Diverse vertebrate assemblage of the Kilmaluag Formation (Bathonian, Middle Jurassic) of Skye, Scotland

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Running Head: Vertebrate assemblage of Kilmaluag Formation

Abstract: The Kilmaluag Formation on the Isle of Skye, Scotland, provides one of the richest Mesozoic vertebrate fossil assemblages in the UK, and is among the richest globally for Middle Jurassic tetrapods. Since its discovery in 1971, this assemblage has predominantly yielded small-bodied tetrapods, including hybodontiforms, salamanders, choristoderes, lepidosaurs, turtles, crocodylomorph, pterosaurs, dinosaurs, non-mammalian cynodonts and mammals, alongside abundant fish and invertebrates. It is protected as a Site of Special Scientific Interest (SSSI) and by Nature Conservancy Order (NCO). Unlike contemporaneous localities from England, this assemblage yields associated partial skeletons, providing unprecedented new data. We present a comprehensive updated overview of the Kilmaluag Formation, including its geology and the fossil collections made to date, with evidence of several species occurrences presented here for the first time. We place the vertebrate faunal assemblage in an international context through comparisons with relevant contemporaneous localities from the UK, Europe, Asia and the United States. This wealth of material reveals the Kilmaluag Formation as a vertebrate fossil assemblage of global significance, both in terms of understanding Middle Jurassic faunal composition and the completeness of specimens with future implications for the early evolutionary histories of mammals, squamates and amphibians.

Key Words: tetrapods, palaeontology, Great Estuarine Group, mammaliaforms, salamanders, squamates

The Middle Jurassic documents key events in the morphological and taxonomic diversifications of many groups of land vertebrates, including dinosaurs (e.g. Benson *et al*. 2014; Lee *et al*. 2014; Rauhut *et al*. 2016; Benson 2018), mammals (Luo 2007; Close *et al*. 2016), squamates (e.g. Jones *et al*. 2013; Burbrink *et al*. 2019), and amphibians (e.g. Roelants *et al*. 2007; Gao & Shubin 2012; Marjanović & Laurin 2014). Middle Jurassic fossils therefore provide vital information on the origins of groups that played central roles in Mesozoic terrestrial ecosystems, many of which persist to the present. However, terrestrial vertebrates from the Middle Jurassic are rare globally, being known predominantly from China (e.g. Sullivan *et al*. 2014; Xu *et al*. 2017), Russia (e.g. Averianov *et al*. 2005, 2016.), and the UK (e.g. Evans & Milner 1994; Wills *et al*. 2019). Within the UK, English Middle Jurassic units yielded the historically earliest discoveries of dinosaurs, pterosaurs, turtles and Mesozoic mammals (Buckland 1824; Blake 1863; Delair & Sarjeant 2002; Anquetin & Claude 2008). More recently, extensive screenwashing of sediment bulk samples at localities in Oxfordshire and Gloucestershire has uncovered abundant isolated remains that document a species-rich assemblage of small-bodied vertebrates including amphibians, reptiles and mammals from sites such as Kirtlington (Freeman 1976, 1979; Kermack *et al*. 1987; Evans 1988, 1990, 1991a, b; 1992, 1994, 1998; Evans *et al*. 1988, 1990; Evans & Milner 1994; Gillham 1994; McGowan 1996; Sigogneau-Russell 1998, 2003a; Gardner *et al*. 2003; Scheyer & Anquetin 2008). While much attention has been paid to Middle Jurassic outcrops in localities in England, it is only recently that Scottish localities have undergone dedicated palaeontological study, particularly on the Isle of Skye.

The Kilmaluag Formation (Harris & Hudson 1980) on the Isle of Skye, part of the Great Estuarine Group, is one of the richest fossiliferous formations for vertebrates in Scotland (Whyte & Ross, 2019). Many of the vertebrates currently known from the Kilmaluag Formation belong to species and genera already reported, but known only from disarticulated remains obtained by bulk sampling of sediments at English Bathonian localities (e.g. Evans *et al*. 2006; Panciroli *et al.* 2018a and herein). However, compared to these the Kilmaluag Formation preserves substantially more complete specimens, including partial and near-complete skeletons that represent some of the oldest salamanders, squamates and crown-group mammals. Due to their significance, outcrops are legally protected as Sites of Special Scientific Interest

(SSSI) and through Scotland's Nature Conservancy Order (NCO) meaning that fossils can only be collected for scientific purposes through permits from Scottish Natural Heritage (SNH).

The first fossils from the 'vertebrate beds' of the Kilmaluag Formation were discovered in 1971 by Michael Waldman, a teacher at Stowe School (Waldman & Savage 1972). Waldman and his colleague and mentor, Robert Savage (University of Bristol), undertook seven field trips between 1971 and 1982. Further fieldwork was undertaken in the early 2000s by a team from the Natural History Museum in London, NMS, University College London, and the University of Oxford, under leadership of Susan Evans and Paul Barrett. Since 2010 fieldwork has continued, led by Roger Benson (University of Oxford), Stig Walsh (National Museums Scotland), Richard Butler (University of Birmingham), and Elsa Panciroli (University of Oxford), along with other participants (see Acknowledgements). A wealth of material collected by multiple expeditions has revealed the Kilmaluag Formation as one of the richest vertebrate fossil localities in the UK, and of global significance both in terms of faunal composition, and the completeness of specimens.

An overview of the fossil finds from the Kilmaluag Formation was last provided in 2006 (Evans *et al*. 2006). New discoveries since then have considerably expanded our knowledge of this assemblage and its global importance as a site for Middle Jurassic vertebrates. Here we provide an up-to-date overview of the geology and collections, and discuss potential collection biases caused by the hard-weathering nature and poor reaction to acid of the limestone, which makes it unsuitable for bulk processing. We make comparisons between the Kilmaluag Formation faunal assemblage—particularly mammals, salamanders and squamates—and relevant contemporaneous localities from the UK, Europe, Asia and the United States. These comparisons provide international context for the Kilmaluag Formation assemblage, and provide evidence regarding proposed global distribution patterns and macroevolutionary trends in various mammal groups and their close relatives.

Institutional Abbreviations—NMS, National Museums Scotland, Edinburgh; NHMUK, Natural History Museum, London; CAMSM, Sedgewick Museum of Earth Sciences, University of Cambridge.

1. Geological Overview

The Kilmaluag Formation (Harris & Hudson 1980) is part of the Great Estuarine Group (formerly Great Estuarine Series [Judd 1878, p722]), a series of near-shore shallow marine, varied salinity lagoon and freshwater lagoon sediments of Bathonian age (Harris & Hudson 1980; Andrews 1985; Barron *et al*. 2012) (Fig. 1). The Great Estuarine Group comprises the Middle Jurassic portion of the Sea of Hebrides Basin and Inner Hebrides Basin: tectonically bound basins with sedimentology that reflects fluctuating sea-levels caused by subsidence and uplift (Morton 1987; Mellere & Steel 1996; Hesselbo & Coe 2000). These Mesozoic sediments are overlain disconformably by Tertiary basalt (Harris & Hudson 1980).

The Kilmaluag Formation crops out on the Scottish Inner Hebridean islands of Eigg, Skye and Muck, and is approximately 25 m in thickness at the most complete section on the Strathaird Peninsula on Skye (Harris & Hudson 1980; Morton & Hudson 1995) (Figs 1–2). It was formerly known as the Ostracod Limestone, and the base of the formation is defined by the occurrence of ostracod-bearing calcareous mudstones and marls/fissile mudstones (Anderson & Dunham 1966; Harris & Hudson 1980; Andrews 1985; Barron *et al*. 2012). It is named for the village of Kilmaluag on the Trotternish Peninsula of Skye, where the type section crops out along the shore of Kilmaluag Bay (Harris & Hudson 1980). Despite being less extensive than exposures on the Strathaird Peninsula in southern Skye, Kilmaluag was chosen as the locality of the type section as it is accessible and fossiliferous, and the base of the formation can be easily defined to within 3 m (Harris & Hudson 1980).

The age of the Kilmaluag Formation correlates with the *Retrocostatum* Zone, and is late Bathonian in age (Barron *et al*. 2012), just over 166.1 Ma (Cohen *et al.* 2019). The similarities in vertebrate faunal composition with that from the Kirtlington Cement Quarry (Forest Marble Formation, see below) in England also support a late Bathonian age. Unlike other formations within the Great Estuarine Group, the Kilmaluag Formation includes predominantly low-salinity and freshwater facies, especially on the Strathaird Peninsula, as demonstrated by the presence of freshwater ostracods (*Darwinula* and *Theriosynoecum*: Wakefield 1995), shallow freshwater to oligohaline conchostracans (such as *Anthronesteria* and *Pseudograpta*: Chen & Hudson 1991) and freshwater gastropods (*Viviparus*: Andrews 1985; Morton & Hudson 1995; Barron *et al*. 2012) (Fig. 3).

The Kilmaluag Formation can be divided into two distinct facies: predominantly siliciclastic facies in northern Skye, including sandstones; and predominantly argillaceous (muddy) limestone facies found on the Strathaird Peninsula in southern Skye, and also in small outcrops on Eigg and Muck, which do not include sandstones (Andrews 1985). Palaeoenvironmental reconstructions of the siliciclastic facies suggest a low-salinity environment of closed lagoons or marginal coastal lakes, fed by small rivers which carried in siliciclastic sediments and plant material (Andrews 1985). Multiple layers of desiccation cracks, and reworked desiccation breccias infilling mudcracks, suggest periodic drying out followed by wetter periods of lagoon expansion. There are also rippled sandsheets in some beds, with tuning-fork bifurcations indicative of wave generation (Andrews 1985).

The argillaceous limestone facies were depositional rather than diagenetic in origin and contain up to 44% acid-insoluble residues (Andrews 1985). These beds are locally altered by metamorphism resulting from Palaeogene igneous intrusions (Hesselbo & Coe 2000). The mud-dominated lower beds, which alternate between muds with high clay content, and muddy-carbonates with lower clay content represent a low-salinity to freshwater lagoon environment, which evaporated in drier seasons and expanded in wetter seasons (Andrews 1985). This environmental interpretation is supported by alternating clay-rich muds, and muddy carbonates that are dominated by disarticulated ostracod bioclasts and structureless micrite introclasts (Andrews 1985). Infrequent dolomites probably represent the dolomitisation of precursor carbonates during extreme periods of desiccation (Andrews 1985:1128). This would have exposed mudflats, forming desiccation cracks and flat-pebble conglomerates. The argillaceous facies were fed by meteoric waters, unlike the clastic facies in the north. This interpretation of a low-salinity closed lagoon environment is supported by a palynoflora that includes *Tasminites* and *Botryoccus* (Riding *et al*. 1991).

Andrews (1985) informally divided the Kilmaluag Formation into a series of numbered horizons, with horizons 9 and 10, near the middle of the sequence, also known as the 'Vertebrate Beds'. These beds are highly fossiliferous, located on the Strathaird Peninsula, and are thought to represent a predominantly wet climatic phase. These beds alternate between muddy carbonates, hard blue-grey limestones, micrites, wackestones and breccia conglomerates, and appear to be predominantly freshwater (Andrews 1985). The lowest MgO content is found in these beds, and in some there is smooth millimetre-scale lamination, and some stromatolitic domed laminations, which suggests a shallow sublittoral depositional environment. Vertebrate fossil remains in the Kilmaluag Formation are black in colour, and are scattered throughout.

Breccia beds that overlie the vertebrate beds also yield body and trace fossil material (see below) (Andrews 1985; Marshall 2003) (Fig. 2). The breccia beds comprise three dolomitic, gradationally bound beds combined into one bedset (Marshall 2003). Each bed consists of silty micrite which becomes brecciated upwards across a desiccation cracked horizon. The brecciation and mudcracks are inferred to result from prolonged subaerial exposure and desiccation (Marshall 2003). This evidence, coupled with the lack of fossilised vegetation, suggests these beds represent a barren or sparsely vegetated supralittoral lagoon margin (Marshall 2003).

2. Fossil Flora and Fauna of the Kilmaluag Formation

2.1 Flora

No in-depth palaeobotanical studies have been made of the plant fossils of the Great Estuarine Group. Floral remains mostly comprise poorly preserved fragments, and only rare small broken pieces of bark and stem occur in the Kilmaluag Formation (EP, pers. obs.). A single palynological study included data from the Kilmaluag Formation in the Trotternish Peninsula of northern Skye as part of a wider analysis of the Jurassic rocks of the Hebrides Basins (Riding *et al*. 1991). They took 16 samples from the Isle of Skye, 12 of them from the type section at Port Gobhlaig in Kilmaluag Bay and four at Prince Charles' Point. These samples indicated low palynological diversity dominated by gymnosperm pollen (up to 87%), with <24% pteridophyte spores (Riding *et al*. 1991:p143).

2.2 Invertebrate fossils

The most abundant invertebrate fossils of the Kilmaluag Formation are arthropods, notably ostracods, principally *Darwinula* and *Theriosynoecum* (Wakefield 1995), and the conchostracans *Anthronesteria* and *Pseudograpta* (Chen & Hudson 1991). There are also molluscs such as the gastropod *Viviparus* and the bivalve *Unio* (Harris & Hudson 1980; Andrews 1985). Trace-fossil burrows attributed to larger decapods are also preserved in the vertebrate beds and breccia beds on the Strathaird Peninsula of southern Skye and are interpreted as dwelling burrows for crabs or shrimps (Marshall 2003).

Only a handful of other invertebrate fossils are known from the Kilmaluag Formation. Insect-bearing strata were discovered by EP in 2017 at an outcrop of Kilmaluag Formation at Lub Score on the Trotternish Peninsula. Subsequently, multiple specimens have been collected and await description (under study by A. Ross). These mainly comprise beetle wing cases that cannot be assigned above ordinal level, but continued collection should yield sufficient data to give some indication of insect faunal diversity in the future.

