 1990) goes on to argue that the Fremdeffekt ('success of the alien') was important too, that he, as a German, came in and could see things the British geologists had long been unable to see. As he says (Kühne 1990, p. 21), 'The "success" of *Rattus* on a pacific island is commensurable with my success in Somerset'. However, his dialectical explanation of why he, as a visiting German, could develop his programme successfully, while the blinkered local geologists could not, is not entirely clearly explained.

Kühne (1990, pp. 17, 132) connected his work at Holwell to Charles Moore, and had read his papers before visiting England. Throughout the book, he discriminates a proletarian vs. a bourgeois division of effort, although he does not use these terms. The bourgeois professor either does no field work, or picks daintily over a site, selecting such beautiful specimens as he can see. The proletarian on the other hand digs deep and processes masses of sediment and thereby secures a much better return, based on heavy labour but also on growing and intimate knowledge of the locality and rock. Kühne himself was on the side of the proletarian, having had to support himself for some 15 years as a commercial palaeontologist, relying on fossil sales to make money. He talks (Kühne 1990, p. 6) of the 'monopoly of learning by the ruling class' and emphasizes that William Smith, founder of stratigraphy, was of the working class (Kühne 1990, p. 12).

Kühne (1990, pp. 87–92) then introduces the pioneering work of Claude W. Hibbard (1905–1973), and he reproduces a long letter Hibbard had written to him in 1961. In this, Hibbard describes how he introduced screen washing in 1928 as a means to recover all the small fossils from Tertiary sites in the American West, and to provide much richer data than could be achieved by the traditional methods advised by the professors, namely to crawl over the sites with a pair of tweezers to pick up small remains. Hibbard constructed a wooden box with a wire mesh base, shovelled fossiliferous dirt into the box and shook it in a flowing stream. The effect was to wash away the mud quickly and to concentrate the debris, comprising grains of sand and microfossils. But the professors from the American Museum, Harvard, Yale, and Princeton ridiculed him and sought to prevent their students from learning Hibbard's method (Hibbard 1949). It is worth noting that, although Hibbard became a professor at the universities of Kansas and Michigan, this was later in life; he had worked his way up from holding short-term technician posts at Michigan in the 1920s and 1930s when he perfected his field methods. Kühne (1990, p. 144) talks about the labour involved in fossil collecting, 'the agricultural labourer, the quarry worker, made direct contact with the earth, not so the geological scientist'. Kühne (1990, pp. 134–135, 145–147) values the earnest endeavours of amateur fossil hunters, disagrees with legislation to limit their collecting activities, and fully understands their need to sell their best finds in order to provide them with a means of sustenance.

It is interesting that, although he mentions Charles Moore with approval, and as his precursor in working the Bristol fissures for microvertebrate fossils, Kühne perhaps did not realize that Moore had in fact used similar bulk processing methods 70 years before Hibbard. Further, Kühne might have appreciated the fact that Moore, as well as many of the other fissure fossil discoverers, such as Frederick Hudson, Tom Fry, and Trevor Thomas, were not professionals, and in fact were amateurs, many of them working men. Tom Fry in particular was always short of money and did his fossil finding at weekends and early in the morning before going to his labouring jobs, often carrying huge weights of rock on his bicycle. Whether the Marxist commentator would class such successful fossil finders as members of the proletariat cannot be said.

TOM FRY AND THE BRISTOL CONNECTION

Tom Fry (1902–1997) was a self-taught geologist (Fig. 7), who had been an enthusiastic fossil collector around Bristol since the 1920s and worked as a palaeontological technician for the University of Bristol from 1947 to 1968 (Large 1994). He made some previously unreported contributions, meeting Kühne in the field in 1947 and 1948, and sharing information. Both were aware that Frederick Hudson had found excellent fossils of the rhynchocephalian *Clevosaurus* at Cromhall Quarry in 1938 (Table 1), but it seems did not follow this up until after World War 2. Fry visited, as described below, but did not find reptile remains, but he did identify the important conchostracan *Euestheria*. Kühne meanwhile did find *Clevosaurus* and archosaur bones in 1946 or 1947, which he sold to the NHMUK in 1948. Fry's collecting included some of the first remains of the gliding reptile *Kuehneosaurus* from Emborough (Fig. 2N).

Fry reported (BRSMG 47/1991; Journal of Personal Happenings of T. R. Fry 1921 onward, 1920–1975, pp. 123–125):

> On July 31st 1947, Professor [Whittard] and I went to Emborough Quarry, where a wide fissure in the Carb. Lst., filled with large limestone boulders and soft Triassic marls, had yielded bones of a small Triassic land reptile. Here I met Dr Kühne and a party of students who were digging for these bones. This Emborough discovery was his latest Mendip find. Professor [Whittard] asked me to go to search at Slickstone [= Cromhall Quarry] in Aug. 1947. I did so but I only found thin calcareous layers of Triassic marl bearing numbers of the ostracod Euestheria (sic), in fissures of the Carb. Limestone.
>
> I next revisited the Emborough fissure now that Dr Kühne and his students had gone. Here I made a new find about 40 yds further along the quarry face southward. Exploring a small pocket of Trias marl not more than 6 or 8 feet from the surface I found a thin sheet or layer of reddish calcareous silt studded with numerous small bones – all separated which later proved to belong to the same small reptile that Kühne and the students were digging out previously. I made seven further visits to the Emborough Triassic deposits.
>
> I visited [Windsor Hill] Quarry on 10 Aug. 1947. The cottager told me that the finds were made by Dr Kuhne (sic) before the war, following his internment as an enemy alien; the Dr resumed work in the Mendips after the war. His finds here included a small reptilian skull which was shown to me later by Dr Robinson. Dr Kühne, following Charles Moore, found more remains of *Microcleptis* (sic) (small mammal of Rhaetic age) in fissures of the Carb Limestone at Holwell near Frome. At least one tooth from this find was sold to Prof. Whittard on behalf of the Geology Department for five pounds.

During her visit to the area in 1951, Pamela Robinson went to Bristol, as she was planning her PhD, and Tom Fry showed her the various fossiliferous fissures, including those discovered by Kühne as well as others he had explored in 1947 and 1948. In the journals already cited, Fry recounts these meetings:

> She visited Slickstone, where she made a lucky strike… there was plenty of bone-rich Triassic infill lying about. After she returned to London… I made several visits and I also collected material. When after a week she returned to the site with Dr Curmack [= Kermack], she was annoyed that I had gone there in her absence although I gave her all my finds. I returned to Slickstone with her and her colleague and they took photos of the fissure.

Figure 7. Tom Fry (1902–1997), pictured as a young man in the foreground with two friends on a geological excursion to the Mendip Hills in 1922 (A), and when he was 90 (B). Photographs by Harry Hodge (A) and Nick Large (B).

> Professor Whittard gave her all Hudson's specimens (collected pre-1939), and I gave her all my Emborough slabs from my own personally discovered fissure. Even so, when she published her general paper on all the occurrences, she never acknowledged any help from myself. This may have been because I went to Slickstone in her absence. In any case I had given her valuable help and my Emborough finds were the best made on that site. When I reproached her later, she said, I will give you full acknowledgement in a forthcoming paper. This promise was never carried out.
>
> 8th Nov.. 1947. A further fissure of indurated Trias Marl was found at Batscombe near Cheddar. It ran two hundred feet or more from the quarry top. This provided lumps crowded with dis-articulated small bones including jaws. I took back several large pieces to the University. The foreman told me that Dr Kuhne (sic) had been there during the summer, and he and his party had taken away most of the lumps of bone-rich material.

Evidently, Fry did not make new discoveries in the Bristol fissures after his excursions from 1947–1951, although a new academic colleague was already interested. Fry was possibly too damning of Robinson, and Robinson mentions Fry among the *Kuehneosaurus* papers at the NHMUK, and in the original version of the *Kuehneosaurus* manuscript, and had apparently intended to keep her word to acknowledge his contributions, but she did not do so when there were further opportunities (e.g. Robinson 1967, 1973).

This new academic colleague was Bob Savage (1927–1998) who came to the University of Bristol in 1954, initially as Curator of the fossil collections and then securing a regular academic post and rising to Professor (Benton 1994). Savage (Fig. 8), like Robinson and Kermack, had been a PhD student at UCL, studying the Oligocene otter *Potamotherium*, and supervised by David Meredith Seares Watson (1886–1973), 'D.M.S.' as he was often called, the doyen of vertebrate palaeontology in the UK for many decades. Savage's first academic post was in Belfast in 1952, and he was aware of the initial work in the fissures by UCL colleagues Kühne, Robinson, and Kermack, so held back from any close involvement at that point. He worked on a broad range of topics concerning mammals, especially from Africa, but kept an eye on the fissures around Bristol, reporting new discoveries through the 1960s and 1970s, culminating in a field guide (Savage 1977) and a detailed, historical review (Savage 1993).

After 1960, whereas Kermack continued visiting and excavating at the South Wales fissure sites, Robinson did not as she shifted her attention to working in India, with regular visits to the Indian Statistical Institute from 1957 to 1974 (Turner 2021), and Bob Savage began expanding his interests in the fissures. He did some exploratory sampling at Holwell in 1961, 'with the encouragement and help of Dr. C.R. Burch FRS (1901–1983) of the University of Bristol, 3½ cwt. of the soft fissure infilling in Qn [= the north quarry] was elutriated and the concentrate sorted on a mechanical separator; the yield was 49 *Birgeria* teeth, 232 *Acrodus* teeth, 227 *Gyrolepis* scales, 18 fish vertebrae and 397 bone fragments, together with brachiopods, belemnites, bradyodont tooth and pyritized rods, spheres, gastropods and lamellibranchs.

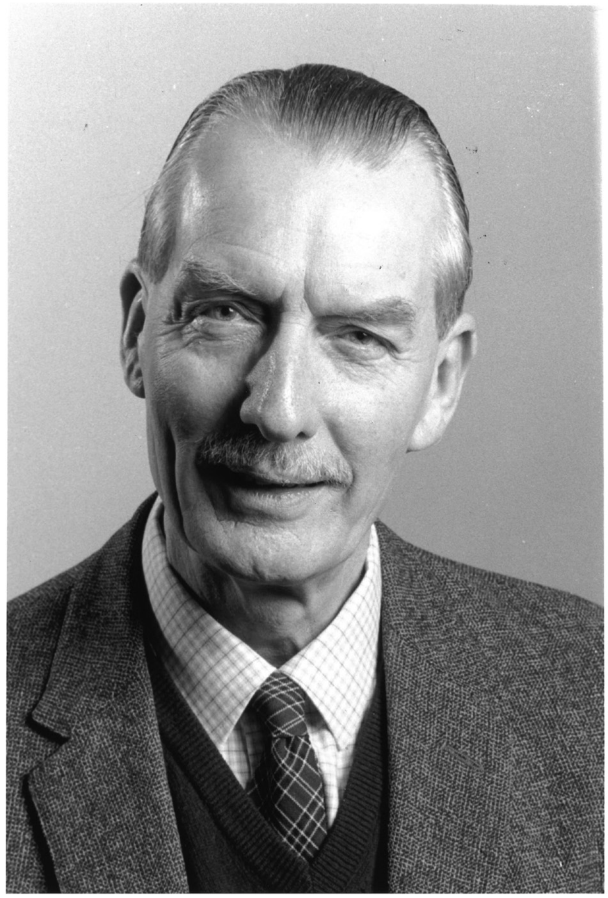

Figure 8. Robert J.G. ('Bob') Savage (1927–1998), pictured about 1980.