2.3 Chondrichthyes and Osteichthyes

Three chondrichthyan and two osteichthyan taxa have been described from the Kilmaluag Formation to date. The chondrichthyans are hybdont sharks: *Acrodus, Hybodus* and an indeterminate hybodont (Rees & Underwood 2006; Evans *et al*. 2006). The *Acrodus* specimens represent new species, and comprise the only non-marine Jurassic occurrences in Europe, and some of the youngest occurrences of this genus known (Rees & Underwood 2006) (Fig. 3). Pycnodont scales are visible at outcrop (EP and RBJB, pers. obs.). The semionotiform *Lepidotes* and an unidentified sarcopterygian (?coelacanth) have previously been recovered (Evans *et al*. 2006), and some partial mandibles belonging to amiiforms were collected recently, but not yet described. All of these are known from isolated scales, teeth and/or tooth fragments. In the last decade of fieldwork more fossil fish have been recovered (e.g.

Fig. 3D), including partial associated skeletons that currently await preparation and study.

2.4 Lissamphibia

Two species of salamander and one albanerpetontid are known from the Kilmaluag Formation (Evans & Waldman 1996; Evans *et al*. 2006). The salamanders, *Marmorerpeton* and (the informally named) 'Kirtlington salamander A', were both originally reported on the basis of isolated elements obtained by screenwashing from the Middle Jurassic Forest Marble Formation of Kirtlington, England (Evans *et al*. 1988; Evans & Milner, 1994; Evans *et al*. 2006). There is currently no evidence of frogs or caecilians from Skye, although frogs have been described from the Kirtlington microvertebrate assemblage (Evans *et al*., 1990).

Marmorerpeton is a relatively large, paedomorphic, aquatic salamander (Evans *et al*. 1988; Evans & Milner 1994; Evans & Waldman 1996). Most material is estimated to come from animals 25-30 cm long (Evans *et al*. 1988). One partial skeleton was collected from Skye by Waldman and Savage (reported in Evans & Waldman 1996), but has not yet been described. Recent fieldwork has recovered a second part of the same skeleton, as well as several addition partial skeletons. Collectively these specimens include most of the skull and postcrania and they are currently under study (Jones *et al*. 2018a).

Accessioned material of *M. kermacki* includes an association of vertebrae, limb and skull elements (NMS G.1992.47.9), two fused caudal vertebrae (NMS G.1992.47.12), multiple isolated vertebrae (NMS G.1992.47.25, NMS G.1992.47.26 and NMS G.1992.47.27), and a partial ilium (NMS G.1992.47.15; Evans & Waldman 1996:fig 1b).

The strongly sculptured skull bones, proportions of the atlas, absence of spinal nerve foramina in the atlas (Evans *et al*. 1988), and features of the ilium suggest that *Marmorerpeton* may be an early karaurid, a group of stem salamanders that are known from the Middle Jurassic to Early Cretaceous of Kyrgyzstan, Kazakhstan, and Russia (Ivakhnenko 1978; Nesov 1988; Nesov *et al*. 1996; Skutschas & Martin 2011;

Skutschas & Krasnolutskii 2011; Skutschas 2013; 2014a, b; Skutschas *et al.* 2018). Whether this group is monophyletic or paraphyletic (sharing several plesiomorphic characters) remains to be established. The proportions of two undescribed atlantes among the Scottish material most closely resemble those of *M. kermacki*, one of the two species named from Kirtlington (Evans *et al*. 1988).

A second salamander, referred to informally as 'Kirtlington Salamander A' (Evans & Milner 1994), is also present at Skye (Evans & Waldman 1996; Evans *et al*. 2006) and is relatively common there, based on recently collected material (Fig. 4H–K). Salamander A was probably smaller than *Marmorerpeton* (Evans & Milner 1994) but was also likely aquatic. Multiple isolated elements of 'Kirtlington Salamander A' from Skye—mostly vertebrae—are accessioned at NMS, including NMS G.1992.47.14. To date the only published image of 'Kirtlington Salamander A' is a dorsal vertebra in lateral view (Evans & Waldman 1996:fig 1a). However, associated skeletons that include skull roof and braincase elements have been found more recently and are currently under study (Jones *et al*. 2018a).

Features of the atlas and vertebrae (e.g. absence of spinal nerve foramina, no interglenoid tubercle) suggest that 'Kirtlington salamander A' is a stem salamander (Jones *et al*. 2018a). It is easily distinguished from *Marmorerpeton* due to its shorter dorsal vertebrae that have shallow rib bearers, less textured skull bones, and wider notochordal canals.

Albanerpetontids are represented by just one specimen, a pair of articulated premaxillae, collected in 2014 (NMS G.2019.34.6) (Fig. 4A–B, D). The specimen shows many similarities with *Anoulerpeton priscus*, previously known only from the microvertebrate assemblage at Kirtlington (Gardner *et al*. 2003).

2.5 Lepidosauromorpha

The Kilmaluag Formation has yielded a diversity of lepidosauromorphs (Waldman & Evans 1994; Evans & Waldman 1996; Evans *et al*. 2006; work in progress), including some of the earliest crown squamates, as well as more basal taxa.

Marmoretta sp. is the most abundant small reptile in the Kilmaluag assemblage, represented by multiple dentaries and maxillae including CAMSM x991, as well as the partial skeleton NMS G.1992.47.1 (Waldman & Evans 1994:fig 6–9), and the maxillae NMS G.1992.47.4 (Fig. 5A–C) and NMS G.1992.47.5 (Waldman & Evans 1994:fig 5). *Marmoretta* was originally described from the microvertebrate assemblage at Kirtlington (Evans 1991a) and other English Bathonian sites (Evans 1992; Evans & Milner 1994) and is also known from the Late Jurassic of Portugal (Evans 1991a). The partial skeleton NMS G.1992.47.1 remains the most complete specimen of *Marmoretta* (Evans 1991a; Evans & Waldman 1994). Only the skull and limited aspects of postcranial morphology have been described so far (Waldman & Evans 1994:figs 6–8). However, microCT scans indicate a more substantially complete and 3D preserved skeleton largely covered by matrix that is currently under study.

Recent fieldwork has substantially extended the number of known lepidosaur fossils from the Kilmaluag Formation, including the collection of more than 20 isolated tooth-bearing elements and several partial or near-complete skeletons. To date these new specimens represent squamates and stem-group lepidosaurs. No rhynchocephalians are currently known. Rhynchocephalians are also rare in other Middle Jurassic assemblages in the UK: only three incomplete bones were reported previously from Kirtlington Cement Quarry (Evans 1992; Evans & Milner 1994) despite bulk sampling of large quantities of sediment (Ward 1984) and abundant remains of other lepidosaurs (e.g. Evans 1988; Evans & Milner 1994).

Two partial dentaries with subpleurodont dental implantation show notable differences from each other and from dentaries of *Marmoretta* (NMS G.1992.47.1 and referred specimens from Kirtlington; Evans 1991a; Waldman and Evans 1994). Both might represent distinct lepidosauromorph species. Lepidosauromorph ‘species A’, NMS G.2019.34.9 (Fig. 5D–E), differs from *Marmoretta* in having a dentary that is dorsoventrally expanded towards the symphysis, giving the ventral margin a strongly curved outline. Seen in lingual view, the anterior end of the bone has an unusual morphology. The rounded subdental shelf develops a sharp-edged and facetted flange, presumably for articulation with a large splenial. Below this, the expanded ventral margin is also facetted.

Lepidosauromorph ‘species B’, NMS G.2019.34.13, is a partial left dentary recovered in 2015 (Fig. 5F–I) with subpleurodont dental implantation may represent a distinct taxon from *Marmoretta*. It differs from *Marmoretta* in possessing conical teeth with apices that are not recurved (those of *Marmoretta* are curved apicoposteriorly). Some teeth have mesiodistally wide bases and others have mesiodistally narrow bases, whereas the teeth of *Marmoretta* vary only gradually (mesial teeth have narrow bases and are smaller). Neither specimen is currently considered sufficient as the basis for a new species but nevertheless these specimens show a potentially larger and as yet unappreciated diversity of primitive lepidosauromorphs in the assemblage.

Several squamates or stem-squamates have been reported so far, based predominantly on tooth bearing elements (dentaries and maxillae), as well as isolated vertebrae. Waldman & Evans (1994) described two isolated dentaries — the almost complete right and a partial left dentary of what they referred to *Paramacellodus* sp. (NMS G.1992.47.2; NMS G.1992.47.3; Waldman & Evans 1994:fig 4) based on overall similarities of the jaw shape (e.g. orientation of the Meckelian canal, elongated lateral depression) and tooth morphology (chisel-shaped striated tooth tips, posteriorly directed). A similar left dentary was collected in 2016 (NMS G.2019.34.11) (Fig. 6C-E). Furthermore, micro-CT scans of NMS G.1992.47.2 reveal a right frontal, left pterygoid with a single pterygoid tooth row, and abraded right humerus within the matrix. These show additional paramacellodid-like features including paired frontals of roughly equal anterior and posterior width with an interdigitating median suture (Evans & Chure 1998). The frontals differ from those of *Paramacellodus* in having a more complex median interdigitation, in lacking any obvious interdigitation of the frontoparietal suture, and in having a deeper anteroventral descending lamina. However, the absence of osteoderms associated with any of these specimens, or even as isolated elements in the matrix, suggests that these specimens do not belong to *Paramacellodus* and they are referred here to Squamata cf. Paramacellodidae indet.

An assemblage of tiny skull bones including a right dentary, partial right maxilla, and a partial right prefrontal collected in 2015 is referred to *Balnealacerta silvestris* (NMS

G.2019.34.3) (Fig. 7A–G). This identification is based on detailed similarities of the anterior part of the dentary, including the anterodorsal angulation of the Meckelian groove at the symphysis and the presence of a long ventrolateral muscle scar. *Balnealacerta silvestris* was originally reported from Kirtlington and referred to Paramacellodidae (Evans 1998) based on similarities of the dentary and tooth morphology to those of other paramacellodids. However, no trace of the characteristic oblong osteoderms characteristic of paramacellodids has been found either at Kirtlington or in the Skye material, raising doubts regarding its paramacellodid affinity.

Evans & Waldman (1996, Fig. 4) reported a dentary and parts of other bones scattered on a slab as Scincomorpha indet. (NMS G.1992.47.10). Here we note strong similarity of that specimen to the holotype of *Bellairsia gracilis*, (NHMUK PV R12678) reported previously from Kirtlington as of the most abundant reptiles in that assemblage (Evans 1998). These specimens share a gracile jaw morphology (slender and parallel-sided rather than 'boat-shaped), open Meckelian groove, and small, lingually striated teeth. Therefore, we refer NMS G.1992.47.10 to *Bellairsia* sp. We also report an incomplete left dentary preserved in two parts (the symphysis and a central portion; NMS G.2019.34.1) (Fig. 7H–M) that shares the slender teeth, relatively simple tooth tips, low subdental shelf and pattern of prearticular and angular faceting with the holotype of *Bellairsia* from Kirtlington (NHMUK PV R12678). Finally, a near-complete, articulated skeleton, probably referable to *Bellairsia*, that was collected in 2016 is currently under study.

Waldman & Evans (1996) reported multiple vertebrae from the Kilmaluag Formation as being similar to subadult specimens of the squamate *Parviraptor* from the microvertebrate assemblage of Kirtlington. The presence of *Parviraptor*-like squamates in the Kilmaluag Formation has been confirmed by the discovery of further material, which is currently under study.

Referrals of individual vertebrae to *Parviraptor* are complicated. *Parviraptor estesi* was originally reported from the Early Cretaceous Purbeck Group of the UK (Evans 1994) and referred to Anguimorpha. Additional species of *Parviraptor* were subsequently erected based on specimens from the Late Jurassic of North America

(Evans 1996; Evans & Chure 1998) and Portugal (Evans 1994, 1996), and specimens from the microvertebrate assemblage from the Middle Jurassic of Kirtlington were referred to *Parviraptor* cf. *P. estesi* by Evans (1994). Recently, many of these specimens were referred to new genera or new genera and species, and this group was attributed to stem-group snakes (Caldwell *et al*. 2015). Here we simply confirm the present of *Parviraptor*-like specimens from the Kilmaluag Formation of Skye that are under ongoing study.

A new squamate dentary, NMS G.1992.47.125, with weakly tricuspid teeth (Fig. 6A–B) was also found during fieldwork in 2004 and is distinct from other specimens both from Skye and from Kirtlington Cement Quarry (Evans *et al*. 2006). Among the as-yet unidentified squamate material is a gekkotan-like vertebra (G.1992.47.13: Evans *et al*. 2006), and multiple fragmentary specimens that cannot yet be identified.

2.6 Testudinata

Turtle fossils are common in the Kilmaluag Formation on the Strathaird Peninsula, mostly comprising broken non-associated portions of turtle carapace and plastron (e.g. NMS G.1992.47.25; Evans & Waldman 1996; Evans *et al*. 2006), but also some significant associated material (Anquetin *et al*. 2009) (Fig. 8A). A new genus and species of stem turtle, *Eileanchelys waldmani* (Anquetin *et al*. 2009; Anquetin 2010), was named from material recovered during field work in 2004. This material included the holotype partial skull, NMS G 2004.31.15 and the paratypes NMS G 2004.31.16a–f, in total comprising at least three associated partial skeletons on the same limestone block. The paratype material includes postcrania and almost complete carapaces. *Eileanchelys waldmani* represents one of the earliest recorded aquatic turtles, and one of the few known from the Middle Jurassic. Its mixture of plesiomorphic and derived characters make it a key taxon in tracking the morphological evolution of the vomer and basicranium from basalmost to crown-group turtles (Anquetin *et al*. 2009).