The concentration was very much less than that recorded by Moore and Kühne and hence the chances of finding further haramiyid teeth was regarded as negligible' (Savage and Waldman 1966, p. 191). Cecil Burch, referred to here, was a noted physics professor at the University of Bristol, elected FRS (Fellow of the Royal Society) in 1944 for his work on high-level vacuums for coating astronomical mirrors. Here, he offered his practical engineering skills, and later developed a vortex machine to help D.I.W. separate bones from sediment, based on their differential density. However, the machine was overly vigorous, and we found it easier to perform these operations with more traditional sieves and water.

KENNETH KERMACK AND THE UCL TEAM

After 1951, stimulated by Kühne's success and following his departure from England and his job at UCL, two colleagues, Kenneth Kermack (1919–2000; often known as K.A.K.) and Pamela Robinson (1919–1994; often known as P.L.R.), began to explore the fossiliferous fissures of the area around Bristol and in South Wales (Fig. 9A, B). There was evidently a firm understanding or agreement that from 1951 onwards, Robinson would concentrate on the reptile-dominated Late Triassic fissures around Bristol and Kenneth Kermack would concentrate on the mammal-rich Early Jurassic fissures of South Wales (Robinson 1957a, p. 262).

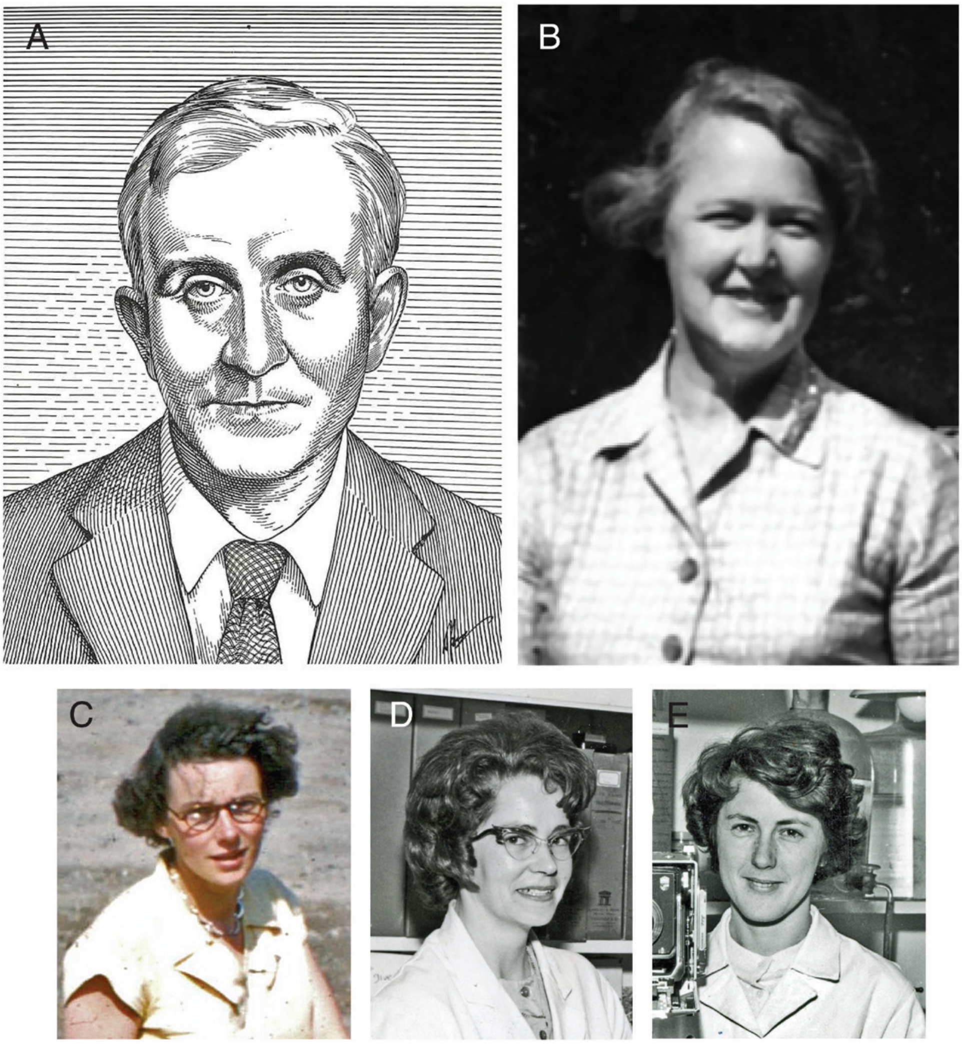

Figure 9. The leaders of vertebrate palaeontology at UCL through the 1950s to the 1980s: Kenneth Kermack (1919–2000; A) and Pamela Robinson (1919–1994; B), and their colleagues, Doris Kermack (1923–2003; C), Frances Mussett (1930–2020; D), and Pat Ferguson (née Lees; E). A, Drawing of Kermack by Tony Lee (UCL), and from the 1984 Kermack Festschrift; (B) courtesy of Saswati Bandyopadhyay; (C) from field photograph by Kenneth Kermack; (D, E) from UCL laboratory photograph supplied by Pat Ferguson.

Kermack and Robinson were the same age, but Kermack already had his doctorate, earned in 1950 for statistical work on the evolution of the echinoderm *Micraster*, and so was senior in the university system. At the time, he had eclectic interests, having already worked on Devonian agnathans, and then on the function of tails in swimming vertebrates following an expedition in 1945–1946 with the Antarctic Whaling Fleet (Simpson 1984). Meanwhile, he co-authored a primer on biometrics with the great J.B.S. Haldane (Kermack and Haldane 1950) and published his PhD research on *Micraster* (Kermack 1954). Kermack (1951) also applied biomechanical arguments to show that the long-necked sauropods could not have drawn air into their lungs if they had walked about in deep lakes, as some suggested at the time.

After 1951, Kenneth Kermack, his wife Doris, and Frances Mussett began regular field trips to the quarries of South Wales, and they assembled huge collections of mammalian teeth and bones, most notably of the primitive mammals *Morganucodon* and *Kuehneotherium*. Their first published work concerned an exhibition of the first fossil finds at the Geological Society of London (Kermack *et al.* 1956). Through the next two decades, Kermack and the UCL team published extensively on these fossils, including monographic works on *Morganucodon* (Kermack *et al.* 1973, 1981).

Doris Kermack, née Carr (1923–2003) was also a zoologist by training (Fig. 9C), and she was a lecturer at Imperial College, London. She worked initially on modern invertebrates, but latterly on Mesozoic mammals, and took the lead on the first publication on Mesozoic mammals by the UCL group (Kermack *et al.* 1956), as well as leading the monographic description of *Kuehneotherium* (Kermack *et al.* 1968) and their textbook (Kermack and Kermack 1984). She served her science through leadership at the Linnean Society in London (Kielan-Jaworowska 2013, pp. 77–78).

Frances Mussett (1930–2020) completed her BSc at Birkbeck and was employed at UCL initially as assistant to Pamela Robinson, but later switched to work with Kenneth Kermack. Initially, she (Fig. 9D) did laboratory and technical work for Robinson (see Robinson 1955), and then concentrated mainly on teaching, some fieldwork, and on preparing and editing manuscript copy for Kermack. She never earned a PhD, but through her research and editorial work was co-author of several key papers about early mammals and earlier synapsids (Kermack DM *et al.* 1956, 1968, Kermack and Mussett 1958, 1959, Kermack KA *et al.* 1973, 1981). Latterly, and after the retirement of Kenneth Kermack in 1984, she taught the bulk of the MSc in Vertebrate Palaeontology at UCL until it ended in 1995.

Pat Ferguson (née Lees) started work with Kenneth Kermack in February 1960, and they visited the Welsh quarries typically twice a year. She had technical qualifications and worked as a technician mainly processing fissure material, extracting fossils, and photographing (Fig. 9E), until the mid-1990s when she retired. She also did technical work for other research groups occasionally in the UCL Department of Zoology.

The Kermack–Robinson research school in vertebrate palaeontology was based in the Zoology Department at UCL, operating from a laboratory area (Fig. 10) in which the fissure sediments were processed by Pat Ferguson and Jackie Papworth. The latter worked mainly for Frances Mussett and was at UCL for 3 years in the early 1970s, then moving to Cambridge to work for Parrington on the Welsh material (Pat Ferguson, letter, 11 April 2023). In terms of processing the fissure sediments, Ferguson recalls, 'both Frances and I used formic acid in preference to acetic; it softened the mud around the bone which was removed by needle. The specimen was then lacquered. My hair was very dark and strong and was used often when splinting was required. I donated a test tube full of my hair'.

There they also ran the UCL MSc in Vertebrate Palaeontology programme, and supervised many PhD students across a wide range of themes in vertebrate palaeontology, including: Brian Gardiner, Colin Patterson, John Maisey (co-supervised by Patterson), and Chris Duffin on fossil fishes; Richard A. (Tony) Thulborn on dinosaurs; Susan Evans on lepidosaur anatomy and Oliver Rieppel on sauropterygian skull kinetics; Peter Crush and Diane Kermack (née Warrener) on archosaurs; Pamela Gill on mammals; and David Pacey on a fissure fauna. From at least the early 1970s, Frances Mussett took an active role in dig supervision and student supervision. Among their rich collections from the South Wales fissures, they found thousands of specimens of *Morganucodon* and *Kuehneotherium*, as well as the diapsid reptile *Gephyrosaurus*, and these collections are now all located at the NHMUK (Fig. 2E–G, K).

How the division of fissure territories between Kenneth Kermack and Robinson was agreed in 1951 is not known, and whether it was amenable to both parties is uncertain. Kühne was evidently unhappy. Jim Hopson (email, 9 March 2023) comments, 'Kühne had no use for Kermack because of the way the latter took over the mammal quarries which I have been told Kühne wanted Pam Robinson to control after Kühne left England for East Berlin. Instead, Kermack somehow gained control of the mammal quarries, leaving the diapsid quarries to Pam. On the post-symposium field trip [1970] led by the Kermacks and Frances Mussett, I watched Kühne being unremitting in his insults to Kermack. The latter always avoided confrontation by laughing off Kühne's gibes'. Nick Fraser (personal communication to D.I.W., 22 February 2023) endorses this, stating 'he (Kühne) took great delight in riling Kermack up at scientific meetings'.

PAMELA ROBINSON

Pamela Robinson (1919–1994) studied initially in Hamburg in 1938 but returned to England that year. She delayed her studies because of war work and completed her first degree at UCL in 1951 (Turner 2021, pp. 287–289), and she then received a UCL Research Scholarship to study for a PhD. Robinson moved to an Assistant Lectureship at UCL in 1955, gaining her PhD in 1957, and remaining at UCL for the rest

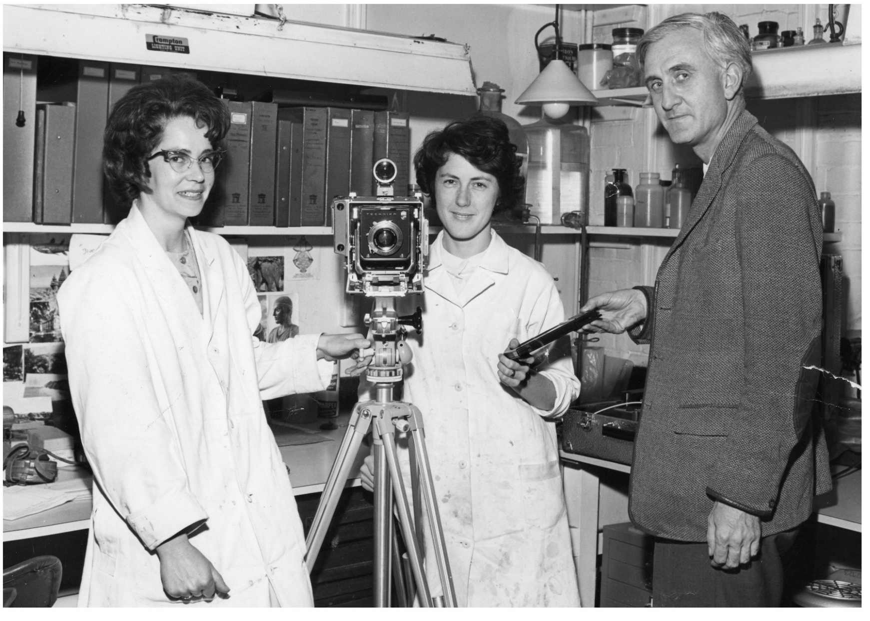

Figure 10. Photograph in the UCL laboratory in the early 1960s, showing Frances Mussett (left), Pat Ferguson, and Kenneth Kermack, in a heavily posed image where Kenneth Kermack is handing Pat Ferguson the camera back with photographic plates. Photograph from Pat Ferguson.

of her research career. Through the influence of J.B.S. Haldane (1892–1964), the renowned geneticist at UCL, Robinson spent considerable time at the Indian Statistical Institute (ISI) in Calcutta and worked on some Indian fossil reptiles and wrote about the impacts of climate and continental drift on Triassic reptiles. Her work in India was innovative and influential, and she is remembered fondly by colleagues in India for all she did at the ISI.