2.7 Choristodera

The choristodere *Cteniogenys* is represented by a partial skull from the Kilmaluag Formation, NMS G.1992.47.11 (Evans & Waldman 1996:fig 3). *Cteniogenys* *antiquus* was originally named on the basis of jaw elements from the Late Jurassic Morrison Formation of North America (Gilmore 1928) and further specimens of *Cteniogenys* were reported from the Late Jurassic of Portugal (Seiffert 1970; *Cteniogenys reedi*). Gilmore and Seiffert interpreted *Cteniogenys* as a stem-squamate, but analysis of abundant elements from the Middle Jurassic microvertebrate assemblage of Kirtlington showed that *Cteniogenys* was an early choristodere (Evans 1989, 1991b). Some specimens of *Cteniogenys* sp. from the Kilmaluag assemblage are more complete and include associated sets of elements (e.g. Evans & Waldman 1996:fig 3). A tiny broken skull of *Cteniogenys,* NMS G.2019.34.4, from the Kilmaluag assemblage is currently under study.

2.8 Reptilia indet.

Four specimens of uncertain affinity are here referred to as Reptilia ‘species A’ (NMS G.1992.17.124 and NMS G.1992.17.126), Reptilia ‘species B’ (NMS G.2019.34.7) and Reptilia ‘species C’ (NMS G.2019.34.12). These specimens all likely constitute new taxa, but lack synapomorphies that would allow them to referred to any of the other clades mentioned herein, and are insufficiently well-known to provide a basis for new species names.

Reptilia ‘species A’ is known from two near-complete dentaries with subthecodont dental implantation and conical teeth (NMS G.1992.47.124 and NMS G.1992.47.126). These dentaries are unusual in that they become dorsoventrally narrow in their anterior one third, even allowing for breakage. Although the dentition is reminiscent of that of *Cteniogenys* in general appearance, these dentaries lack the double rows of grooved labial neurovascular foramina that characterise the jaws of choristoderes.

Reptilia ‘species B’ is known from a single left dentary (NMS G.2019.34.7). It is shorter than the dentary of Reptile A, or *Cteniogenys*, and lacks the marked anterior taper of Reptile A and the double row of neurovascular foramina seen in *Cteniogenys*.

Reptilia 'species C' is based on a remarkably small tooth-bearing portion of dentary, NMS G.2019.34.12 which was discovered in 2016. It has subthecodont dental implantation and differs from *Cteniogenys* in possessing slightly recurved teeth and lacking the characteristic labial foramina.

2.9 Crocodylomorpha

The first crocodylomorph material described from the Kilmaluag Formation comprised an indeterminate partial postcranial skeleton, NMS G.1992.47.6, belonging to an animal approximately 1 metre in length (Waldman & Evans 1996) (Fig. 8B). This includes elements of the right hind limb and scapula, fragments of rib, three dorsal vertebrae and multiple osteoderms. The authors suggested the small size and postcranial morphology of the material was not suggestive of a goniopholid, although goniopholid teeth are common in other Bathonian sites. A crocodylomorph left pubis (NMS G.1992.47.51), some osteoderms (NHMUK PV R36713), and a single goniopholid tooth (NHMUK PV R36713) were described by Wills *et al*. (2014) from the Kilmaluag Formation of the Strathaird Peninsula and comprised the first figured crocodylomorph material from that region. The pubis was collected in 1992, and the osteoderms and tooth in 2006. These specimens are attributed to indeterminate goniopholid neosuchians. Isolated crocodylomorph material is also included in faunal lists (Evans & Milner 1994; Evans *et al*. 2006), but not described or figured. Evans *et al*. (2006) mention atoposaurid material, although it is not figured or described. Atoposaurid teeth are regularly visible at outcrop.

2.10 Pterosauria

Two associated skeletons of pterosaurs are currently under study from the Kilmaluag Formation: one that represents a monofenestratan pterosaur, NHMUK PV R37110 (Martin-Silverstone *et al.* 2019); and one as yet unprepared specimen that appears to be non-pterodactyloid (Fig. 8D). Several teeth thought to represent pterosaurs have also been identified (Evans *et al*. 2006).

2.11 Dinosauria

Although dinosaur body and ichnofossils are known from other parts of the Great Estuarine Group (see Clark [2018] for overview), very little dinosaur material has been recovered from the Kilmaluag Formation to date. However, the scant material that does exist currently represents the geologically youngest non-avian dinosaur material in Scotland. The trackways of small bipedal tridactyl dinosaurs at Lub Score on the Trotternish Peninsula (Clark *et al*. 2005) possibly represent adult and juvenile theropods, most likely the same ichnospecies. They were found in two distinct stratigraphic layers: a silty mudstone, and a sandstone containing darker organic layers. Both are suggested to represent freshwater depositional settings, but exact correlation with the stratigraphy in other parts of the Isle of Skye has proven problematic (Clark *et al*. 2005).

The only dinosaur body fossil remains reported so far from the Kilmaluag Formation are an isolated sauropod tooth, NMS G 2004.31.1 (Fig. 8C), which represents the first dinosaur tooth described from Scotland (Barrett 2006), an incomplete taxonomically indeterminate femur, NMS G.2003.31.20, and theropod tooth, NMS G.1992.47.50, all from the Strathaird Peninsula (Wills *et al*. 2014). The sauropod tooth comprises a complete crown with partial root, with morphology suggesting it is referable to either a basal eusauropod or basal titanosauriform (Barrett 2006). Further material that may be attributable to dinosaurs is currently being prepared for further study.

2.12 Mammaliamorpha

The first non-mammalian cynodont from Scotland was found in the Kilmaluag Formation on the Isle of Skye. It was placed in a new species, *Stereognathus 'hebridicus'*, based on four isolated postcanines (holotype BRSUG 20572; paratypes BRSUG 20573, BRSUG 20574, BRSUG 20575), which appeared to be larger than the English *S. ooliticus* (Waldman & Savage 1972). Following detailed morphological comparison of specimens assigned to these two species, with the addition of better-preserved specimens recovered from the Kilmaluag Formation since the 1970s, these species were synonymised under *S. ooliticus* (Panciroli *et al*. 2017a) (Fig. 9A–B). *S. ooliticus* in the UK is almost entirely represented by isolated postcanine teeth, with only two partial maxillae: one edentulous, and the other the holotype, BGS GSM113834, consisting of three postcanines in a maxillary fragment. Isolated limb bones from English Jurassic sites such as Kirtlington Cement Quarry (Forest Marble

Formation) have been assigned to Tritylodontidae (Simpson 1928; Kühne 1956), but their identification as *Stereognathus* is unconfirmed.

The first Mesozoic mammaliaform from Scotland came from the Kilmaluag Formation: the new genus and species of docodont, *Borealestes serendipitus* (Waldman & Savage 1972). Only one specimen of *Borealestes* was described, the holotype partial dentary BRSUG 20570 (Fig. 9K), which bears three premolars and six molars (Waldman & Savage 1972). Further specimens (BRSUG 20571 and BRSUG 29007) were collected subsequently during fieldwork in the 1970s and 1980s, but were not described until recently (Panciroli *et al*. 2018c, 2019). *Borealestes* was the third docodont genus to be named (after *Docodon victor* [Marsh 1880] and *Peraiocynodon inexpectatus* [Simpson 1928]—although the latter was synonymised with *Docodon* [Butler 1939], only to be resurrected again later [Sigogneau-Russell 2003a]), and the original diagnosis was not comprehensive. Later authors expanded the diagnosis of *B. serendipitus* for upper and lower molars, and added a second species (*B. mussettae*) based on individual molars found at Kirtlington Cement Quarry (Sigogneau-Russell 2003a; Luo & Martin 2007), although their attribution to *Borealestes* is now being re-evaluated (Panciroi *et al.* in review).

Multiple dentaries of *Borealestes* are now known from the Kilmaluag Formation, including an almost complete dentary NMS G.1992.47.121.3 (Panciroli *et al.* 2019) (Fig. 9L–M), which belongs to the associated skeleton NMS G.1992.47.121.1 (Panciroli *et al*. in review). Most of these specimens were collected in the 1970s, but a new, almost complete dentary was recovered during fieldwork in 2016 (NMS G.2018.27.1), and another associated skeleton was recovered in 2018 belonging to a new species of *Borealestes* (Panciroli *et al*., in review). Together these specimens have permitted the clarification of the diagnosis of *Borealestes* (Panciroli *et al*. 2019; manuscript in review), and they include some of the most complete crania and postcrania for any Mesozoic mammaliaform from the British Isles.

Further mammaliaform material was recovered and recorded in published faunal lists (Evans & Milner 1994; Evans *et al*. 2006), including a molar from the docodont genus *Krusatodon*. An exceptionally complete skeleton collected in the 1970s is also confirmed as belonging to a docodont (NMS G.1992.47.122.1) and is currently under study by EP.

Recent fieldwork recovered another mammaliaform dentary, belonging to the morganucodontan *Wareolestes rex* (Panciroli *et al*. 2017b) (Fig. 9C–E). The first crown-group mammal from the Kilmaluag Formation, the cladotherian *Palaeoxonodon ooliticus* was also recently described (Close *et al*. 2016; Panciroli *et al*. 2018b) (Fig. 9d). Both taxa were known previously from isolated teeth from the Forest Marble Formation (Freeman 1976, 1979; Butler & Sigogneau-Russell 2016), but the Scottish specimens are more complete, consisting of teeth set within near-complete dentaries.

The specimen of *Wareolestes rex*, NMS G.2016.34.1, is the most complete for this taxon, consisting of two erupted molars and two unerupted premolars in a partial dentary (Panciroli *et al*. 2017b). The *in situ* molars settle disagreement over the orientation within the tooth row of previously recovered isolated molars from the Forest Marble Formation (thought to be upper molars, but now identified as lowers) (Freeman 1979; Hahn *et al*. 1991; Butler & Sigogneau-Russell 2016; Panciroli *et al*. 2017b). Erupting teeth present below the alveolar margin of the dentary suggest a derived tooth replacement pattern for this early-diverging mammaliaform.

The nearly complete dentary of *Palaeoxonodon ooliticus*, NMS G. 2015.17.10, includes an incisor, canine, three premolars and five molar teeth *in situ* within the dentary (Close *et al*. 2016) (Fig. 9F–H). A second portion of dentary, NMS G.2017.37.1, includes a portion of the coronoid base that is missing from NMS G. 2015.17.10 (Fig. 9G–H), and provides additional information for phylogenetic analyses, further supporting this genus as a stem cladotherian closely related to *Amphitherium* (Panciroli *et al*. 2018b). The morphological variation along the tooth row in NMS G. 2015.17.10 indicates that the morphologies of previously erected cladotherian taxa, *Palaeoxonodon ooliticus, P. leesi, P. freemani*, and *Kennetheridium leesi* (Sigogneau-Russell 2003b), all fall within the range of variation observed in *P. ooliticus*. They are therefore considered to be junior synonyms of *P. ooliticus* (Close *et al*. 2016). Postcranial material from *Palaeoxonodon* is currently under study by EP.

Postcrania and crania belonging to *Phascolotherium* have also been recovered (Fig. 9N) and are currently under study by EP.

3. Comparisons to Vertebrate Faunas from Other Sites

The vertebrate fauna of the Kilmaluag Formation represents one of the richest Mesozoic vertebrate-bearing sites in the British Isles. Nevertheless, the vertebrate faunal list (Table 2) essentially represents a subset of the species found in the Forest Marble Formation of England (see Supplementary material), with many of the same taxa represented. The Kilmaluag Formation vertebrate fauna also resembles those from other Middle Jurassic localities such as the Anoual Formation (Guelb el Ahmar fauna) in Morocco and Itat Formation in Russia, with broad compositional similarities based on the shared presence of higher taxa. The Kilmaluag assemblage shares fewer taxa in common with those represented in Late Jurassic localities such as the Alcobaça Formation in Portugal, or the Yanliao Biota in China (Supplementary material). We have also included the Purbeck Group in England, which is Latest Jurassic to Early Cretaceous in age.

Below we provide comparisons for broadly contemporaneous and well-sampled vertebrate faunas from different biotas globally, beginning with the coeval Forest Marble Formation, and then looking globally at comparable sites, from the geologically oldest formation included herein (the Itat Formation in Russia) to the geologically youngest (the Purbeck Group) (Fig. 10).

3.1 Forest Marble Formation, England

The Forest Marble Formation of England yields the most similar vertebrate fauna to the Kilmaluag Formation and is thought to be broadly coeval. The Forest Marble Formation is part of the Great Oolite Group (Bathonian), and comprises greenish grey silicate mudstones with cross-bedded limestone units and channel fills (Barron *et al*. 2012). It crops out across the southern half of England, but the main localities that have yielded fossil vertebrate fauna are Kirtlington Cement Quarry in Oxfordshire and Watton Cliff in Dorset (Evans 1992; Evans & Milner 1994) (Fig. 10).

The vertebrate beds at Kirtlington Cement Quarry near the village of Kirtlington in Oxfordshire comprise an unconsolidated brown marl, forming lenses of variable thickness between ooidal limestone (Freeman 1979). These lenses are now believed to be exhausted at surface exposure (Freeman 1979). The Forest Marble Formation at Kirtlington represents an estuarine environment, brackish to marine in nature, and to lie within the *Retrocostatum* to *Discus* Zones (possibly the *Oppelia aspidoides* Zone [Cope *et al*. 1980]), making it late Bathonian in age, although the exact dating is uncertain (Evans & Milner 1994; Barron *et al*. 2012). Kirtlington Cement Quarry was collected intensively in the 1970s and 1980s, with many tonnes of matrix processed for vertebrate fossils, and it is one of the most diverse and productive microvertebrate assemblages in the UK (Evans & Milner 1994).

The Kilmaluag Formation assemblage includes a subset of the taxa known from the Forest Marble Formation. Many of the same genera are found in both formations: the fish *Hybodus* and *Lepidotes*; the lissamphibian *Marmorerpeton*; the lepidosauromorph *Marmoretta*; the squamates *Balnealacerta*, *Bellairsia* and *Parviraptor*; the choristodere *Cteniogenys*; the mammaliamorph *Stereognathus*; the mammaliaforms *Wareolestes rex*, *Borealestes* and *Krusatodon*; and the mammalians *Phascolotherium* and *Palaeoxonodon* (Table 2 and Supplementary material). In addition, similar groups are represented at higher taxonomic levels, such as pycnodont and amiiform fishes, testudinates, goniopholid and atoposaurid crocodylomorphs, and pterosaurs. Although there is evidence of dinosaur material at both sites, most cannot be identified to a higher taxonomic level, particularly in the Kilmaluag Formation, limiting comparisons.

The similarities between these vertebrate assemblages support the hypothesis that they were deposited at approximately the same time. However, there are a few key differences between the Kilmaluag and the Forest Marble formations. Many of the same mammaliamorph and mammaliaform taxa are present in both, with the exception of haramiyids and multituberculates. These are abundant in the Forest Marble Formation—five species to date (Kermack *et al*. 1998; Butler & Hooker 2005)—whereas there are currently none from the Kilmaluag Formation. Rhynchocephalians and anurans are not currently known from the Kilmaluag Formation, but are present in the Forest Marble Formation (Evans 1992). These differences may be attributed to the slightly different environments represented by each: the Kilmaluag Formation is predominantly freshwater, rather than brackish or shallow marine. However, the absence of certain taxa from the Kilmaluag Formation may also be the result of differences in collection methods: bulk processing of Forest Marble sediments might have permitted a wider diversity of fauna to be recovered and identified (for more on the effects of sampling, see below).

3.2 Guelb el Ahmar Fauna, Morocco

The Guelb el Ahmar Fauna comes from the Middle Jurassic Anoual Formation, a predominantly continental sequence of ‘red beds’ located on the northeastern rim of the High Atlas Mountains (Haddoumi *et al*. 2016). The marine upper member of the Anoual Formation is Bathonian (Haddoumi *et al.* 1998), whereas the lower member represents a flood plain or deltaic depositional environment. Most vertebrate fossils located in a thin bed of dark-brown, partially lignitic marls, and the presence of palynoflora including *Callaliasporites* constrains the age as no older than Toarcian. (Haddoumi *et al*. 2016).

Both the Guelb el Ahmar Fauna and the Kilmaluag Formation include *Lepidotes*, albanerpetontids and other lissamphibians and caudates, testudinates, lepidosaurs including *Parviraptor* species, choristoderes, theropods, pterosaurs, crocodylomorphs and cladotherians (see Supplementary material). These broad similarities are also seen in the Itat Formation (see section 3.3). However, the Guelb el Ahmar Fauna is known from very incomplete material, so unlike in the Kilmaluag Formation and other better-known assemblages, most groups are represented by isolated material that cannot be assigned to genus level.

Unlike the Kilmaluag Formation, osteoglossiform, actinistan and dipnoi fish are all known from the Guelb el Ahmar Fauna. Indeterminate rhynchocephalian material is also present, as in the Forest Marble, Alcobaça and Morrison formations. The Guelb el Ahmar Fauna currently lacks several groups represented in the Kilmaluag Formation: hybodont, amiiiform and picnodont fish, sarcopterygians, paramacellodids, sauropod dinosaurs, mammaliamorphs, mammaliaforms and eutriconodont mammalians (Table 1).

The Guelb el Ahmar Fauna is significant in that it represents one of the few Middle Jurassic assemblages from Gondwana—all of the other localities compared here are Laurasian. The similarity between the Kilmaluag Formation assemblage and fauna collected from this southern site is intriguing, as the north of Africa was separated from Europe by the emerging Central Atlantic Sea during the Middle Jurassic (Haddoumi *et al*. 2016). This indicates a Pangean distribution for many of these groups, and this may be supported by the fauna recovered so far from Middle Jurassic localities in Madagascar (Flynn *et al*. 2006) and India (Prasad & Manhas 2002). However, the partial nature of the material from these sites limits higher taxonomic comparisons.

3.3 Itat Formation, Russia

Pollen from the Upper Member of the Itat Formation includes *Cyathiditesminor*, *Piceapollenites*, *Eboracia*, *Quadraeculina*, and *Classopollis*, which suggests a Bathonian age for this unit (Averianov *et al*. 2005), but possibly slightly older than either the Forest Marble or Kilmaluag formations. The Itat Formation comprises a series of fossiliferous clays, sandstones and siltstones representing a fluvial floodplain deposit (Averianov *et al*. 2005, 2016). The most productive site is Berezovsk Quarry in western Siberia, Russia (Fig. 10). Vertebrate fossils are found in a fluvial flood-plain deposit ~50 m in thickness. The nature of the depositional environment is thought to contribute to the disarticulation and abrasion of specimens (Averianov *et al.* 2016).

The chondrichthyan fish *Hybodus* is the only genus present in both the Kilmaluag and Itat formations. *Eodiscoglossus* (anuran), which is present in the Forest Marble Formation (but not the Kilmaluag Formation), has also been found in the Itat Formation (Averianov et al. 2016). However, similar groups are represented in both the Scottish and Russian deposits: salamanders, testudines, scincoid lizards, choristoderes, lepidosauromorphs, goniopholid crocodylomorphs, pterosaurs, tritylodontid mammaliamorphs, docodontan mammaliaforms, and eutriconodont and cladotherian mammalians (see Supplementary materials).

A key difference between the Itat and Kilmaluag formations is that the former has yielded multiple haramiyidan taxa (Averianov *et al*. 2011, 2019), a group that is so far absent from the Kilmaluag Formation, although five haramiyidan species are present in the Forest Marble Formation. The Itat Formation has recently yielded two multituberculates taxa (Averianov *et al.* 2020), but none are present in the Kilmaluag Formation.

3.4 Yanliao Biota, China

The Yanliao Biota takes its name from the Yanliao area in northeast China, including parts of Inner Mongolia, and Liaoning and Hebei Provinces, which contains extensive exposures of Middle to Late Jurassic fossiliferous strata (Fig. 10). The term Yanliao Biota is used here following Xu *et al*. (2016, 2017) to include the Juilongshan/Haifenggou Formation and Tiaojishan/Lanqi Formation, as well as the 'Daohugou Biota' (Sullivan *et al*. 2014). The strata yielding the Daohugou Biota (including sites at Linglongta, Wubaiding, Mutoudeng, Guancaishan, Nanshimen, Daxishan, Daxigou and Youlugou) are likely to correlate with the Tiaojishan/Lanqi Formation, and possibly the youngest part of the Juilongshan/Haifenggou Formation (Sullivan *et al*. 2014; Xu *et al*. 2017). Some confusion persists over the exact correlations between different outcrops in the Yanliao area. Radiometric dates have provided a wide age range of 146–188 Ma, but a more conservative range is 157 ± 3 Ma (Xu *et al*. 2017), making it Bathonian to Oxfordian (Fig. 10). Biostratigraphical correlations support this Middle–Late Jurassic age (Sullivan *et al*. 2014; Xu *et al*. 2017).

The Yanliao Biota comes from a series of sedimentary and volcanic cycles, but despite there being multiple formations over such a large geographic area, the fossil-bearing strata are somewhat similar. These mostly comprise laminated tuffaceous mudstones and shales, yielding exceptionally complete skeletons with soft tissue preservation—resulting in recognition of the sites yielding the Yanliao Biota as a globally significant Lagerstätte (Xu *et al*. 2017). The palaeoenvironment varied laterally, but overall represents a freshwater ecosystem similar in many ways to that preserved in the Kilmaluag Formation, but it was lacustrine rather than lagoonal, with a humid, warm climate and highly aquiferous soil (Xu *et al*. 2017).

No genera are shared between the Yanliao Biota and the Kilmaluag Formation, but there are some similarities in the vertebrate groups represented. Both sites have caudates, pterosaurs, and theropod dinosaurs, but all of these groups are represented by much higher diversity in the Yanliao Biota; conversely, squamates have a greater diversity in the Kilmaluag Formation; and docodontan mammaliaforms and eutriconodonts are similar in diversity.

Few fish have been reported from the Yanliao Biota, and fewer groups are recorded in comparison to the Kilmaluag Formation. Testudines and crocodylomorphs are also unknown in the Yanliao Biota currently. Differences in the relative abundance and presence/absence of higher taxa may reflect the continental (non-marine) nature of the Yanliao Biota, although some sampling and publication factors may partly influence their absence from faunal lists.

Similar mammaliaform and mammalian groups are present in the Yanliao Biota and the Kilmaluag, Forest Marble, and Itat formations, with multiple docodontans, one or more eutriconodontans, and at least one cladotherian (Table 2 and Supplementary material). As in the Forest Marble and Itat formations, but unlike the Kilmaluag Formation, the Yanliao Biota includes haramiyidans (e.g. Zhou *et al*. 2013; Xu *et al*. 2017). Unlike the other formations discussed so far, the Yanliao includes an australosphenidan (*Pseudotribos robustus* [Luo *et al*. 2007]). The genera represented are also exceptionally ecologically diverse, with specialised swimming (*Castorocauda* [Ji *et al*. 2006]), digging (*Docofossor* [Luo *et al*. 2015]) and gliding (*Maiopatagium* [Meng *et al*. 2017]) forms. However, this ecomorphological diversity is likely the result of the completeness of the skeletal material known for these animals—their counterparts in other localities globally are often represented by more partial cranial and dental material, which provide limited information about ecomorphology (see below for further discussion).

3.5 The Alcobaça Formation, Portugal

The Alcobaça Formation is Kimmeridgian in age (Fig. 10), and represents a shallow-marine to brackish deltaic depositional environment (Mateus *et al*. 2017). One of the most productive localities of the Alcobaça Formation is the vertebrate-bearing Guimarota Coal Mine, where it is approximately 20 m in thickness, comprising a layer of limestone between two coal seams (Schudack 2000). These seams are composed of alternating marls, and represent a shallow lagoon environment with fluctuating water levels, resulting in changes in salinity that are reflected in the evidence from ostracods and charophytes (Helmdach 1971; Schudack 2000).

Several genera are shared between the Alcobaça Formation and the Kilmaluag formations: the chondrichthyans *Acrodus* and *Hybodus*; the lepidosauromorph *Marmoretta*; the squamate *Parviraptor*; and the choristodere *Cteniogenys*. Similar groups are represented by different genera, for example albanerpetontids, lissamphibians of uncertain identity, paramacellodids, goniopholid and atoposaurid crocodylomorphs, pterosaurs, docodont mammaliaforms and cladotherian and eutriconodont mammals are all found in both formations. Scincoids, testudines, crocodylomorphs, pterosaurs, dinosaurs and mammalians are so far found in much greater diversity in the Alcobaça Formation. The Alcobaça Formation also includes groups not represented in the Kilmaluag Formation: multiple groups of fishes, anurans, dorsetisaurids, rhynchocephalians, multituberculates and symmetrodonts (Mateus 2006). The only groups represented in the Kilmaluag Formation that are not found in the Alcobaça Formation are sarcopterygian fishes, tritylodontids and morganucodontans.

As in most of the other sites compared herein, the Alcobaça Formation has multituberculates—in fact they represent the most speciose mammal group at this locality, with 12 genera (Martin & Krebs 2000; Martin 2001), whereas the Kilmaluag Formation currently lacks multituberculates, indicating a substantial difference between higher taxa. The lack of haramiyidans in the Alcobaça Formation distinguishes this mammal assemblage from the Forest Marble, Itat, and Morrison formations and the Yanliao Biota and Purbeck Group (see Supplementary material).

3.6 Morrison Formation, North America

The Morrison Formation in North America also yields globally significant Jurassic mammal material. Historically it was one of the first Jurassic fossil localities in the world to be exploited systematically, since 1877 (Foster 2003a; Weishampel *et al.* 2004), and a great deal of attention has been given to its dinosaur assemblage. This rock unit extends across an enormous area of the west and central United States—with significant outcrops in Arizona, Montana, Wyoming, Utah, and Oklahoma—and north into Canada (Turner & Peterson 2004). The Morrison Formation is between

155–148 Ma (Kowallis *et al*. 1998; Maidment & Muxworthy, 2019) (Fig. 10), and it largely comprises terrestrial deposits, with a huge range of lithologies including aeolian, fluvial and floodplain sandstones, floodplain/lacustrine mudstones and coal, and wetland and lacustrine carbonates (see Maidment & Muxworthy, [2019] for comprehensive geological overview).

The only genera in common between the Kilmaluag and Morrison formations are the parviraptorid squamates, possible paramacellodids, and the choristodere *Cteniogenys*. However, both formations also yield: amiiform, semionotiform and pycnodont fishes; salamanders; testudinates, scincoids; goniopholid crocodiles; pterosaurs and dinosaurs; docodont mammaliaforms and eutricondont mammals (Table 2 and Supplementary material). In almost all cases, the diversity known from the Morrison Formation is much higher than the Kilmaluag Formation, especially crocodylomorphs, dinosaurs, pterosaurs and mammalians. The Morrison Formation also yields several rhynchocephalian taxa (Simpson 1926; Rasmussen & Callison 1981; Foster 2003b; Jones *et al*. 2018b), which are so far unknown in the Kilmaluag Formation. The enormous extent of the Morrison Formation compared the small locality represented in Scotland by the Kilmaluag Formation undoubtedly contributes to the difference in diversity, as does the longer history of collecting in the Morrison Formation.

There are around 45 species of Mesozoic mammal known from the Morrison Formation, including eutriconodontans, docodonts, multituberculates and cladotherians (Chure *et al*. 2006; Supplementary material). Docodonts were among the first taxa to be found and described (Marsh 1880) and subsequently five species of the genus *Docodon* were erected (Marsh 1887; Simpson 1928; Rougier *et al*. 2015). These have since been synonymised under *D. victor* and *D. apoxys* (Chure *et al*. 2006; Schultz *et al*. 2018), which now makes Docodonta the least speciose group of Mesozoic mammals in the Morrison Formation. Nevertheless, the overall mammalian diversity is greater than the other Jurassic formations known globally (Chure *et al*. 2006). Like the Kilmaluag Formation, but unlike the Yanliao Biota, Forest Marble and Itat formations, there are currently no haramiyidans known from the Morrison.