But it is Robinson's PhD work that concerns us here, which was focused on the reptiles of the Bristol fissures, and especially the gliding diapsid *Kuehneosaurus*. Robinson (1957a) published a detailed account of the fissures, in fact the most thorough such account yet, and this, her paper on *Tricuspisaurus* and *Variodens* (Robinson 1957b), and the geology and dating of the 'slot fissures' comprised her thesis; her slot fissure description and analysis was published much later (Robinson 1971). In fact, the UCL library copy of Robinson's thesis consists of a total of 25 pages plus her two papers. However, she was also making a thorough study of the gliding kuehneosaurid reptiles while working on her thesis (Milner and Hughes 1995) which started in 1951–1952 according to a draft of an undated letter to the *New Scientist* she wrote in 1962 (NHMUK, Section of Fossil Reptiles, Amphibians and Birds [SFRAB] archive); her unpublished kuehneosaurid work comprises three volumes of illustrated manuscript (NHMUK, SFRAB archive). It was widely known that she was engaged on this additional large project on reptiles from the Bristol Late Triassic fissures, based on a short paper in which she named *Kuehneosaurus* (Robinson 1962), and a later paper (Robinson 1967) in which she showed that *Kuehneosaurus* occurred at Emborough and a second taxon, *Kuehneosuchus*, at Batscombe.

Robinson's third major project, also largely unpublished, was on the sphenodontian *Clevosaurus*, based on the original material of Swinton (1939) plus excellent articulated materials collected by her (Fig. 2O) from the new fissure exposure at Cromhall and others given to her from the Hudson and Fry collections at Bristol. These specimens formed the basis of Robinson (1973) where she revealed that *Clevosaurus*, 'a problematic reptile', had an incomplete lower temporal arcade and therefore was an unusual rhynchocephalian. The wealth of *Clevosaurus* specimens collected by Robinson are in the NHMUK (see e.g. O'Brien *et al.* 2018), and, in the absence of a full description by her, Fraser (1988) produced the most complete description of the Cromhall clevosaur based on excellent specimens held at CAMZM.

Turner (2021, p. 288) notes that 'The process of thesis production and her reluctance to publish all was the source of contention between Pamela and student Tarlo (Halstead …)'. This introduces a new name, Beverley Tarlo (= Halstead; 1933–1991), her new PhD student at UCL who had started in 1955. He wanted to work on Devonian fossil fishes following enthusiasms he had developed during his undergraduate days at Sheffield University and his interest in the Triassic lepidosaurs emerged while he was engaged in his PhD work (Sarjeant 1993), but Robinson suggested a project on Jurassic plesiosaurs. Tarlo decided to do the work quickly, publishing it as a series of papers, so he could then spend his time on other projects. The fact he submitted published work rather than a thesis for his PhD infuriated Pam Robinson and the degree award was delayed until 1959.

Tarlo also had a huge row with Robinson in 1962 over the Bristol fissures. Sarjeant (1993, p. 9) quotes an extensive reminiscence from Colin Patterson (1933–1998):

> The "spectacular quarrel" that I mentioned in the *Independent* obituary was with Pamela. She and Kermack were both working on fragmentary terrestrial vertebrates recovered from late Triassic and early Jurassic fissure fillings in the Carboniferous Limestone of South Wales and the Mendips. Pamela was laboriously reconstructing the skeleton of what appeared to be the earliest flying reptile, an animal that she named *Kuehneosaurus* in 1962 (*Proc. Geol. Ass.*, 1601, 137–146). That paper was published on 31st July 1962, and it is headed "submitted 16 July 1962". Two weeks between submission and publication is not normal in leisurely places like PGA [he is mistaken here; it was the *Proceedings of the Geological Society of London*, not the Geologists' Association], and the reason for the rush can be found in *New Scientist* for 5 July 1962, pp. 32–34, where Bev has an article called "Ancient animals of the upland" in which he names Pamela's flying lizard *Plesiodraco* and comments on other members of the fissure faunas without anywhere mentioning Pamela. The name *Plesiodraco* was a *nomen nudum*, but the "theft" was enough to send Pamela to the typewriter and the editors of PGA into an unprecedented rush into print. There is a bit of background on this in *Proc. Geol. Soc.*, 1568, 63–64, published in March [Tarlo 1959]. The note describes Bev's exhibit at the Geol. Soc. of reptiles from a Triassic fissure filling in Poland, collected in 1958, and mentions lizards from a fissure filling at Slickstones Quarry near Bristol, "although no description of them has yet appeared." Pamela was (slowly) writing the description, and Bev's remark was a sideswipe at her. Her name is conspicuously absent from the list of names in Bev's acknowledgements at the end of the note.

Tarlo's (1962) article in *New Scientist* rankled for all sorts of reasons. Robinson accused Tarlo of having covertly studied her materials of *Kuehneosaurus*, but he denied this, stating that he had been given fossils of a gliding lizard from Batscombe by Dr M.L. Curtis of BRSMG (Tarlo 1962), and threatened legal action (letter from Halstead to Robinson 30 July 1962; NHMUK SFRAB archive) and Robinson retracted the claim. However, the dispute forced Robinson to publish her preliminary note on the kuehneosaurids (Robinson 1962) and a further short paper (Robinson 1967) with her views on these gliding reptiles and the suggestion they occupied upland habitats, as previewed by Tarlo (1962). She wrote to noted American palaeontologist, Alfred S. Romer (letter dated 12 May 1967; courtesy of Barry Hughes, digital copy, NHMUK SFRAB) about her 1967 paper, 'Had to be done in a disgusting hurry as a certain young gentleman was interfering yet again and trying to split it himself – *Plesiodraco* and all and all. So finally got a bit cross and wrote this in 36 hours, sent it to India on 20th April and it was published on 30th April (good old Professor Mahalanobis) and that has settled that … Hell, it's all so petty, but I'm fed up with attempts to muck about with my work by someone who knows nowt and cares less about fossil Eolacertilia, Kuehneosauridae, Prolacertiformes and Eosuchia. Well, got that off my chest'.

Later, Halstead and Nicholl (1971, pl. 24) returned to the fissure topic, showing photographs of sphenodontian jaws from Cromhall Quarry which they identified as *Clevosaurus*. However, this turned out to be the first published illustration of a different taxon, *Planocephalosaurus robinsonae* described by Fraser in 1982. The Halstead and Nicholl (1971) paper is the first to illustrate a procolophonid or archosauromorph from Cromhall. There is no record of Robinson's response to this short paper, also like Tarlo (1962) and Robinson (1967), published in an unusual venue, but she had already recognized that *Planocephalosaurus* (her reptile 'E' or 'wavy line maxilla') was distinct from *Clevosaurus*. In her unpublished faunal list from Cromhall (Robinson archives, NHMUK SFRAB) she also recognized a procolophonid and archosauromorphs, so she had again been pre-empted.

Much of Robinson's work in excellently illustrated manuscripts on, for example, *Kuehneosaurus*, was never published which may have been affected by her ill health, and by the growing scale of the project. Colbert (1970) published his description of the very similar North American kuehneosaurid *Icarosaurus*, and this meant she would have had to rewrite parts of her unpublished manuscript. In those days it was the norm for vertebrate palaeontologists to consider all aspects of a new fossil reptile, including anatomy, relationships, evolution, and mechanical function, by themselves and not to think of recruiting students or colleagues to help complete the project.

Her last paper was Robinson (1976), and others referred to her ill health. Bob Carroll of McGill University wrote to Robinson on 8th December 1976 and commented, 'I hope that this year finds you in better health and spirits than last'. Mick Oates (5 November 2021 email to M.J.B.) confirms that, as a student of Robinson in the 1970s, she was an 'extremely addicted smoker'. Her chain smoking may have been the reason that she did not use her allocated room or research her fossils further in the NHMUK following the deposition of her collection in 1986. The late Angela Milner, former Assistant Keeper of Palaeontology at the Natural History Museum, in a personal communication to Sandra Chapman, former Curator of Fossil Reptiles & *Archaeopteryx*, said that Pamela found it very difficult to comply with the no-smoking rules in the collections of the NHMUK. This is despite NHMUK staff trying 'to persuade Pamela to get back to her research by offering to collect her by car from her home or planning a ciggie stop on the way' (Sandra Chapman, email to D.I.W., 13 March 2023). Certainly by 1987 she had apparently lost motivation in research. In a 11 March 1987 note to D.I.W. written by her confidante, Barry Hughes, requesting a copy of Whiteside (1986) on *Diphydontosaurus* (Robinson's reptile 'D'; Robinson 1955) he states of Robinson, 'she speaks of returning to work on her collection, but I fear she never will; knowledge of your work might provide activation'.

Turner (2021, p. 287) writes about Robinson, 'On the few occasions I met her at meetings she seemed rather dour and even her obituarist, R.J.G. "Bob" Savage (1994), noted her steely nature. But then, I was probably tarred with my supervisor's brush as Halstead (Tarlo) and Pamela Robinson had not got on'. Milner (2004) confirms these impressions. One of the authors (P.G.G.) adds a more positive note, at least from knowing Robinson in the early 1970s. 'Robinson was preparing to leave for fieldwork in India and, although I was a student of Kermack at the time, she discovered that I was looking for accommodation. She suggested that I move into her flat in Kensington, a wonderful location near Hyde Park, and on her return from India allowed me to stay for about a year. Although we did not generally socialise together, I found her to be kind and caring, sharing her interest in music and literature. The one time she did talk about the Kermack team to me, was to express annoyance that Kermack's Mesozoic mammals seemed to be getting all the headlines, and funding in the UK, and flippantly referred to them as the "Holy Hairies"'. Nick Fraser (personal communication to D.I.W., 22 February 2023) also has good memories of Robinson: he was shown her Cromhall collection of fossil reptiles in the late 1970s and remarks that she 'was perfectly delightful to talk with' and seemed to expect that he 'would become her doctoral student'. Fraser (1982) named the Cromhall rhynchocephalian *Planocephalosaurus robinsonae* in her honour.

NEW FISSURE DISCOVERIES IN THE 1950S

Kermack and Robinson at UCL had already been shown the key fissure sites Kühne had discovered, including Holwell, Windsor Hill, Emborough, Cromhall (Slickstones), and the Duchy and Pant quarries in South Wales. After Kühne's return to Germany in 1951, Robinson (1957a, p. 262) reported that, 'I found a new Triassic fissure deposit at Slickstones Quarry, near Cromhall in Gloucestershire in 1951, from which a fauna of small reptiles has been collected (Robinson *et al.* 1952). In 1952 my colleague Dr. K.A. Kermack joined in the hunt, and we discovered bone-rich material containing at least five different reptiles at Pant-y-ffynnon Quarry, near Cowbridge, Glamorgan. This locality was the first to yield associated bones … In future all limestone quarries in work in the Bristol Channel area will be inspected annually, those in South Wales by Dr. Kermack, and those in Somerset and Gloucestershire by myself'. Over the years, both researchers collected from many sites, and Kenneth Kermack explored widely across South Wales, visiting quarries in Carboniferous limestone, some of which yielded fissures and fissure faunas and some of which did not (Figs 11–13); he took back huge volumes of sediment for processing at UCL, using a variety of techniques to concentrate the bones (Savage 1993, p. 158). These discoveries, and others, are summarized in the timeline (Table 1; Supporting Information, Table S1).