3.7 Purbeck Group, England

The Purbeck Group includes the Lulworth and Durlston formations, and is Tithonian to Berriasian in age (Late Jurassic to Early Cretaceous). It crops out in southern England (Fig. 10), and yields one of the most diverse vertebrate assemblages in the Mesozoic of the British Isles. The group comprises a series of interbedded mudstones, limestones and evaporites of marine, brackish and freshwater origin (Westhead & Mather, 1996).

Although the Purbeck Group is geologically much younger than the Kilmaluag Formation (Ensom 2007), there are some similarities between the vertebrate faunas. Both sequences contain the genera *Hybodus* and *Lepidotes*, the squamate *Parviraptor*, paramacellodids, and several other squamate taxa. They also both have semionotiform fish; albanerpetontids, caudates, testudinates, goniopholid crocodylomorphs, pterosaurs, dinosaurs, morganucodontan and docodontan mammaliaforms, and cladotherian and eutricondont mammalians. The sampled diversity of almost all of these shared groups is far greater in the Purbeck Group.

Vertebrates represented in the Purbeck Group that are absent from the Kilmaluag Formation at present include batrachosauridid salamanders, frogs, lacertoid and dorsetisaurid squamates, rhynchocephalians, marine reptiles (plesiosaurs and ichthyosaurs), ornithischian dinosaurs, and multituberculate and symmetrodontan mammals. Groups represented in the Kilmaluag Formation that are absent from the Purbeck Group include pycnodont and sarcopterygian fish, choristoderes, and tritylodontid mammaliamorphs.

The mammaliaform orders Docodonta and Morganucodonta are much less speciose in the Purbeck Group than in the Kilmaluag Formation, contrasting with the exceptionally diverse multituberculate and cladotherian mammalians (Kielan-Jaworowska & Ensom 2002; Ensom 2007). This pattern is similar to that seen in the Alcobaça and Morrison formations, and may reflect the faunal replacement of earlier diverging orders with more derived mammalian groups. The presence of a possible morganucodontan in the Purbeck Group (Butler *et al*. 2012) is unusual, as they are entirely absent from the geologically older Alcobaça and Morrison formations, and it would represent the youngest-known occurrence of this group.

4. Collection Methods and Potential Biases

The collection approach employed at Kilmaluag Formation sites since its discovery in 1971 has focussed on more complete specimens visible at outcrop, with no batch processing of bulk samples. This is partly to ensure minimal impact on the SSSI where this formation crops out, but is also influenced by the nature of the sediments. At Kirtlington Cement Quarry, Forest Marble Formation matrix was processed using a process of wet sieving followed by drying and hand picking (Freeman 1979; Evans & Milner 1994). More complete associated skeletons would be unlikely to be retrieved using this method. A sample of matrix processed in batches by previous researchers indicated no evidence of associated remains, suggesting possible taphonomic disassociation of specimens. The same method of batch processing has been employed to process Itat Formation sediments at the Berezovsk coal mine (Averianov *et al*. 2016), and the Guelb el Ahmar fauna from the Anoual Formation (Haddoumi *et al.* 2016). Similarly, at Guimarota the coal lignite sediment of the Alcobaça Formation was dissolved in an alkaline bath and screen washed (Martin 2001)—although some more complete specimens were found in lumps of lignite prior to this process (Martin 2005). The Morrison Formation crops out in multiple localities, and these have been both screenwashed and collected by eye (Foster & Lucas 2006; Foster & Heckert 2011). This ability to bulk process sediments constitutes a key difference between sampling the Kilmaluag Formation and most of the other formations and vertebrate assemblages discussed herein, and limits the quantity of isolated remains that have been recovered from the Kilmalaug Formation compared to other units.

Collection from Yanliao Biota localities is usually through concentrated excavation efforts, without screen-washing, and initial discoveries come often from local farmers spotting fossil material during their work (Xu *et al*. 2016, 2017). Therefore, a collection bias may exist towards more complete material visible at outcrop.

The hard-weathering nature and poor reaction to acid of the limestones in the vertebrate-rich strata of the Kilmaluag Formation are not suited to bulk processing. This limits the volume of fossil material collected from these outcrops, and introduces collection bias towards more readily visible material—such as bone associations, dentaries containing teeth, and single elements—that appear diagnostic at outcrop. Micro-CT scans of collected specimens occasionally reveal isolated dental and skeletal fragments scattered throughout the limestone matrix. These commonly include tritylodontid teeth, salamander vertebrae, and fish remains (RBJB and EP, pers. obs.). These finds suggest that if the Kilmaluag Formation could be bulk processed it would potentially yield a similarly rich assemblage of incomplete and isolated microvertebrate remains to those of the Forest Marble Formation.

There have been three main periods of collecting from the outcrops of the Kilmaluag Formation along the Strathaird Peninsula. From 1971–1982 collecting was carried out over the course of seven field trips by Michael Waldman and Robert Savage (hereafter referred to as: W&S) and their team. In 2004 and 2006 collecting was carried out by SE and Paul Barrett (hereafter referred to as: E&B) and their team. Collecting has been carried out since 2010 by SW, RBJB, EP and RJB and their teams (hereafter referred to as: SRER). There are marked differences in the collections made by each team (Fig. 11): W&S collected substantially more mammaliamorphs and mammaliaforms (42%), mainly in the form of tritylodontid teeth, whereas E&B collected more fish (37%), which were predominantly shark teeth. For SRER the largest proportion of finds has been lepidosaurs (21%), including multiple dentaries and small partial skeletons (Fig. 11). Of all finds made by all teams since 1971, 37% remain unidentified, usually because they are too fragmentary to assign to any taxonomic group. This figure may reduce in the next decade due to changing collection practices. Although 25% of specimens collected by SRER are categorised as ‘unknown ID’, many of these possess diagnostic characters and await CT-scanning to facilitate identification.

The application of micro-CT scanning as routine by SRER means collecting practices have changed dramatically. Previously mainly fossils that appeared likely to produce good specimens when observed at outcrop tended to be collected. It is now evident that the much less superficially compelling material exposed along the Strathaird Peninsula can be highly informative once µCT-scanned. This is particularly true for microvertebrates such as small amphibians, reptiles and mammaliaforms, which may appear unpromising and indistinct even when observed under magnification.

5. Discussion

The Kilmaluag Formation is currently producing novel insights into the Middle Jurassic vertebrate fauna of the UK. The assemblage appears to constitute a subsample of that found within the Forest Marble Formation, but unlike those from Kirtlington Cement Quarry the specimens from the Kilmaluag Formation are most often preserved in association, preserving more complete morphology. This attribute has already permitted re-evaluation of the anatomy, taxonomy and diversity of various mammal groups (Close *et al*. 2016; Panciroli *et al*. 2017a, b, 2018b and c, 2019) and it is clear from the material currently under study that it will do the same for multiple squamate and lissamphibian clades.

The new skeletal material of *Marmorerpeton* and ‘Kirtlington salamander A’ from Skye has huge potential for understanding early salamander evolution. These specimens will also be highly valuable for interpreting the taxonomy of isolated salamander material from other Middle Jurassic sites (e.g. Kirtlington). The identification of jaws and vomers remains particularly problematic (Evans *et al*. 1988, 1994)

The discovery of more complete skeletal material for known taxa has changed our understanding of the diversity of Middle Jurassic vertebrate assemblages in the UK. With more complete dental and skeletal material, it has been possible to clarify the amount of anatomical variation among taxa, resulting in a reduction in species diversity for some taxonomic groups (e.g. *Stereognathus* and *Palaeoxonodon*), but increases for others as new taxa are recognised that were not identifiable from less complete material (e.g. *Borealestes*, new salamander and reptile material).

The outcrops of the Kilmaluag Formation are in areas protected by SSSI and NCO, ensuring that only minimal collecting takes place, and only for scientific research. Due to the mode of fossil preservation and its limestone matrix, data on these fossils can only be obtained thanks to the application of micro-CT scanning as routine by researchers. It is vital that protections remain in place to ensure key specimens are not lost to science through destructive unauthorised collecting.

6. Conclusions

The Kilmaluag Formation contains undoubtedly one of the most important vertebrate assemblages in the world. Although it appears less diverse than either the contemporaneous Forest Marble or Itat formations, the Middle–Late Jurassic Yanliao Biota, the Upper Morrison and Alcobaca formations, or the latest Jurassic–Cretaceous Purbeck Group, this is likely partly a result of restricted outcrop and an inability to bulk process the limestone of the Kilmaluag Formation. Despite this, it contains many similar genera, and adds to our picture of the biogeographical distributions of these groups in the Middle Jurassic. The Kilmaluag Formation appears to comprise a subsample of the taxa known from the Forest Marble Formation, but this subset is represented by more complete material including partial skeletons. The ongoing protection of the sites where the Kilmaluag Formation crops out is vital. Scientific collection is selective, poses minimal impact and is producing a steady volume of material that promises more information on new, and previously poorly represented taxa. Using μCT, it is possible to exploit the rare three-dimensional preservation of these fossils. This combination of taxonomic diversity, completeness, and three-dimensional preservation, makes the Kilmaluag Formation one of the most important sites in the world for understanding Middle Jurassic ecosystems, as well as the anatomy and evolution of multiple major lineages of Mesozoic vertebrates.

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Figure captions

Figure 1. The location of surface outcrops of the Kilmaluag Formation and overview of the stratigraphy of the Great Estuarine Group (A). Outcrops north of Elgol (B), and the appearance of bone (black) against the micritic blue-grey limestone (C). Map adapted from Wikimedia Commons. Stratigraphy compiled and adapted from Cohen *et al*. (2018), Andrews (1985), and Barron *et al*. (2012).

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Figure 4. Amphibians. Premaxillae of Albanerpetontidae cf. *Anoulerpeton priscus* NMS G.2019.34.6 in lingual (A), labial (B), and occlusal view (C). *Marmorerpeton* roofing bone (field number ELGOL.2019.15) in dorsal view (D). Partial atlas of *Marmorerpeton* (ELGOL.2016.019) in rostral view with left right side reflected to represent the right side (D). Dorsal vertebra of *Marmorerpeton* (ELGOL.2016.024) in rostral view (F) and left lateral view (G). Atlas of 'Salamander A' (field number ELGOL.2016.004) in rostral view (H) and left lateral view (I). Dorsal vertebra of 'Salamander A' (field number ELGOL.2016.004) shown in anterior (J) and left lateral view (K). Abbreviations: brk=breakage; cen=centrum; DEN=dentary; fac=facet; fac.pro=facial process; for=foramen; fu.sut.se= fused suture seam; lin.sh= lingual shelf; MAX=maxilla; Mck.gro=Meckelian groove; muc.sca=muscle scar; nar=naris; neu.arc=neural arch; not.can= notochordal canal; neu.cre=neural crest; pmx.fact=premaxilla facet; prezyg=presygapophyses; PRF=prefrontal; res.pit=resorption pit; rib.ber=rib bearer; spl.fac=splenial facet; sub.sh=subdental shelf; sym=symphysis; too=tooth; tr.pro=transverse process. All scale bars = 1 mm.

Figure 5. Lepidosauromorphs from the Kilmaluag Formation: *Marmoretta* NMS G.1992.47.4 in lingual (A), apical (B) and labial (C) view; Lepidosauromorph 'species

A' NMS G.2019.34.9 in lingual (D), labial (E) and apical (H) views; and Lepidosauromorph 'species B' NMS G.2019.34.13 in lingual (F), labial (G) and apical (I) views. Abbreviations as for Fig. 4. Scale bar = 5 mm.

Figure 6. Squamates: tricuspid squamate dentary, NMS G.1992.47.125 in lingual (A) and labial (B) views; Squamata cf. Paramacellodidae NMS G.2019.34.11 in lingual (C) labial (D) and apical view (E). Abbreviations as for Fig. 4. Scale bar = 5 mm.

Figure 7. Squamates from the Kilmaluag Formation: *Balnealacerta silvestris* NMS G.2019.34.3 dentary and partial maxilla (A), with the dentary in lingual (B), labial (C), and apical (D) views, and maxilla in lingual (E), labial (F), and apical (G) views; *Bellairsia gracilis* NMS G.2019.34.1 in labial (H and I), lingual (J and K), and apical (L and M) views. Abbreviations as for Fig. 4. Scale bar = 5 mm.

Figure 8. Reptile fossils from the Kilmaluag Formation: turtle *Eileanchelys waldmani* NMS G.2004.31.16d (A) (image: J. Anquetin); crocodylomorph osteoderms NHMUK PV R36713 (B) (adapted from Wills *et al.* [2014; fig 4a]); sauropod dinosaur tooth NMS G.2004.31.1 (C) (adapted from Barrett [2006: fig 1]); and a non-pterodactyloid pterosaur collected in 2016 (D) (Photo by R Close). Scale bars: B = 50 mm, for C = 5 mm.

Figure 9. Mammaliamorphs from the Kilmaluag Formation: *Stereognathus ooliticus* NMS G.2017.17.2 (A), and NMS G.1992.47.120 (B) (adapted from Panciroli *et al.* [2017b;5 and 7]); *Wareolestes rex* NMS G.2016.34.1, photographed in matrix (C), digitally segmented in labial view (D) and lingual view (E) (adapted from Panciroli *et al.* [2017; fig 2 and 3]); *Palaeoxonodon ooliticus* NMS G.2016.17.1 in the field (F) (image: R. Close), and combined with NMS G.2017.37.1 (red) in labial (G) and lingual view (H); *Palaeoxonodon ooliticus* NMS G.1992.47.123 in labial (I) and lingual view (J) (adapted from Panciroli *et al.* [2018a; figs 1 and 3]); *Borealestes serendipitus* BRSUG 20570 holotype (K), *Borealestes serendipitus* NMS G.1992.47.121.3 in lingual (L) and labial view (M); *Phascolotherium* sp. (field number ELGOL2017.023) in labial view (N). Abbreviations: dent.cond=dentary condyle; mass.foss=masseteric fossa; man.sym=mandibular symphysis; Mck.gro=Meckelian groove. Scale bar = 5 mm, same scale throughout.