After her first visit to Bristol and field guidance by Tom Fry in 1951, Robinson (Fig. 9B), together with Kermack, and a new UCL PhD student Ken Joysey (Fig. 12B) embarked on a survey of the limestone quarries of the Bristol region (Robinson *et al.* 1952) discovering a newly opened large, cavernous fissure at Cromhall in 1951. Robinson and Kermack discovered the Pant-y-ffynnon fauna in a spoil heap in 1952 (Robinson 1957a, Kermack *et al.* 1973) in the northern quarry of the complex (Keeble *et al.* 2018) but could not locate the fissure(s) from which it derived; this was the first fissure locality to yield associated bones (Robinson 1957a, p. 262). Diane Kermack's personal communication (email to D.I.W., 16 November 2021) confirmed it is likely that all the archosaurs and lepidosaurs were found on the same day and in the same spoil heap. In her thesis, she (Warrener 1983) remarked that the old rock screening plants were not efficient at separating clay from the valuable limestone so that the fissure material was either dumped in a heap or, if

Figure 11. Field photographs of fieldwork by the Kermack team in the 1950s and 1960s. A, Doris Kermack at Cnap Twt Quarry in 1953; (B) Doris Kermack taking tools from the field car at Argoed Ishaf Quarry, Glamorgan, in Spring 1956; (C) Pat Ferguson at Longlands Quarry in April 1962; and (D) Kenneth Kermack at Pontalun Quarry in September 1963. Images are C-1-8, B-VI-40, B-VI-64, and C-V-72, respectively, in the NMW archives.

the fissure was large, the quarrying operations simply excavated around it.

In 1954, Robinson received funding from the Geological Society of London for her field work and made annual visits to the known fissure sites around Bristol and the Mendips, travelling on foot and by bus (Turner 2021, p. 288). These visits were lengthy and thorough, and Robinson expressed her gratitude to Kühne for all his initial work in identifying fissures and in handing over the research theme to her, by remaining in touch and helping Kühne edit some of his papers to improve the English and tighten the science. Nick Fraser comments (personal communication to D.I.W., 22 February 2023) 'Kühne himself spoke to me quite fondly of Pamela – perhaps in a way that he never did about others'.

As a result of all her field work, Robinson (1957a) presented a major overview of the fissures of the Bristol and Mendips

Figure 12. Field photographs of fieldwork by the Kermack team in the 1950s and 1960s. A, Doris Kermack packing specimens at Cnap Twt in 1953; (B) Ken Joysey at Longlands Quarry inspecting the Jurassic shell beds unconformably banked up against the Carboniferous limestones in 1954; (C) Frances Mussett checking specimens at Duchy Quarry in Spring 1956; (D) Doris Kermack (left) and Frances Mussett (right) at Beaufort Quarry, Chepstow, in September 1958. Images are C-1-29, B-VI-59, C-1-41, and B-11-39, respectively, in the NMW archives.

area. She discriminated four types of fissures, two of them originating under the sea and being filled with marine sediment dating from the Rhaetian to Middle Jurassic, and the other two forming entirely on land and dating from the Late Triassic. Importantly, she documented the fissures known to date and their faunas and discriminated their ages. The Neptunian dyke fissures at Holwell contained a mix of fossiliferous sediments from the Rhaetian to Middle Jurassic in age, and those at Windsor Hill are Early Jurassic in age. In some of these she identified invertebrates of definite Jurassic age. Kühne had also discriminated between a suite of Early Jurassic fissures, generally those with mammals, and older, red-bed fissure fills of Late Triassic age. Robinson (1957a, pp. 271–275) was the first to present detailed evidence of the formation of the fissures in the context of changing landscape relief and she assigned them a Late Triassic age. This was confirmed by the relationship of the fissures at Emborough that, she predicted from mapping (Robinson 1957a, fig. 6), would have lain below a thin bed of marine Rhaetian. Kühne in the 7 November 1952 letter to Robinson (NHMUK SFRAB) had also suggested that 'Emborough was a lagger, viz. high in the Trias, if your Geology is right'. Finally, the faunas themselves, being dominated by diapsids, compare best with Late Triassic faunas from elsewhere. The understanding that there were two ages of fissure deposits, Late Triassic, predominantly containing red or yellow sediments, and Early Jurassic, generally containing grey-coloured sediments, with some red colours at Pant and Pontalun, is also the current thinking (Savage 1993, Whiteside *et al.* 2016). This assumes two distinct episodes of fissure filling, which might not be the case, and fissure-filling sedimentation might have been continuous through the Late Triassic and much of the Jurassic (Whiteside *et al.* 2016). Interestingly, Parrington (1971, 1978) regarded the reptile and mammal fissures all as Late Triassic. Robinson was reluctant to consider research involvement by others in fissure geology. When told in 1971 by Mick Oates, one of her UCL students, of a Natural Environment Research Council sponsored PhD on the Triassic/Jurassic transgression of the Mendip Hills, including investigation of the fissures, Robinson 'nearly exploded' and exclaimed 'Over my dead body' which, as Oates remarks 'probably adequately demonstrates how she regarded this as her territory'.

Robinson's work at Cromhall in the 1950s has had lasting impacts, even though she was unable to publish many of the exceptional specimens she collected. She donated her collection to the NHMUK on the proviso that it was not available to other visiting researchers (letter of 20 August 1986 from Angela Milner to Robinson; NHMUK SFRAB). However, her collection of reptiles from Cromhall, Emborough, and Batscombe is now being studied, providing new insights into function (e.g.

Figure 13. Field photographs of fieldwork by the Kermack team in the 1950s and 1960s. A, Doris Kermack preparing lunch at Ruthin Quarry in April 1962; (B) Pat Ferguson at Pant Quarry in July 1962; (C) Pant Quarry in September 1968, showing a new fissure (left arrow) in relation to Kühne's fissure (right arrow); (D) students at Holwell Quarry in April 1974. Images are B-IV-40, C-11-18, C-VII-6 and E-111-13, respectively, in the NMW archives.

Stein *et al.* 2008) and anatomy through computed tomography (CT) scanning (O'Brien *et al.* 2018, Chambi-Trowell *et al.* 2019, Whiteside *et al.* 2022). Susan Evans is currently leading a project to describe the kuehneosaurs using Robinson's manuscripts, but with much new input.

THE PARRINGTON–KERMACK BUST-UP

Parrington and Kermack had had a tense relationship over the years, disagreeing about many aspects of their respective views about synapsids and the origin of mammals, as well as the relative merits of the names *Eozostrodon* and *Morganucodon*. As Tom Kemp reported (interview, 15 March 2022), 'the idea of multiple origins of mammals from reptiles was received wisdom. And the argument was the rather circular one that given selective forces powerful enough anything would evolve in the same direction, so we would expect parallel evolution of practically everything. If we consider the middle ear, the idea that the ear ossicles of monotremes and therians could evolve independently from some pelycosaur, was only to be expected because of the power of natural selection. The same with the teeth. Any synapsid in the Middle Triassic was bound to evolve complex occluding teeth because they were such a good thing. So Kermack was happy to have monotremes and therians going back to ancient ancestors. Parrington was probably the first one to say how similar *Kuehneotherium* and *Morganucodon* are, the beginning of the monophyletic theory of the origin of mammals'. The observation that both *Morganucodon* and *Kuehneotherium* are similar in their development of cusp-based wear facets would subsequently lead to a new hypothesis that mammals are monophyletic (Hopson and Crompton 1969). Kermack and Mussett (1959), in a popular article, showed an extreme model for the polyphyletic origin or mammals, depicting five separate origins for the various groups. This was the common view; in a review of the evidence for the origin of mammals, Simpson (1959) wrote that Kühne saw 'Mammalia' as merely a grade, and that the reptile to mammal line must have been crossed at least twice, but probably at least four times, as Simpson (1928) had proposed. Parrington and Kermack had disagreed over these and other questions at meetings and in print, but they maintained a civil relationship.

Everything changed in 1967. The dispute concerned a large quantity of richly fossiliferous fissure-fill clay from a new fissure (Pontalun 3), discovered at Pontalun Quarry in South Wales (Fig. 11D) in 1962 by the Quarry Manager, Les Middleton. The UCL team outlined their account of the situation in the Kermack Field Notes folder (NHMUK SFRAB archive). There was so much matrix that it was intermittently stored in an old boiler at the then disused Ewenny Quarry. Some matrix was gradually transferred to UCL, but a large quantity was still there in 1966 and was picked up by a party from CAMZM and taken to Cambridge. This was discovered by Kenneth Kermack and Frances Mussett on their next visit in June 1967, and they were not pleased. The Field Notes state 'Found that Joysey and Cambridge party had hired a lorry and taken all our stored matrix – 4 tons...... Very stiff letter sent to Parrington on this. Paid Les Middleton £5 to keep an eye on things'. This 'stiff letter' did indeed elicit a response, and in September the notes state that 'Parrington and Joysey visited quarry immediately on receipt of our letter; explained it was all a misunderstanding to Les'.

Pat Ferguson reported the story from the UCL side (letter to M.J.B., 15 March 2023):

> It was very bitter. Parrington felt and said in public that K.A.K. should publish his work on *Morganucodon* etc. I did feel some sympathy for him (P.) on this point. K.A.K. was asked by Joysey if Cambridge could have a small amount of some of the fissure material that was stored in the quarry. We received a telephone call from the quarry manager saying that Joysey had come down with a lorry and taken the lot. I am afraid that was the end of any friendly feelings between Cambridge and UCL. Both Kermack and Frances were furious. It was a pity as Parrington used to come and see K.A.K. every so often when he was in London, and they chatted together happily. This was a period when coffee was always drunk in my room. So I was at my microscope, listening. As far as I know there were no public debates or arguments.

Parrington had said that he just collected loose, discarded material from the quarries, but Pat Ferguson and others at UCL were adamant that the material taken was stored under a tarpaulin.

As it turned out, fissure 3 in Pontalun Quarry, Glamorgan, produced some very important fossils (Fig. 2D, E, H, K; it is the type locality for *Gephyrosaurus*) so perhaps this is more than just a notional argument. Four years later, Parrington (1971) described new material (e.g. Fig. 2D, H) of *Eozostrodon* (= *Morganucodon*) and *Kuehneotherium* from Pontalun, found by Cambridge student Alex Baynes, and he thanked (Parrington 1971, p. 238), 'Dr K. A. Joysey who carried out the necessary salvage operations and worked out the most efficient procedures whereby the bones and teeth have been extracted from the clay'. Tom Kemp (interview, 15 March 2022) provides further information:

> The cause of the bust up between Parrington and Kermack was a pile of fissure sediment in one of the South Wales quarries. One of the Cambridge students about 1967, Alex Baynes, had arranged to go to Australia to work with David Ride on fossil marsupials, but he had the long summer in Cambridge before he went. Ken Joysey arranged to teach him some basic field geology, so he took him to South Wales to look at fissure stuff. Alex Baynes contacted Joysey, and said he was in one of the quarries, and found a pile of sediments full of bits of bone. He had talked to the quarry manager, Les Middleton, who said this stuff came from a different quarry where they had been keeping stuff for Kermack. He had told Kermack that they had found this new fissure stuff, several tons of it, and what to do with all the piles of sediment and reported that Kermack had said 'Oh dump it''. So, the quarrymen took and dumped it in a different quarry.
>
> So, there was Parrington hearing about these earliest-known mammals, in large amounts potentially in this clay, and not only had the sediment been abandoned by Kermack, which was bad enough, but it had actually been salted in another quarry, which was unforgiveable. So, Parrington persuaded himself and us that Kermack, having behaved like this, it was perfectly legitimate for Cambridge to go and collect the stuff. So, we duly hired a lorry and along came 15 sacks full of clay, which we dumped in the basement. And Parrington got to work on it; in fact we all did. Joysey experimented with ways to break it up with acetic acid, and we spent hours, Anne Warren, Parrington, and me, sorting through the sediment under the binocular microscope, picking out individual teeth, thousands of them, little bits of jaws, and we experimented with ways of breaking the stuff up without acid so you might get whole jaws, and that's how Parrington got hold of the specimens of *Eozostrodon* and *Morganucodon*, and some pieces of *Kuehneotherium* appeared as well.
>
> Well, by all accounts, Kermack was incandescent, and he accused Parrington of stealing the material, which he certainly hadn't meant to leave, and he meant to collect it, and this was the worst behaviour he had encountered. That was the beginning of the serious battle. Parrington was one of those characters who was a bit black or white. From that point, everything Kermack said or did was at least wrong and probably wicked. And I dare say Kermack felt the same.
>
> I don't know whether Kermack ever accused Parrington of stealing the material in public, probably not so directly, but it was certainly intimated that he had behaved very, very badly. Cope and Marsh writ small.

Kermack reports his stiff letter of complaint to Parrington, but Kemp did not know about this, and reported that Ken Joysey acted as intermediary. Joysey had done his PhD at UCL, and so maintained relationships with people both there and at Cambridge, where he worked in the CAMZM.

Jim Hopson, as an uninvolved but keen observer of the older men, wrote (email, 9 March 2023):

> when his student came back from the field to tell him that a large mass of fissure-fill material containing *Morganucodon* bones had been dumped in a corner of a different limestone quarry from where it originally came on Kermack's orders (according to the quarryman), Parrington's moral outrage burst all bounds and he felt justified in collecting the material for his own use. He told me that rather than lose this material to science, Kermack should have notified colleagues that the material was available for them to collect. Apparently, Kermack subsequently claimed that he had not abandoned this material, but, if the quarryman is to be believed, this is unlikely in my view.

Adrian Friday, former member of staff in the Department of Zoology at Cambridge (email, 23 February 2023) added, 'Parrington regarded it as sacrilegious that any material at all should be dumped. An affidavit was extracted from Les Middleton the quarry manager, to the effect that he had had clear instructions from Dr Kermack. Thus indemnified, Cambridge sent a truck to Pontalun and liberated the rest of the material'.

The Pontalun matrix in Cambridge was a major focus of research by Parrington and his students through the 1970s. As Tom Kemp reported (above), he and the others processed the matrix and spent hours extracting fossils. Adrian Friday (email, 23 February 2023) reports:

> The clay matrix was broken down by puddling and using hydrogen peroxide. There was a flotation method of separating bone/teeth from sediment by using their different specific gravities in toxic organic solvents (bromoform). Some of this methodology had been pioneered in the UCL lab! The enriched bone/teeth fraction was then manually sorted, under a microscope… When I was taught in the Museum in my final year as an undergraduate, material of *Eozostrodon*/*Morganucodon* and of *Kuehneotherium* was made available to us for study, together with the papers resulting from the work up to that point. Camera lucida drawings were made by Parrington himself, and by Doug Norman, who also photographed the teeth, and another assistant, Jack Henderson (who had previously been assistant to Sir James Gray). The photography was particularly tricky, and Doug excelled using the techniques and equipment available to him… Parrington retired to relative isolation in Scotland in 1970; but after a couple of years, he returned to the Museum, and resumed work on the material. Funding became available for a dedicated technician… At various times, all those who had an interest would be asked to graphically restore cone heights on the two original *Eozostrodon* teeth. This was with a view to establishing the extent of tooth variation, with the ultimate aim of sinking Kermack's creation of the new genus *Morganucodon* on the basis of the copious Pontalun material, and retaining *Eozostrodon* as the generic name based on the priority of description of the Holwell teeth… The long episode of study in Cambridge was brought to an end when Parrington finally retired.

Following the bust-up in 1967, Tom Kemp recalls, 'At conferences, SVPCA [Society of Vertebrate Palaeontology and Comparative Anatomy], there was a definite sense of stand-off between the Cambridge lot, which was me, Barry Cox, Alex Panchen and Alan Charig on the one hand and their lot on the other. There was very little fraternising'. In his obituary of Parrington, Charig (1990) refers briefly to the Kühne–Kermack debates (p. 365), and says, 'It was unfortunate that divergent views on these earliest mammals provoked some controversy and (uncharacteristically for Parrington) some personal hostility towards certain colleagues'. Kermack is not mentioned. Chris Duffin, former student of Kermack's (MSc, 1974; PhD, 1977) recalls (email, 15 November 2021), 'I remember standing next to Parrington in the gentlemen's lavatory (a great leveller), I think at the Reading SVPCA [Society of Vertebrate Palaeontology and Comparative Anatomy] meeting, when Kermack came in and stood the other side of me—the chill in the atmosphere was palpable'.

CHARACTER AND WORK MODE

The depth of loathing between Parrington and Kermack may be typical of scientific disputes where one person has wronged another. However, the nature of vertebrate palaeontology at the time did not help. Then, specimens were all. If a researcher had excellent specimens, they could write papers; if not, they could not. Even though Kermack had trained as a statistician and biometrician, as shown in his early papers on aquatic locomotion and biometrics in evolution, he still craved specimens. In fact, through the 1970s and 1980s as his research team grew, his need for specimens as a basis for PhD projects became greater. This then meant that any original agreement that he would study the mammal and synapsid fossils and Robinson the reptiles was not firmly adhered to. Kermack students worked on a diversity of reptilian projects, such as Peter Crush on the crocodylomorph *Terrestrisuchus*, Diane Warrener on the dinosaur *Thecodontosaurus*, and Susan Evans on the lepidosaur *Gephyrosaurus*.

In assigning so many distinctive PhD topics, Kermack was following principles that would be familiar today in a successful research group. However, then he, like others, assigned taxa, not questions—each student studies a different genus or species, not a question in phylogeny, function, or evolution. His UCL students report that he gave them considerable freedom. He was innovative in initial tasks for postgraduates that made a huge difference in their research on the fissure fossils such as providing disarticulated bones of extant animals, lizards for Susan Evans (email, 5 February 2023), and fish for Colin Patterson to aid in their identification of faunal specimens. Susan Evans still uses the disarticulated bone technique in her supervision of new postgraduate students. Kermack even encouraged her to read Willi Hennig's *Phylogenetic Systematics* even though he was no cladist, but he must have recognized the new methods should be encompassed.

In comparing Parrington and Kermack, Tom Kemp commented, 'Parrington was a bit stuffy I suppose, but he was very kind. He was very kind to me. Kermack had a way of being very unpleasant. He could cut people, and really be seriously offensive. I'm not sure he ever quite knew who I was'. Charig (1990), who had been a PhD student of Parrington's in the 1950s, stated that his supervisor had been a gentleman of the old school, endlessly kind to colleagues and students, but shy and reserved. Jim Hopson (email, 9 March 2023) gave a succinct overview, 'Kermack avoided becoming embroiled with Parrington, so maintained himself above the fray, whereas Parrington, fortified by the righteousness of his cause, did not feel he needed to be more politic. Parrington was certainly self-righteous and very conservative as a member of the wealthy establishment and a believer in the empire. He did look down on Kermack, who was not of the upper class and who did not respect traditional conservative values. Kermack's University College PhD students definitely resented Parrington's superior Cambridge attitude. I believe these social differences contributed to the antagonism between Parrington and Kermack'. Adrian Friday, a younger colleague of Parrington's at Cambridge in the 1970s, comments further (email, 17 February 2023), 'Kermack had been in the orbit of Haldane and the vaguely to stridently left-wing tendencies of the London axis (UCL, NHMUK). Parrington, on the other hand, had a private income through the family brewing interests, Harding & Parrington, based in Liverpool. This represented privilege. Also, Parrington's manner of dress, military rank and bearing suggested a certain tendency to the establishment and even to the right'.

Pat Ferguson added (letter to M.J.B., 15 March 2023) that Kenneth Kermack believed in encouraging women in the workplace, and it was much commented at the time that an unusual number of women were working in his laboratory, as technical support, PhD students, and colleagues. She notes that she always got on very well with Kenneth Kermack through her 30 years at UCL (1960–1990). 'I know KAK could be difficult but for a long time we always worked together amicably – or reasonably so. Also, we "knew out positions in the hierarchy." He always backed me though … However, Frances Mussett and KAK could argue fiercely but seemed to work together very successfully'.

Sadly, relations between Kenneth Kermack and Pamela Robinson were no better. As Pat Ferguson recalls (letter to M.J.B., 15 March 2023), 'when I arrived in the KAK lab in February 1960, PLR and KAK didn't have a relationship and never worked together. For the first couple of years of my time there, Frances Mussett worked for both of them. She was very discreet, but I was observant. She coped superbly but I think was very relieved when she stopped working for PLR. There was not I think a formal ending. PLR was just spending more and more time in India and no longer doing much work in Somerset'.

A positive feature of Kenneth Kermack's work is that he generally published as part of his team and then not always as a lead, insisting that author names were listed in alphabetical order (P.G.G.). Also, authors without higher level qualifications (e.g. Mussett, Ferguson) were included in the author lists. He acknowledged in detail where others had made a major contribution (e.g. that the quadrate and stapes and most of the specimens of the articular of the *Morganucodon* skull were found by Susan Evans; Kermack *et al.* 1981). In these aspects he was perhaps ahead of his time especially in the team approach to publication.

LATER DEBATES ON THE MAMMALS

In the comments quoted at the start of this article, Kühne (1973) argued provocatively that the name *Eozostrodon* given by Parrington (1941) should be abandoned in favour of the name *Morganucodon* which Kühne (1949a) gave later (Kühne 1973, Clemens 1979). Parrington (1971) reviewed the entire story up to that point, and expressed his disagreements with both Kühne and Kermack, and especially his unhappiness with many of the suggestions by Kermack. The language of this paper is sharp, and the name Kermack (both Kenneth and Doris) appears 76 times: in reporting their numerous published contributions since the 1950s, Parrington uses terms like 'claimed', 'supposed', and 'would suppose' in reference to their work. He is also sharper in specifics where he disagrees with them. For example, in reference to Kermack and Mussett's (1958) proposed revisions to the nomenclature of early mammals, Parrington (1971, p. 234) writes, 'Such muddling of the literature is not to be accepted. Instead of proposing a new name for the so-often discussed Pantotheria, all that was necessary was to put forward a name for the new Infraclass and all confusion would have been avoided'. Later, Parrington (1971, p. 239) reports Kenneth Kermack's changing views on the synonymy or not of *Eozostrodon* and *Morganucodon*—Parrington always argued they were synonyms and his *Eozostrodon* should be the name used—and summarizes, 'Kermack *et al.* do not appear to dispute this though, curiously, they do not appear to be able to recognize the tooth as an upper premolar. But they claim that it cannot be distinguished from a tooth they identify as belonging to *Kuehneotherium praecursoris*. Their reasoning is curious'. This comment is responded to in Kermack *et al.* (1973; p.105 footnote), noting that the premolars of *Kuehneotherium* are known from the Pontalun 1 pocket. One of the authors (P.G.G.) at the time noted the similarity to a *Kuehneotherium* penultimate upper premolar. Parrington (1971, p.241) writes further, 'Such is the reasoning which satisfies D.M. Kermack *et al.* that *Eozostrodon* is indeterminable'. There is a distinct feeling of antipathy behind the language.