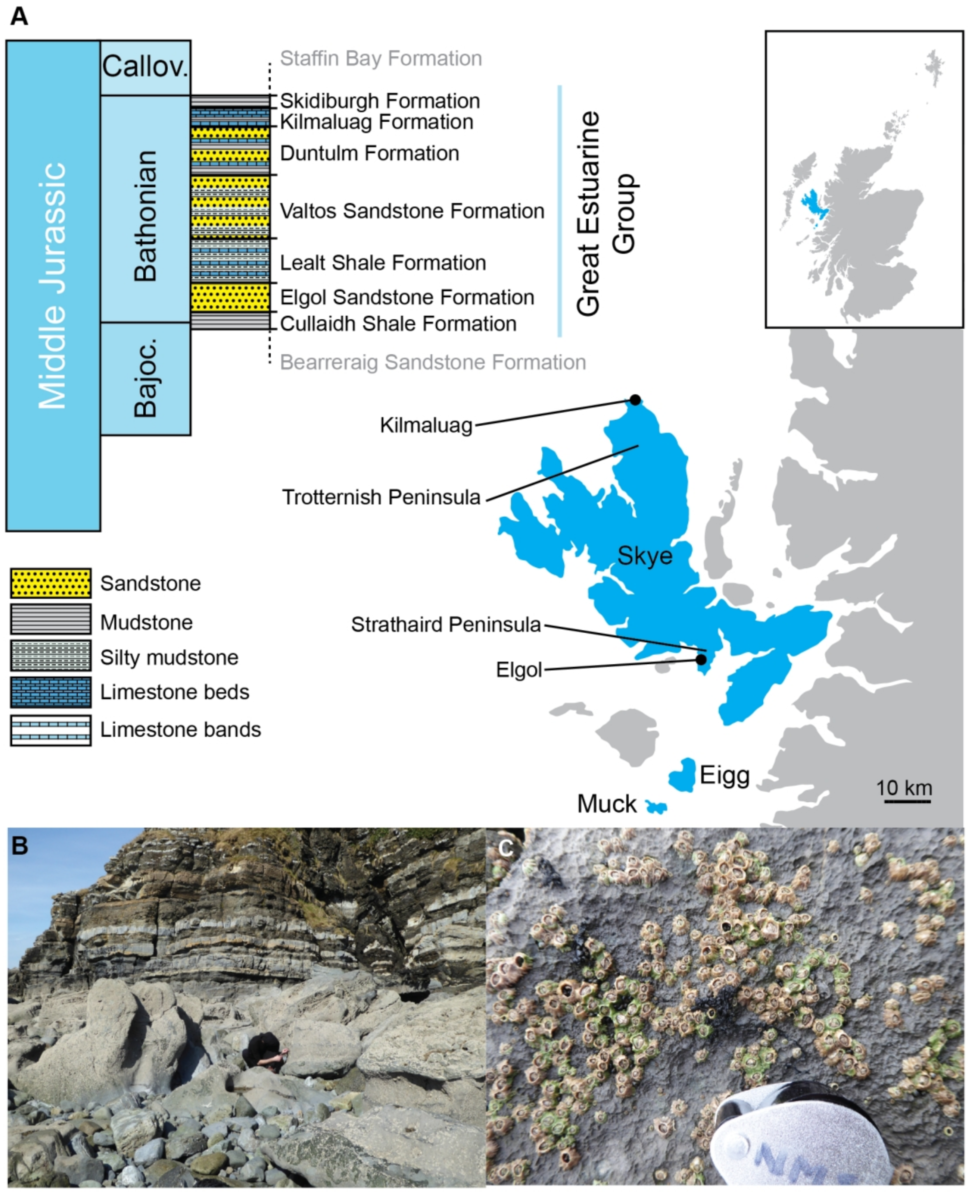
Figure 10. Location and age of the Jurassic and Cretaceous vertebrate assemblages discussed.

Figure 11. Proportion of each vertebrate group collected by research teams from the Kilmaluag Formation: since the sites discovery in 1971 (A); in the 1970-80s by Dr Michael Waldman and Prof Robert Savage (B); in the early 2000s by Prof Susan Evans and Prof Paul Barrett (C); and since 2010 by the universities of Oxford, Birmingham, and National Museums Scotland (D). Silhouettes created by EP.

Table 1: *Updated vertebrate faunal list for the Kilmaluag Formation, Scotland*.

Chondrichthyes	Hybodontiformes		*Acrodus caledonicus*
			Hybodus sp.
			Hybodont indet.
Osteichthyes	Amiiformes		Amiiformes indet.
	Pycnodontiformes		Pycnodontiformes indet.
	Semionotiformes		*Lepidotes*
Sarcopterygii	Coelacanthiformes		?coelacanth
Lissamphibia		Albanerpetontidae	cf.*Anoualerpeton* sp.
		Caudata	*Marmorerpeton kermacki*
			'Kirtlington Salamander A'
Sauropsida	Testudinata		*Eileanchelys waldmani*
			Chelonia indet.
	Lepidosauromorpha	Lepidosauromorph a indet	*Marmoretta* sp.
			Taxon A
			Taxon B
		Squamata indet	*Parviraptor* sp.
			Taxon nov. A
			Taxon nov. B
			Bellairsia sp.
		?Paramacellodidae	*Balnealacerta sp.*
			? Paramacellodid indet
		Incertae sedis	Taxon nov.
	Choristodera		*Cteniogenys* sp.
			Choristodera indet.
	Archosauromorpha	Crocodylomorpha	Goniopholidae indet.
			Atoposauridae indet.
			Unnamed Crocodylomorpha
			Goniopholidae indet.
		Dinosauria indet.	Dinosauria indet.
		Sauropoda	Neosauropoda indet. (not *Cetiosaurus*)
			Sauropoda indet.
		Theropoda	Theropoda indet.
		Pterosauria	Rhamphorhynchoidea indet.
			Pterodactyloidea indet.
		Reptilia indet.	Reptilia A
			Reptilia B
			Reptilia C
Synapsida	Mammaliamorpha		*Stereognathus ooliticus*
	Mammaliaformes	Morganucodonta	*Wareolestes rex*
		Docodonta	*Borealestes serendipitus*
			Borealestes sp. nov.
			Krusatodon kirtlingtonensis
			Krusatodon sp.
	Mammalia	Cladotheria	*Palaeoxonodon ooliticus*
		Eutriconodonta	*Phascolotherium* sp.
	Incertae sedis		Mammalia indet.

Table 1: *Updated vertebrate faunal list for the Kilmaluag Formation, Scotland.*



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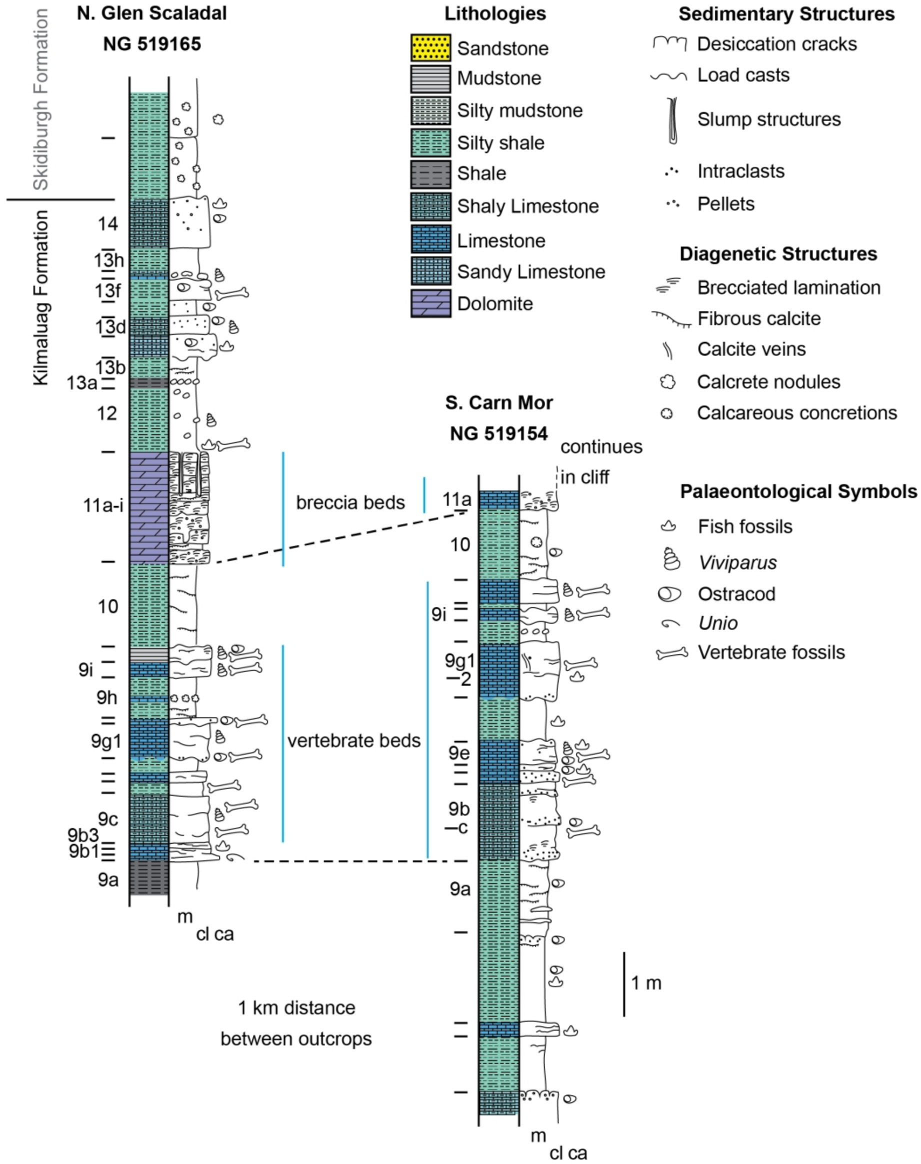

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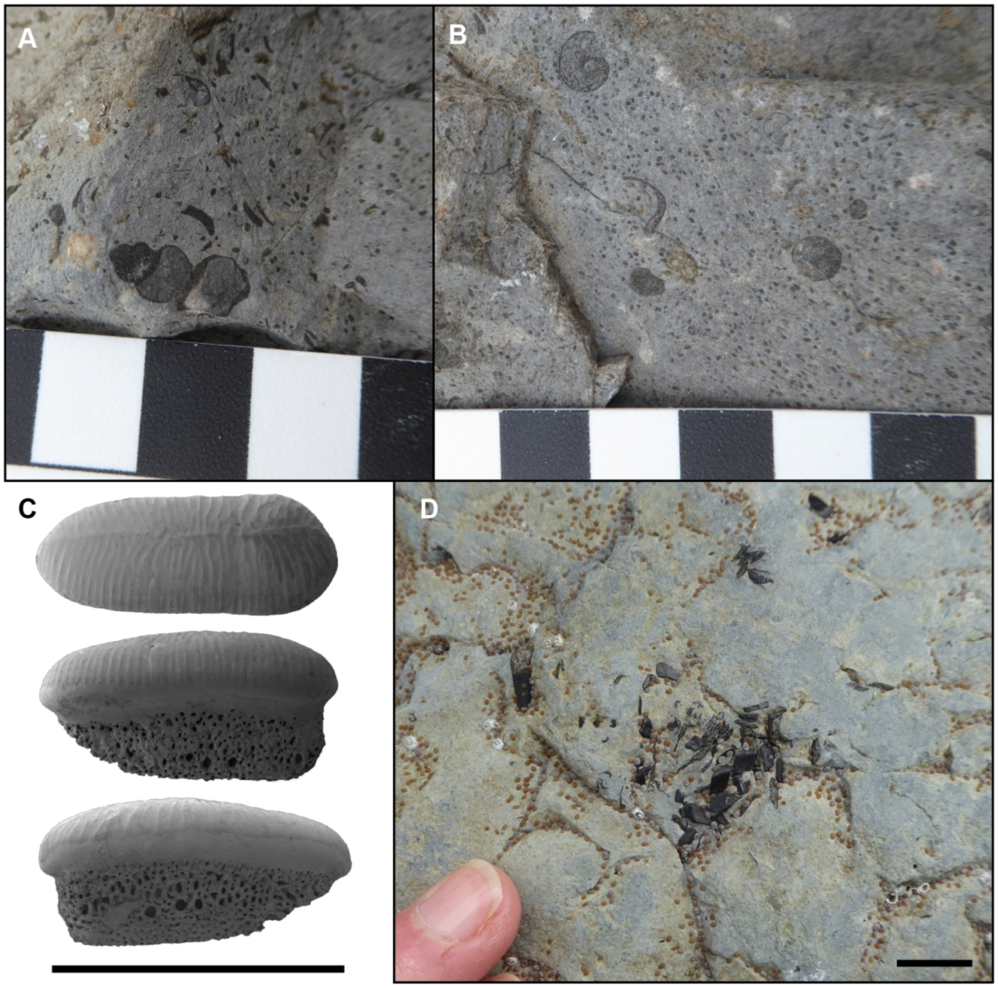

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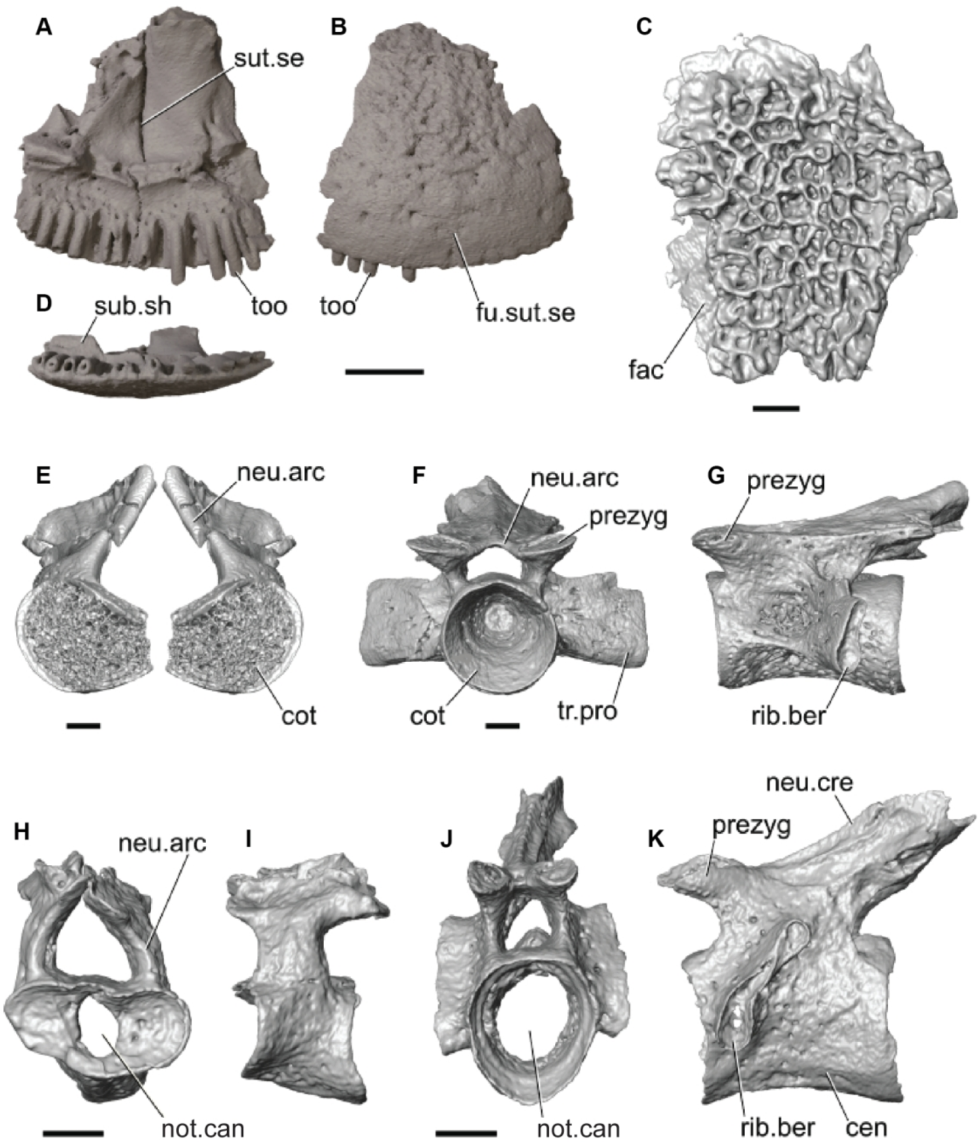

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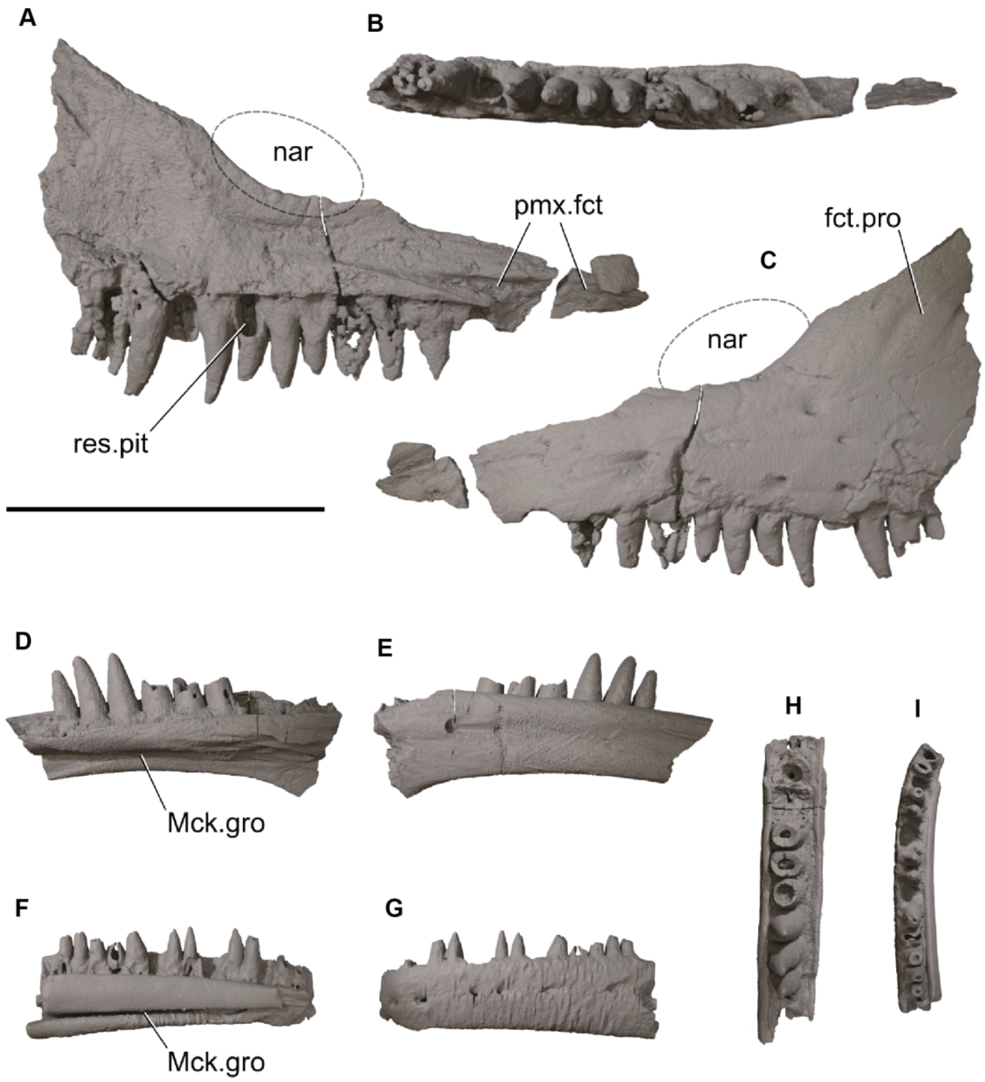

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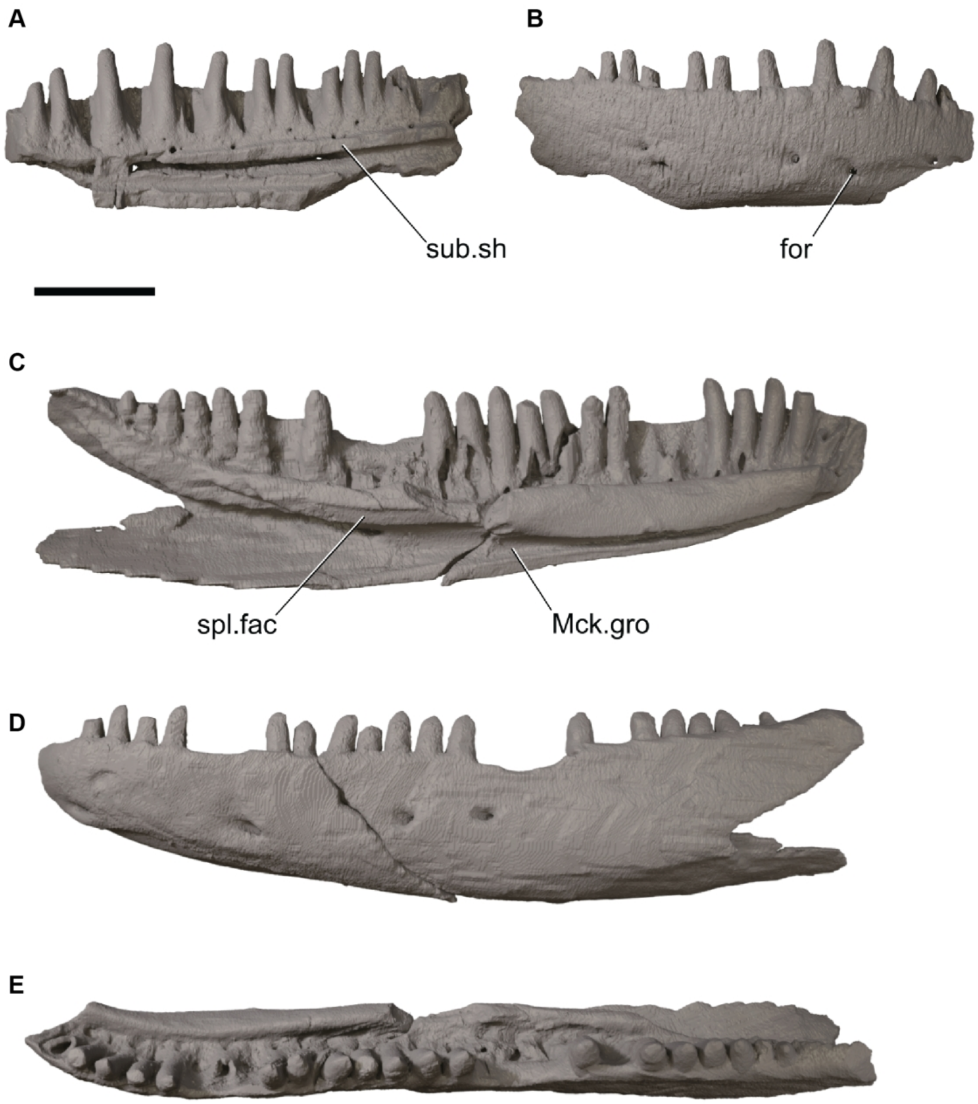

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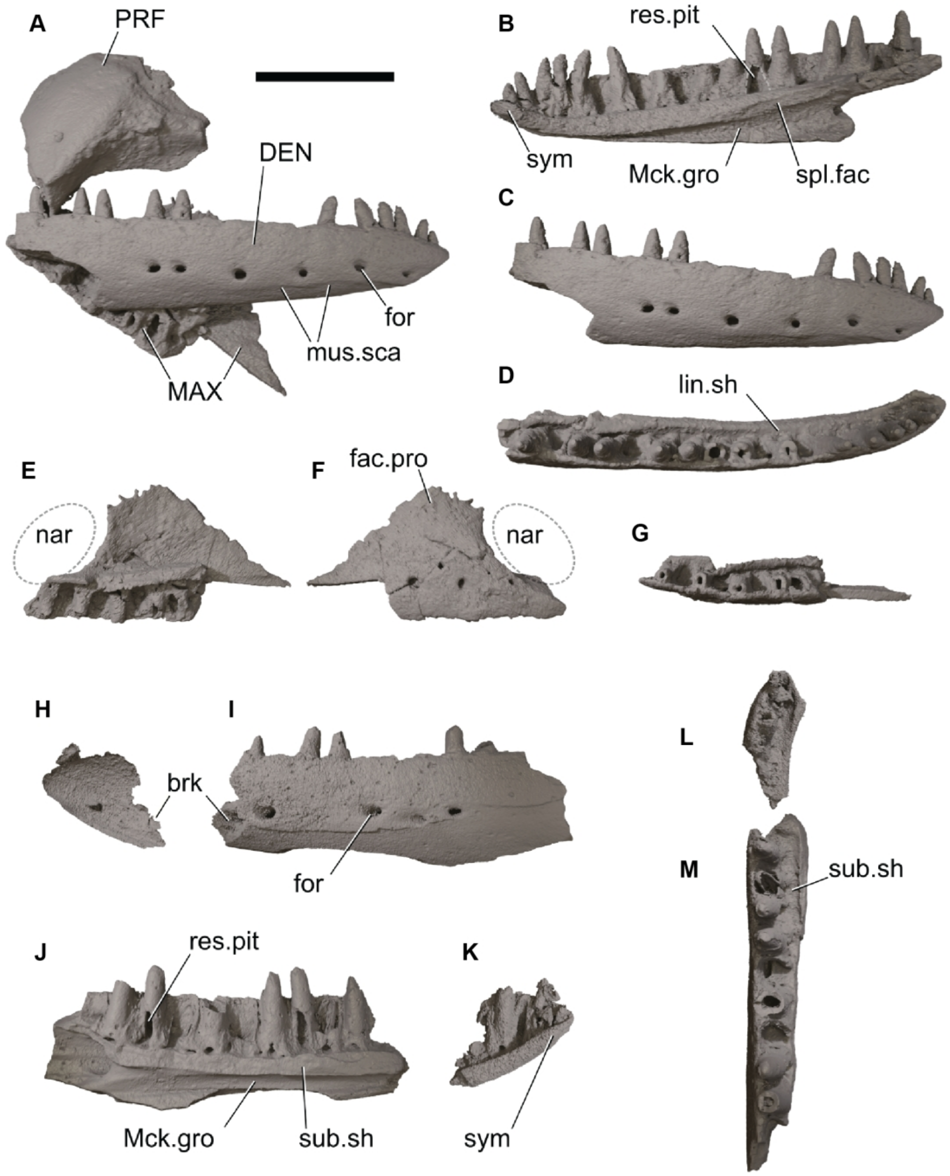