In a follow-up paper, Parrington (1978) continues the public filleting of everything Kermack had written, focussing especially on responding to Kermack *et al.* (1973, pp. 180, 187), referring to 'Kermack and his associates'. Parrington (1978, p. 186) says, for example, 'Contrary to what stands in print, Kermack *et al.* (1973, p. 107) state that Mills had shown that in the tooth replacement of *Eozostrodon* (called by him *Morganucodon*) was "not of the therian pattern", which he did not … Kermack *et al.* (1973) do not make any mention of the work on tooth replacement by either Crompton or Parrington, leaving their readers in total ignorance of it'. Further (Parrington 1978, p. 191), 'Contrary to what stands in print Kermack *et al.* (1973, p. 106) make a very misleading statement'. On the question of synonymy or not between *Eozostrodon* and *Morganucodon*, 'Kermack achieves his second *volte face* in this matter' (Parrington 1971, p. 194). There then follows a detailed critique of various measurements of the teeth: 'It was for a short time difficult to follow just what Kermack had been measuring' (p. 194), and 'The explanation of appendix 1 of Kermack *et al.* (1973) was then reread when it was realized that the D/V figures were not obtained from carefully made, enlarged drawings, but by putting a graticule in the eyepiece and measuring imagined complete cusps and unworn valleys! Anyone who cares to try this will soon realize that it is impossible to feel satisfied with such measurements' (Parrington 1971, p. 196); 'the conclusion drawn in their appendix 1 is null and void. It has been a waste of everybody's time. Moreover, no knowledge of statistical methods is needed to reduce this impressive looking exercise to nothing' (Parrington 1971, p. 197); 'It is a pity that Kermack *et al.* did not check their student's figures by referring to Parrington's (1941) photographs and drawings' (Parrington 1971, p. 197). His conclusion (Parrington 1978, pp. 197–198) is devastating, 'Finally Kermack *et al.* (1973) supported Mills's contentions and also claimed that the once despised lower molar (*E. problematicus*) could be studied metrically and examined statistically, and claimed, in a most misleading appendix to their paper, that they had proved the two genera to be distinct. It has been shown that their conclusions are based on serious methodological errors. There are no grounds whatsoever for maintaining the genus *Morganucodon*. It is a junior synonym for the genus *Eozostrodon*'.

The student in question, one of the authors (P.G.G.), would like to set the record straight though, that the drawing (a sketch, made with a camera lucida in Cambridge, with Parrington's permission) was sitting on her desk at UCL, and she did not know that Kermack was going to use it until Parrington's paper came out. It was very embarrassing at the time, although she remained on good terms with Parrington. In defence of both Kermack and Parrington, though, neither of them let their dispute stand in her way, and Kermack encouraged her to visit Cambridge to see the collection of Pontalun material, and Parrington and Joysey were always helpful and welcoming.

Parrington (1978, p. 200), however, continued the careful dissection of his perception of Kenneth Kermack's many flaws, saying 'In the course of his three classifications K.A. Kermack has put forward names for two subclasses, one infraclass, one order and five suborders—all new (the two names for subclasses refer to the same animals). His five varying opinions on the nature of *Eozostrodon*, the last the most seriously questionable, leave one supporting his remark (1967), 'Rather, a worker in this field may be gratified if his concepts are still regarded as valid five years after he put them forward'. The sarcasm continues, 'here's prescience indeed!' (Parrington 1978, p. 200), 'Kermack *et al*.... scorn this comment'. Tom Kemp speculated (interview, 15 March 2022), 'I've no idea whether Parrington was able to write in such a sharp way in his 1970 and 1978 papers in the *Proceedings of the Royal Society*—Stanley Westoll was the editor, so maybe he let him get away with things'.

This approach is not seen in the three major Kermack papers to which Parrington was responding. Kermack *et al*. (1968) mention Parrington only twice, as author of the name *Eozostrodon*. Kermack *et al*. (1973, p. 105, footnote) refer to 'some confusion' from Parrington (1971). On the following page, they note, 'We can only repeat that we have been quite unable to match *E. problematicus* with *Morganucodon*. If Dr Parrington can, it would be helpful if he will publish the specimen'. Perhaps the only sharp remark by Kermack (1973, p. 165) is, 'Spurious resemblances may be obtained by cusp rotation without regard to the mode of functioning of the teeth'. Kermack *et al.* (1981) refer to Parrington on only three out of 158 pages, disputing points he made, but only some of his older papers from 1946 and 1949.

Kermack did not openly evince much interest in the Parrington publications, apart from the nomenclature question. Jim Hopson (email, 9 March 2023) comments, 'I believe that Kermack had the upper hand here because, after all, he had the better material, facilities, and staff, and a superb artist. What he did not have was, in my opinion, a passion for knowledge and understanding of the biology of *Morganucodon* that Parrington had. Parrington wanted the answers to biological questions on tooth succession and other aspects of the animal, but he was frustrated by Kermack having a total corner on the material that could answer these questions. He had a low regard for Kermack's intellectual achievements and believed he was wasting the potential of the material'. Others would perhaps argue that both Parrington and Kermack had a deep interest in the wider intellectual questions around evolution and function. Kühne expressed himself acerbically concerning Parrington. He wrote to Robinson (letter, 15 April 1973, NHMUK SFRAB; last known letter from him to Robinson), 'the idea that I would lower myself as Parrington has done is really slanderous'. The context of the letter is to express deep annoyance with Robinson about her continuing to correspond with him about her 250-page *Kuehneosaurus* monograph but not publishing it. He says, 'to achieve perfection is impossible and is the trait of a deseased [sic] mind'.

However, things could be rather more heated face to face, for example at the Linnean Society Early Mammal symposium in London in 1970 (Fig. 14). One of the authors (P.G.G.) had just started as a PhD student with Kermack, when she attended the meeting. She was amazed to see Kermack and Parrington shouting at each other at the front of the lecture theatre, until Simpson, who was the session chair, intervened.

Figure 14. The old and the new generations, Jim Hopson (left), Kenneth Kermack (centre), and George Gaylord Simpson (right), at the meeting on 'Early Mammals' in the rooms of the Linnean Society, London, 1970. At this point, Simpson, with his walking stick on his lap, was 68 years old, Kermack 51, and Hopson 35.

CONSEQUENCES

Much of what we have described might be seen as ancient history and not relevant to the modern study of Mesozoic mammals. However, the British Triassic and Jurassic mammal fossils dominated the discussion on early mammals for palaeontologists worldwide, until the 1990s, and papers by Simpson, Kermack, and Parrington are still widely quoted. Indeed, a case could be made that Kermack's scientific legacy has been more substantial than that of Parrington. For example, Kermack's most cited paper has had more success than Parrington's most cited paper: Kermack *et al.* (1981) has 326 citations against Parrington (1971) with 102 citations (Google Scholar, April 2023). Other papers by the Kermack team also achieved high citations [e.g. Kermack *et al.* (1968) has 152 citations], and students of Kermack also wrote highly cited papers from their thesis work, for example, Evans (1980; 202 citations) and Crush (1984; 223 citations). Evans went on the write many highly cited papers often on lepidosaurs (e.g. Evans 2008) which is a key reference on the skull of lizards and *Sphenodon*, achieving at least 339 citations. Parrington's student Tom Kemp was particularly successful, achieving, for example, 587 citations for Kemp (2005).

Both Kermack and Parrington left substantial collections of early fossil mammals, and these are widely studied today. Arguably, because of his long-term, industrial-scale processing of fissure material, Kermack has left the larger legacy here as well. The main Parrington collection is in the CAMZM, and the Kermack collection now in the NHMUK, but the latter comprises many more specimens and is associated too with large numbers of important specimens of reptiles, also from the fissures.

The research publications by both Kermack and Parrington established the importance of the very oldest triconodont-like mammaliaforms, including *Morganucodon*, and this has been the basis for much later research worldwide. Such mammals have turned out to be far more diverse worldwide than initially suspected, with, for example, *Megazostrodon* (Crompton & Jenkins, 1968) and *Erythrotherium* (Crompton, 1964) from southern Africa and *Dinnetherium* (Jenkins, Crompton & Downs, 1983) from Arizona. A further important discovery from Yunnan is *Hadrocodium* (Luo *et al.* 2001, 2022). Several new taxa have also been described from Saint-Nicolas-de-Port in France, including *Brachyzostrodon* (Sigogneau-Russell and Hahn 1994, Debuysschere *et al.* 2015), and the UK fissure mammaliaform fauna has turned out to be more diverse than previously thought, as evidenced by the identification of the new genera *Bridetherium* and *Paceyodon* (Clemens 2011). The 'symmetrodont'-like mammaliaforms including *Kuehneotherium*, although less widely distributed, include *Kotatherium* from India (Prasad and Manhas 1997) and new taxa from Saint-Nicolas-de-Port in France (Debuysschere 2017).

In terms of fundamental science, it might be said that Parrington's views have prevailed. He was an early convert to the idea of a monophyletic modern Mammalia, whereas Kermack firmly held the diphyletic view (Kermack and Kielan-Jaworowska 1971; Kermack and Kermack 1984). Earlier in their lifetimes, the multiple-origin view was the dominant one (Simpson 1959), but subsequently the monophyletic view emerged, firmly based on application of cladistic analysis (Kemp 1982, 2005, Rowe 1988). However, Kermack was very influential in promoting the view of two divisions of mammals (therians vs. non-therians), based on the structure of the braincase and molar form (Kermack 1967, Kermack and Kielan- Jaworowska 1971). Non-therians included docodonts, in which Kermack included *Morganucodon* (Kermack 1967), multituberculates and monotremes, and therians included the 'pantotheres', in which Kermack included *Kuehneotherium* (Kermack *et al.* 1968), 'symmetrodonts' and Eutheria. Non-therians are characterized by formation of the lateral braincase wall by the petrosal anterior lamina and by *Morganucodon*-like triconodont teeth. Therians are characterized by formation of the lateral braincase wall by the alisphenoid and squamosal and by triangulated teeth, either in the simple form seen in *Kuehneotherium*, or the therian tribosphenic (then called tritubercular) pattern. This 'two-division' mammal phylogeny was a prevailing idea, also adopted by Hopson (1969), Hopson and Crompton (1969), and Crompton and Jenkins (1973), and the idea came from the new petrosal fossils and abundant teeth prepared from the Glamorgan fissure sediments. Although not the only scientist promoting this, Kenneth Kermack, was certainly the earliest, and the idea became the mainstream opinion in the late 1960s through to the 1970s, until being challenged by Presley (1981) and Kemp (1983) who demonstrated that the lateral braincase wall and straight cusp alignment of molars are not suitable characters to define a clade. When Rowe (1988) published the first formal matrix-based phylogeny, Kermack's diphyletic origin of mammals simply collapsed [see Luo *et al.* (2002) for a discussion of these historical contexts]. It should also be noted that the basic definition of a mammal (= Mammaliaformes) often used today (Kemp 2005), is the one given by Kermack *et al.* (1981) based on the dentary-squamosal jaw joint and molar occlusion, a key distinction from earlier cynodonts.

The Bristol and South Wales fissures continue to produce excellent fossils, including, for example, the dinosaur *Thecodontosaurus* (Benton *et al.* 2000, Ballell *et al.* 2021, 2022), sphenodontians and other small reptiles (Evans 1980, Whiteside 1986, Fraser 1988, Chambi-Trowell *et al.* 2020), as well as mammals, although most of the newer work on the South Wales fossils (e.g. Fig. 2E) is based on specimens collected in the 1950s to 1970s (e.g. Gill *et al.* 2014, Newham *et al.* 2020). However, the world has moved on, and the old rivalries between Kühne, Parrington, and Kermack, came to an end after their deaths in 1991, 1981, and 2000, respectively. It is good to know that, whereas their teams of research students might have variously sided with their supervising professors at the time, these feelings did not persist after Parrington and Kermack retired.

CONCLUSION

Much of the story of the Triassic and Jurassic fissures around Bristol and South Wales might now seem pointless in the face of the spectacular complete fossils of Mesozoic mammals that have been found in China this century. However, up to the year 2000, the isolated teeth, jaws, and partial skeletons from the British Late Jurassic and Early Jurassic were some of the best materials we had to illustrate the origin of mammals. Then current arguments about the polyphyletic origins of mammals held sway, and so there was great excitement with the discovery of early mammals such as *Morganucodon* (*Eozostrodon*) with its cingulum and three-pointed molar teeth, interpreted as an early occurrence of the triconodont tooth type, and *Kuehneotherium* with the three cusps of its molar teeth arranged in a triangle, as in modern therians. Did these specimens capture two of the possibly multiple lines of parallel evolution from ancestral forms to mammals that occurred in the Late Triassic?

Since the papers by Kühne, Parrington, and Kermack, the overall picture of early mammalian evolution has changed radically, with widespread acceptance that Mammalia or Mammaliaformes are monophyletic groups (Kemp 1982, 2005, Rowe 1988, Luo *et al.* 2002, Kielan-Jaworowska *et al.* 2004). Also, much of the former obsession with fine details of cusps and their geometrical arrangements as the key to major trends in early mammalian evolution has dissolved in the face of richer evidence from more complete fossils.

Nonetheless, and despite all these advances in the diversity and quality of specimens coupled with huge advances in methods of phylogenetic analysis and access to computed tomography scanning to extract fine-scale details of anatomy in three dimensions, the British Late Triassic and Early Jurassic fissure mammals are crucial for understanding the first 50 Myr of mammalian (= mammaliaform) evolution. The fact that the fissures produced not just teeth and jaws, but also other elements of the skull and skeleton, so allowing more-or-less detailed accounts of the entire cranial anatomy (e.g. Kermack *et al.* 1973, 1981) sets these locations apart from many others of similar age that yield just teeth. Further, the excellent quality of preservation of the fossils means that modern technologies such as tooth-wear analysis, 3D CT micro-scanning to create accurate 3D digital models, tooth and jaw biomechanical analysis, and even analysis of growth rings in the cementum that fixes the teeth into the sockets to estimate growth rates and physiology can be applied (Gill *et al.* 2014, Newham *et al.* 2020).

SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* Journal online.

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REFERENCES

Ballell A, King JL, Neenan JM *et al.* The braincase, brain and palaeobiology of the basal sauropodomorph dinosaur. *Zoological Journal of the Linnean Society* 2021;**193**:541–62.

Ballell A, Rayfield EJ, Benton MJ. Walking with early dinosaurs: appendicular myology of the Late Triassic sauropodomorph *Thecodontosaurus antiquus*. *Royal Society Open Science* 2022;**9**:211356.

Benton MJ. Professor R. J. G. Savage: an appreciation. *Zoological Journal of the Linnean Society* 1994;**112**:3–12.

Benton MJ. Naming the Bristol dinosaur, *Thecodontosaurus*: politics and science in the 1830s. *Proceedings of the Geologists' Association* 2012;**123**:766–78.

Benton MJ, Juul L, Storrs GW *et al.* Anatomy and systematics of the prosauropod dinosaur *Thecodontosaurus antiquus* from the Upper Triassic of southwest England. *Journal of Vertebrate Paleontology* 2000;**20**:77–108.

Butler PM, Sigogneau-Russell D. Diversity of triconodonts in the Middle Jurassic of Great Britain. *Palaeontologia Polonica* 2016;**67**:35–65.

Chambi-Trowell SAV, Whiteside DI, Benton M *et al.* Biomechanical properties of the jaws of two species of *Clevosaurus* and a reanalysis of rhynchocephalian dentary morphospace. *Palaeontology* 2020;**63**:919–39.

Chambi-Trowell SAV, Whiteside DI, Benton MJ. Diversity in rhynchocephalian *Clevosaurus* skulls based on CT reconstruction of two Late Triassic species from Great Britain. *Acta Palaeontologica Polonica* 2019;**64**:41–64.

Charig AJ. Francis Rex Parrington. 20 February 1905–17 April 1981. *Biographical Memoirs of Fellows of the Royal Society* 1990;**36**:360–78.

Clemens WA. A problem in morganucodontid taxonomy. *Zoological Journal of the Linnean Society* 1979;**66**:1–14.

Clemens WA. New morganucodontans from an Early Jurassic fissure filling in Wales (United Kingdom). *Palaeontology* 2011;**54**:1139–56.

Colbert EH. The Triassic gliding reptile *Icarosaurus*. *Bulletin of the American Museum of Natural History* 1970;**143**:85–142.

Cromie WJ. Oldest mammal is found. *Harvard Gazette* 2001;**2001**:5. https://news.harvard.edu/gazette/story/2001/05/oldest-mammal-is-found-2/

Crompton AW. A preliminary description of a new mammal from the Upper Triassic of South Africa. *Proceedings of the Zoological Society of London* 1964;**142**:441–52.

Crompton AW, Jenkins FA Jr. Molar occlusion in Late Triassic mammals. *Biological Reviews* 1968;**43**:427–58.

Crompton AW, Jenkins FA Jr. Mammals from reptiles: review of mammalian origins. *Annual Reviews of Earth and Planetary Sciences* 1973;**1**:131–55.

Crush PJ. A Late Upper Triassic sphenosuchid crocodilian from Wales. *Palaeontology* 1984;**27**:131–57.

Debuysschere M. The Kuehneotheriidae (Mammaliaformes) from Saint-Nicolas-de-Port (Upper Triassic, France): a systematic review. *Journal of Mammalian Evolution* 2017;**24**:127–46.

Debuysschere M, Gheerbrant E, Allain R. Earliest known European mammals: a review of the Morganucodonta from Saint-Nicolas-de-Port (Upper Triassic, France). *Journal of Systematic Palaeontology* 2015;**13**:825–55.

Duffin CJ. Charles Moore and Late Triassic vertebrates – history and reassessment. *Geological Curator* 2019;**11**:143–60.

Evans SE. The skull of a new eosuchian reptile from the Lower Jurassic of South Wales. *Zoological Journal of the Linnean Society* 1980;**70**:203–64.

Evans SE. The skull of lizards and tuatara. In: Gans C, Gaunt AS, Adler K (eds), *Biology of the Reptilia, Volume 20. Morphology H: The Skull of Lepidosauria*. Ithaca: Society for the Study of Amphibians and Reptiles, 2008, 1–344.

Evans SE, Kermack KA. Assemblages of small tetrapods from the Early Jurassic of Britain. In: Fraser NC, Sues HD (eds), *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*. Cambridge: Cambridge University Press, 1994, 271–83.

Foffa D, Whiteside DI, Viegas PA *et al.* Vertebrates from the Late Triassic *Thecodontosaurus*-bearing rocks of Durdham Down, Clifton (Bristol, UK). *Proceedings of the Geologists' Association* 2014;**125**:317–28.

Fraser NC. A new rhynchocephalian from the British Upper Triassic. *Palaeontology* 1982;**25**:709–25.

Fraser NC. The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida). *Philosophical Transactions of the Royal Society of London B* 1988;**321**:125–78.

Gill PG, Purnell MA, Crumpton N *et al.* Dietary specializations and diversity in feeding ecology of the earliest stem mammals. *Nature* 2014;**512**:303–5.

Halstead LB, Nicoll PG. Fossilized caves of Mendip. *Studies in Speleology* 1971;**2**:93–102.

Hibbard CW. Techniques of collecting microvertebrate fossils. *Contributions of the Museum of Paleontology, University of Michigan* 1949;**8**:7–19.

Hopson JA. The origin and adaptive radiation of mammal-like reptiles and nontherian mammals. *Annals of the New York Academy of Sciences* 1969;**167**:199–216.

Hopson JA, Crompton AW. Origin of mammals. *Evolutionary Biology* 1969;**3**:15–72.

Jäger KRK, Gill PG, Corfe I *et al.* Occlusion and dental function of *Morganucodon* and *Megazostrodon*. *Journal of Vertebrate Paleontology* 2019;**39**:e1635135.

Jenkins FA Jr, Crompton AW, Downs WR. Mesozoic mammals from Arizona: new evidence on mammalian evolution. *Science* 1983;**222**:1233–5.

Keeble E, Whiteside DI, Benton MJ. The terrestrial fauna of the Late Triassic Pant-y-ffynnon Quarry fissures, South Wales, UK and a new species of Clevosaurus (Lepidosauria: Rhynchocephalia). *Proceedings of the Geologists' Association* 2018;**129**:99–119.

Kemp TS. *Mammal-like Reptiles and the Origin of Mammals*. New York: Academic Press, 1982.

Kemp TS. The relationships of mammals. *Zoological Journal of the Linnean Society* 1983;**77**:353–84.

Kemp TS. *The Origin and Evolution of Mammals*. Oxford: Oxford University Press, 2005.

Kermack DM, Kermack KA. *The Evolution of Mammalian Characters*. New York: Springer, 1984.

Kermack DM, Kermack KA, Mussett F. New Mesozoic mammals from South Wales. *Proceedings of the Geological Society London* 1956;**1533**:31.

Kermack DM, Kermack KA, Mussett F. The Welsh pantothere *Kuehneotherium praecursoris*. *Journal of the Linnean Society of London, Zoology* 1968;**47**:407–23.

Kermack KA. A note on the habits of the sauropods. *Annals and Magazine of Natural History, Series 12* 1951;**4**:830–2.

Kermack KA. A biometrical study of *Micraster coranguinum* and *M.* (*Isomicraster*) *senonensis*. *Philosophical Transactions of the Royal Society of London B* 1954;**237**:375–428.

Kermack KA. An ancestral crocodile from South Wales. *Proceedings of the Linnean Society, London* 1956;**166**:1–2.

Kermack KA. The interrelations of early mammals. *Journal of the Linnaean Society, Zoology* 1967;**47**:241–9.

Kermack KA, Haldane JBS. Organic correlation and allometry. *Biometrika* 1950;**37**:30–41.

Kermack KA, Kielan-Jaworowska Z. Therian and non-therian mammals. *Zoological Journal of the Linnean Society* 1971;**50**:103–16.

Kermack KA, Mussett F. The jaw articulation of the Docodonta and the classification of Mesozoic mammals. *Proceedings of the Royal Society B* 1958;**149**:204–15.

Kermack KA, Mussett F. The first mammals. *Discovery* 1959;**20**:144–51.

Kermack KA, Mussett F, Rigney HW. The lower jaw of *Morganucodon*. *Zoological Journal of the Linnean Society* 1973;**53**:87–175.

Kermack KA, Mussett F, Rigney HW. The skull of *Morganucodon*. *Zoological Journal of the Linnean Society* 1981;**71**:1–158.

Kielan-Jaworowska Z, Cifelli RL, Luo ZX (eds). *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure*. New York: Columbia University Press, 2004.

Kielan-Jaworowska Z. *In Pursuit of Early Mammals*. Bloomington: Indiana University Press, 2013.

Kohring R, Schluter T. In memoriam Walter Georg Kühne (26.2.1911–16.3.1991). *Berliner Geowissenschaftliche Abhandlungen A* 1991;**134**:3–8.

Krebs E. Walter Georg Kühne 26.2.1911–16.3.1991. *Paläontologie Aktuell* 1991;**24**:18–22.

Kretzoi M. Zur Benennung des ältesten Symmetrodonten. *Vertebrata Hungarici* 1960;**2**:307–9.