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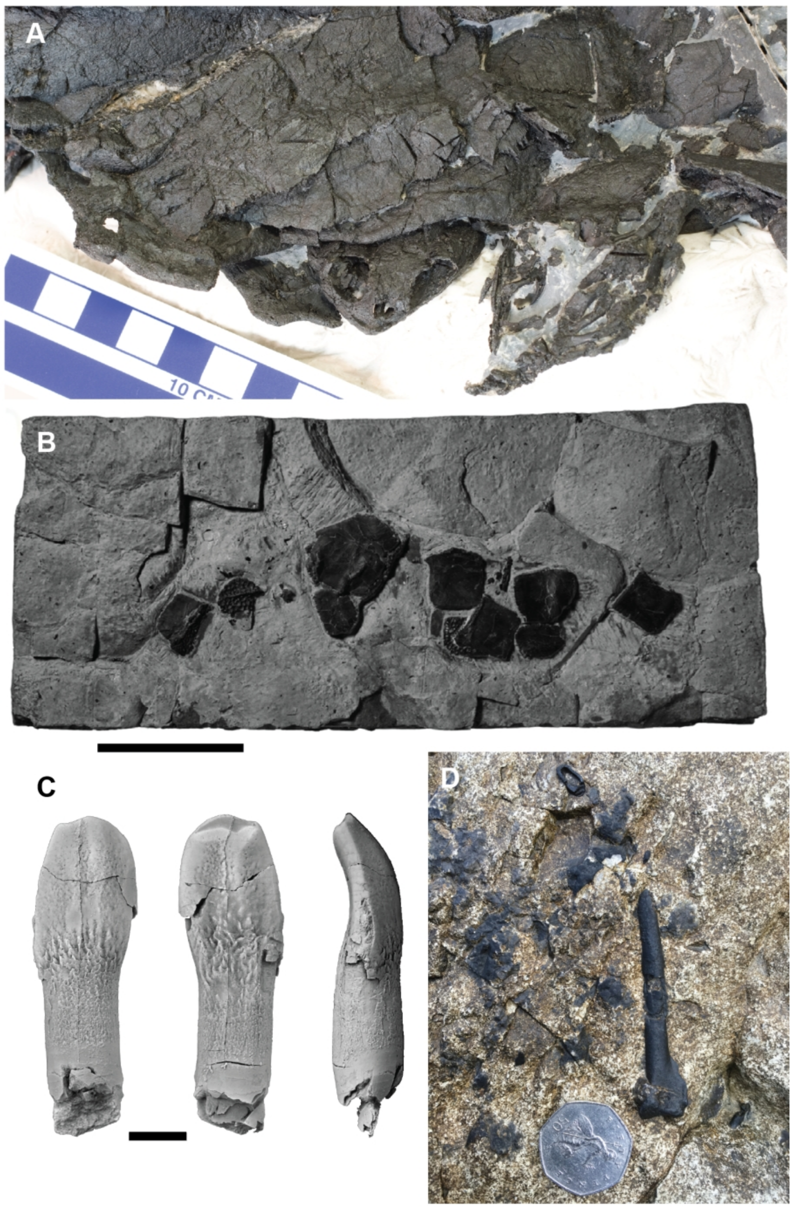

Figure 8. Reptile fossils from the Kilmaluag Formation: turtle *Eileanchelys waldmani* NMS G.2004.31.16d (A) (image: A. Anquetin); crocodylomorph osteoderms NHMUK R36713 (B) (adapted from Wills *et al*. [2014; fig 4a]); sauropod dinosaur tooth NMS G.2004.31.1 (C) (adapted from Barrett [2006: fig 1]); and a non-pterodactyloid pterosaur collected in 2016 (D) (Photo by R Close). Scale bars: B = 50 mm, for C = 5 mm.

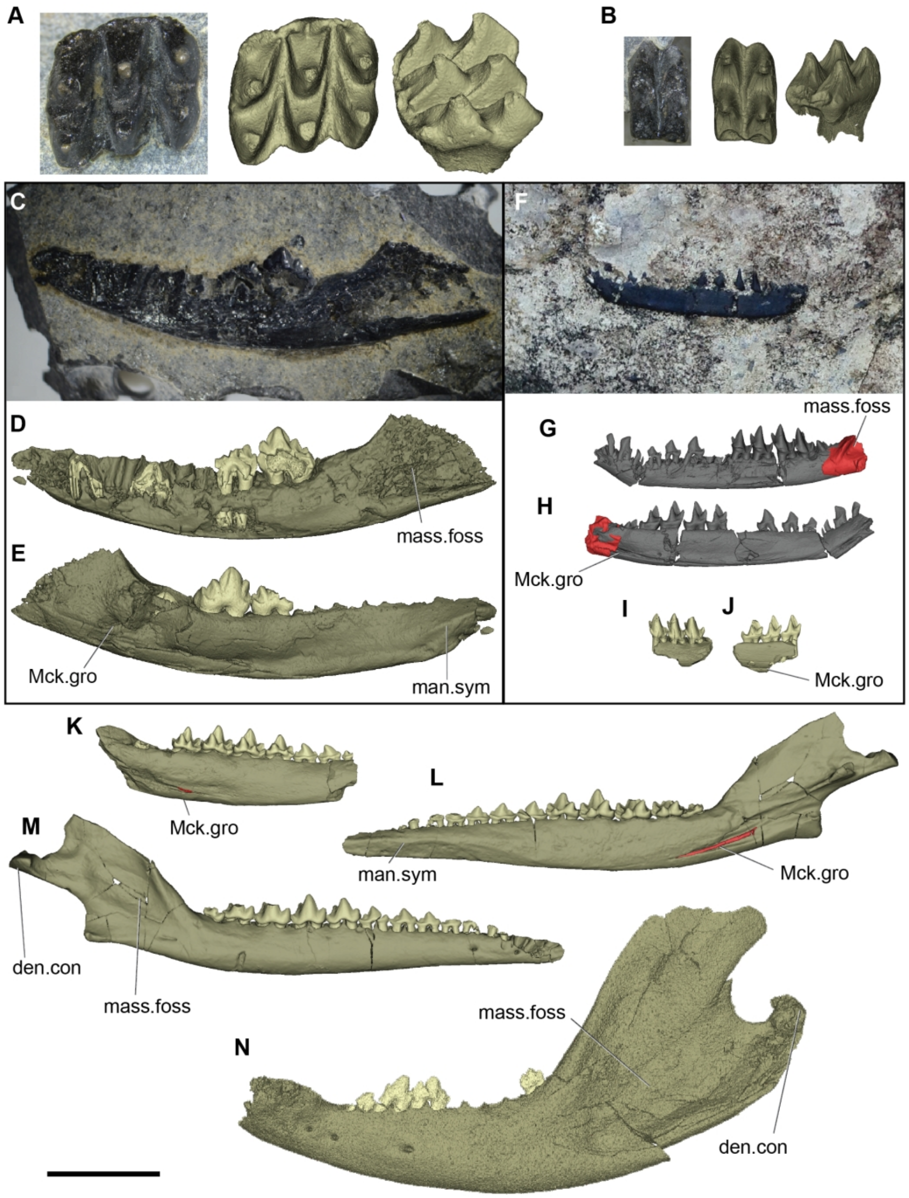

Figure 9. Mammaliamorphs from the Kilmaluag Formation: *Stereognathus ooliticus* NMS G.2017.17.2 (A), and NMS G.1992.47.120 (B) (adapted from Panciroli *et al*. [2017;5 and 7]); *Wareolestes rex* NMS G.2016.34.1, photographed in matrix (C), digitally segmented in labial view (D) and lingual view (E) (adapted from Panciroli *et al*. [2017; fig 2 and 3]); *Palaeoxonodon ooliticus* NMS G.2016.17.1 in the field (F) (image: R. Close), and combined with NMS G.2017.37.1 (red) in labial (G) and lingual view (H); *Palaeoxonodon ooliticus* NMS G.1992.47.123 in labial (I) and lingual view (J) (adapted from *Panciroli et al*. [2017; figs 1 and 3]); *Borealestes serendipitus* BRSUG 20570 holotype (K), *Borealestes serendipitus* NMS G.1992.47.121.3 in lingual (L) and labial view (M); *Phascolotherium* sp. (field number ELGOL2017.023) in labial view (N). Abbreviations: dent.cond=dentary condyle; mass.foss=masseteric fossa; man.sym=mandibular symphysis; Mck.gro=Meckelian groove. Scale bar = 5 mm, same scale throughout.

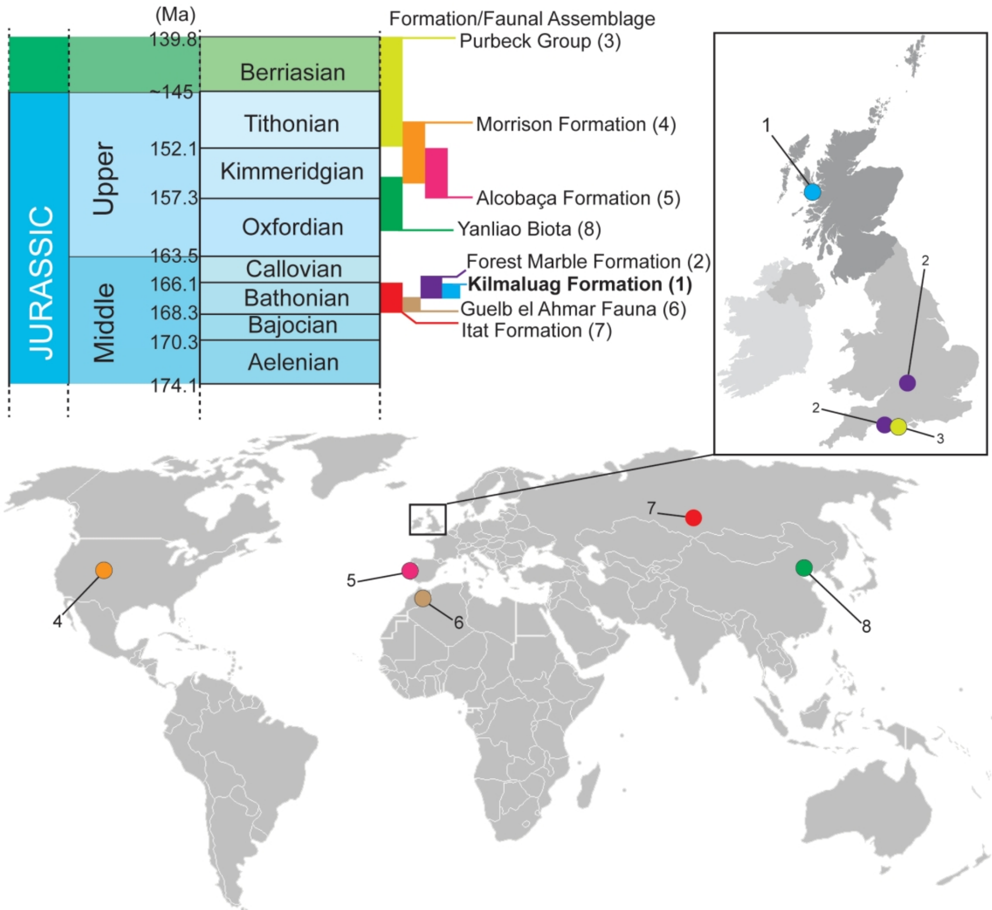

Figure 10. Location and age of the Jurassic and Cretaceous vertebrate assemblages discussed.

747x687mm (72 x 72 DPI)

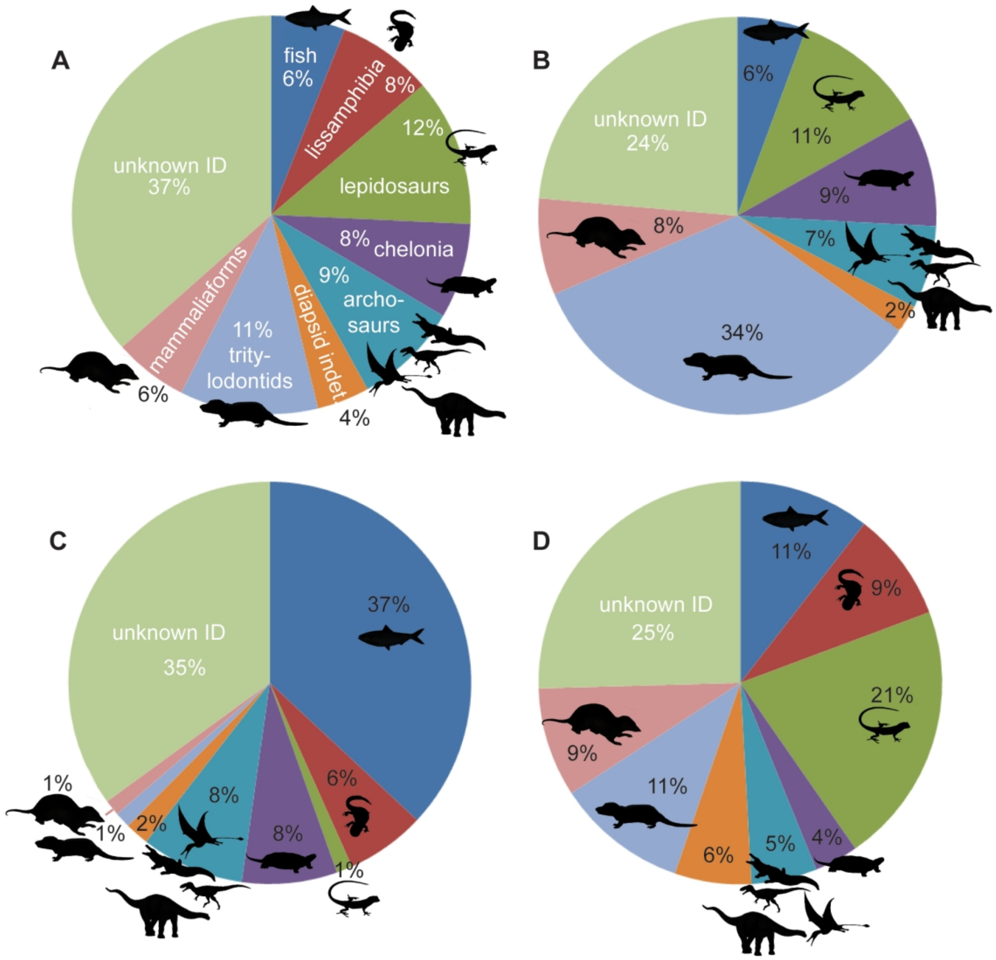

Figure 11. Proportion of each vertebrate group collected by research teams from the Kilmaluag Formation: since the sites discovery in 1971 (A); in the 1970-80s by Dr Michael Waldman and Prof Robert Savage (B); in the early 2000s by Prof Susan Evans and Prof Paul Barrett (C); and since 2010 by the universities of Oxford, Birmingham, and National Museums Scotland (D). Silhouettes created by EP.

682x655mm (72 x 72 DPI)