Kühne WG. The geology of the fissure filling 'Holwell 2'; the age determination of the mammalian teeth therein; and a report on the technique employed when collecting the teeth of *Eozostrodon* and Microclepidae. *Proceedings of the Zoological Society of London* 1947;**116**:729–33.

Kühne WG. On a triconodont tooth of a new pattern from a fissure-filling in South Glamorgan. *Proceedings of the Zoological Society of London* 1949a;**119**:345–50.

Kühne WG. Exhibition of specimens from localities of Mesozoic terrestrial vertebrates in the Bristol Channel area. *Proceedings of the Geological Society of London* 1949b;**1448**:53–4.

Kühne WG. A symmetrodont tooth from the Rhaeto-Lias. *Nature* 1950;**166**:696–7.

Kühne WG. *The Liassic Therapsid Oligokyphus*. London: British Museum (Natural History), 1956.

Kühne WG. Rhaetische Triconodonten aus Glamorgan, ihre Stellungzwischen den Klassen Reptilia und Mammalia und ihre Bedeutung fur die Reichart'sche Theorie. *Palaeontologische Zeitschrift* 1958;**32**:197–235.

Kühne WG. The systematic position of monotremes reconsidered (Mammalia). *Zeitschrift für Morphologie und Okologie der Tiere* 1973;**75**:59–64.

Kühne WG. *Paläontologie und Dialektischer Materialismus*. Jena: Gustav Fischer, 1979.

Kühne WG. Palaeontology and dialectics. *Documenta Naturae* 1990;**62**:1–167.

Large N. *Tom Fry, the Fossil Finder*. Winter: The Countryman, 1994, 95–100.

Lillegraven JA, Kielan-Jaworowska Z, Clemens WA. *Mesozoic Mammals, The First Two-Thirds of Mammalian History*. Berkeley: University of California Press, 1979.

Luo ZX, Bhullar BAS, Crompton AW *et al.* Reexamination of the mandibular and dental morphology of the Early Jurassic mammaliaform *Hadrocodium wui*. *Acta Palaeontologica Polonica* 2022;**67**:95–113.

Luo ZX, Crompton AW, Sun AL. A new mammaliaform from the Early Jurassic of China and evolution of mammalian characteristics. *Science* 2001;**292**:1535–40.

Luo ZX, Kielan-Jaworowska Z, Cifelli RL. In quest for a phylogeny of Mesozoic mammals. *Acta Palaeontologica Polonica* 2002;**47**:1–78.

Meng J. Mesozoic mammals of China: implications for phylogeny and early evolution of mammals. *National Science Review* 2014;**1**:521–42.

Milner AC. Robinson, Pamela Lamplugh, (1919–1994). In: *Oxford Dictionary of National Biography*. Oxford: Oxford University Press, 2004. https://doi.org/10.1093/ref:odnb/63228 (22 October 2021, date last accessed).

Milner AC, Hughes B. Pamela Lamplugh Robinson (1919–1994). *Society of Vertebrate Paleontology Bulletin* 1995;**164**:54–5.

Moore C. On Triassic beds near Frome, and their organic remains. *Report on the Twenty-Eighth Meeting of the British Association for the Advancement of Science* 1859;**1859**:93–4.

Moore C. On the contents of three cubic yards of drift. *Report of the British Association for the Advancement of Science* 1861;**1860**:87–8.

Moore C. On abnormal conditions of secondary deposits when connected with the Somersetshire and South Wales Coal Basin; and on the age of the Sutton and Southerndown Series. *Quarterly Journal of the Geological Society of London* 1867;**23**:449–568.

Moore C. On the age of the Durdham Down deposit, yielding *Thecodontosaurus* &c. *Annual Report of the British Association for the Advancement of Science* 1876;**1875**:77–8.

Moore C. On abnormal geological deposits in the Bristol district. *Quarterly Journal of the Geological Society* 1881;**37**:67–82.

Newham E, Gill PG, Brewer P *et al.* Reptile-like physiology in Early Jurassic stem-mammals. *Nature Communications* 2020;**11**:5121.

O'Brien A, Whiteside DI, Marshall JEA. Anatomical study of two previously undescribed specimens of *Clevosaurus hudsoni* (Lepidosauria: Rhynchocephalia) from Cromhall Quarry, UK, aided by computed tomography, yields additional information on the skeleton and hitherto undescribed bones. *Zoological Journal of the Linnean Society* 2018;**183**:163–95.
Owen R. Monograph of the fossil Mammalia of the Mesozoic formations. *Palaeontographical Society Monograph* 1871;**24**:1–115.
Parrington FR. On two mammalian teeth from the Lower Rhaetic of Somerset. *Annals and Magazine of Natural History (Series 11)* 1941;**8**:140–4.
Parrington FR. On a collection of Rhaetic mammalian teeth. *Proceedings of the Zoological Society, London* 1947;**116**:707–28.
Parrington FR. On the Upper Triassic mammals. *Philosophical Transactions of the Royal Society B* 1971;**261**:231–72.
Parrington FR. A further account of the Upper Triassic mammals. *Philosophical Transactions of the Royal Society B* 1978;**282**:177–204.
Plieninger WH. Zähne aus der oberen Grenzbreccie des Keupers bei Degerloch und Steinenbronn. *Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg* 1847;**3**:164–7.
Prasad GVR, Manhas BK. A new symmetrodont mammal from the Lower Jurassic Kota Formation, Pranhita-Godavari Valley, India. *Geobios* 1997;**30**:563–72.
Presley R. Alisphenoid equivalents in placentals, marsupials, monotremes and fossils. *Nature* 1981;**294**:668–70.
Rigney HW. A specimen of *Morganucodon* from Yunnan. *Nature* 1963;**197**:1122–3.
Robinson PL. Exhibition of specimens from Slickstones Quarry, Gloucestershire. *Proceedings of the Geological Society, London* 1955;**1527**:113–5.
Robinson PL. The Mesozoic fissures of the British Channel area and their vertebrate faunas. *Zoological Journal of the Linnean Society of London* 1957a;**43**:260–82.
Robinson PL. An unusual sauropsid dentition. *Zoological Journal of the Linnean Society of London* 1957b;**43**:283–93.
Robinson PL. Gliding lizards from the Upper Keuper of Great Britain. *Proceedings of the Geological Society of London* 1962;**1601**:137–46.
Robinson PL. Triassic vertebrates from lowland and upland. *Science and Culture* 1967;**33**:169–73.
Robinson PL. A problem of faunal replacement on Permo-Triassic continents. *Palaeontology* 1971;**14**:131–53.
Robinson PL. A problematic reptile from the British Upper Trias. *Journal of the Geological Society, London* 1973;**129**:457–79.
Robinson PL. How *Sphenodon* and *Uromastyx* grow their teeth and use them. In: Bellairs AD'A, Cox CB (eds), *Morphology and Biology of Reptiles*. Linnean Society Symposium Series. London: Academic Press, 1976, 43–67.
Robinson PL, Kermack KA, Joysey KS. Exhibition of a new Upper Triassic land fauna from Slickstones Quarry, Gloucestershire. *Proceedings of the Geological Society of London* 1952 ;**1485**:86–7.
Rowe TB. Definition, diagnosis, and origin of Mammalia. *Journal of Vertebrate Paleontology* 1988;**8**:241–64.
Sarjeant WAS. Lambert Beverley Halstead (1933–1991): his life, his discoveries and his controversies. In: Sarjeant WAS (ed.), *Vertebrate Fossils and the Evolution of Scientific Concepts*. London: Gordon & Breach, 1993, 2–58.
Savage RJG. The Mesozoic strata of the Mendip Hills. In: Savage RJG (ed.), *Geological Excursions in the Bristol District*. Bristol: University of Bristol, 1977, 85–100.
Savage RJG. Vertebrate fissure faunas with special reference to Bristol Channel Mesozoic faunas. *Journal of the Geological Society, London* 1993;**16**:153–62.
Savage RJG. Pamela Lamplugh Robinson (1919–1994). *Annual Report of the Geological Society* 1994;**1994**:19–20.
Savage RJG, Waldman M. *Oligokyphus* from Holwell Quarry, Somerset. *Proceedings of the Bristol Naturalists* 1966;**31**:185–92.
Schlüter T. Walter Georg Kühne 70 Jahre alt—eine biographische Skizze. *Berliner Geowissenschaftliche Abhandlungen A* 1981;**32**:1–17.
Schmitt M. *From Taxonomy to Phylogenetics: Life and Work of Willi Hennig*. Leiden: E.J. Brill, 2013.
Şengör AMC. An outstanding scientist, a great book and an infernal title. *International Journal of Earth Sciences* 2021;**110**:759–65.
Sigogneau-Russell D. Haramiyidae (Mammalia, Allotheria) en provenance du Trias supérieur de Lorraine (France). *Palaeontographica A* 1989;**206**:137–98.
Sigogneau-Russell D, Hahn G. Late Triassic microvertebrates from central Europe. In: Fraser NC, Sues HD (eds), *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*. Cambridge: Cambridge University Press, 1994, 197–213.
Simpson GG. *A Catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum*. London: British Museum (Natural History), 1928.
Simpson GG. American Mesozoic mammals. *Memoir of the Peabody Museum, Yale* 1929;**3**:1–236.
Simpson GG. *Haramiya*, new name, replacing *Microcleptes* Simpson, 1928. *Journal of Paleontology* 1947;**21**:497.
Simpson GG. [Review of Kühne 1956.]. *Science* 1957;**126**:1250.
Simpson GG. Mesozoic mammals and the polyphyletic origin of mammals. *Evolution* 1959;**13**:405–14.
Simpson GG. Preface. *Zoological Journal of the Linnean Society* 1984;**82**:3–5.
Skinner M, Whiteside DI, Benton MJ. Late Triassic island dwarfs? Terrestrial tetrapods of the Ruthin fissure (South Wales, UK) including a new genus of procolophonid. Proceedings of the Geological Associatio 2020;**131**:535–61.
Stein K, Palmer C, Gill PG *et al.* The aerodynamics of the British Late Triassic Kuehneosauridae. *Palaeontology* 2008;**51**:967–81.
Swinton WE. A new Triassic rhynchocephalian from Gloucestershire. *Annals and Magazine of Natural History* 1939;**4**:591–4.
Tarlo LB. A new Middle Triassic reptile fauna from fissures in the Middle Devonian limestones of Poland. *Proceedings of the Geological Society of London* 1959;**1568**:63–4.
Tarlo LB. Ancient animals of the upland. *New Scientist* 1962;**15**:32–4.
Thomas TM. Notes on the structure of some minor outlying occurrences of littoral Trias in the Vale of Glamorgan. *Geological Magazine* 1952;**89**:153–62.
Turner S. Far-flung female (and fossil bone hunting) fellows: an autoethnographical approach. *Geological Society, London, Special Publications* 2021;**506**:277–302.
Warrener D. An archosaurian fauna from a Welsh locality. *Ph.D. Thesis*. Department of Zoology, University College London, 1983, 384 pp. (unpublished).
Whiteside DI. The head skeleton of the Rhaetian sphenodontid *Diphydontosaurus avonis* gen. et sp. nov. and the modernizing of a living fossil. *Philosophical Transactions of the Royal Society of London B* 1986;**312**:379–430.
Whiteside DI, Chambi-Trowell SAV, Benton MJ. A Triassic crown squamate. *Science Advances* 2022;**8**:eabq8274.
Whiteside DI, Duffin CJ. Late Triassic terrestrial microvertebrates from Charles Moore's '*Microlestes*' quarry, Holwell, Somerset, UK. *Zoological Journal of the Linnean Society* 2021;**179**:677–705.
Whiteside DI, Duffin CJ, Gill PG *et al.* The Late Triassic and Early Jurassic fissure faunas from Bristol and South Wales: stratigraphy and setting. *Palaeontologica Polonica* 2016;**67**:257–87.