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A new ankylosaurian osteoderm from the Middle Jurassic Oxford Clay Formation, United Kingdom

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Abstract: Ankylosaurs are a characteristic group of dinosaurs recognized by their extensive coverings of dermal bony armour, known as osteoderms, across their bodies. The Oxford Clay Formation (Callovian–Oxfordian, Middle Jurassic) in the UK is important for understanding early ankylosaur evolution as it contains some of the earliest known ankylosaur material, including a cranial osteoderm from the basal-most ankylosaur *Sarcolestes* (and probable postcranial osteoderms). Here, we describe an isolated osteoderm from the Oxford Clay of Peterborough that exhibits a different morphology to other osteoderms from this formation. The specimen, although incomplete along its transverse axis, measures 52.7 mm by 41 mm. The osteoderm is subrectangular with a concave ventral surface and a low, rounded keel on its dorsal surface that protrudes beyond the posterior margin of the specimen base. This morphology is superficially more similar to the thoracic osteoderms of more derived Cretaceous ankylosaurs from North America (e.g. *Borealopelta*), than to *Sarcolestes* and other Jurassic ankylosaurs (e.g. *Dracopelta*, *Mymoorapelta*, *Tianchisaurus*), but could represent a currently unknown *Sarcolestes* morphology. Although its isolated nature prevents reliable identification of the taxon and the body part to which it belonged, the osteoderm nevertheless indicates a larger morphological diversity in the body armour of the earliest ankylosaurs than currently appreciated.

Supplementary material: A photogrammetric .obj model of the osteoderm is available at https://doi.org/10.6084/m9.figshare.c.7255842

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Anklyosauria (= ankylosaurs) is an iconic group of ornithischian dinosaurs characterized by their wide quadrupedal bodies and widespread coverings of dermal armour on their skulls and postcrania (Vickaryous *et al.* 2004; Pond *et al.* 2023). The estimated origins of ankylosaurs date to the late Early or early Middle Jurassic when they split from their sister group, the stegosaurs (Maidment *et al.* 2020; Raven *et al.* 2023), although the earliest conclusive ankylosaur material is from the Bajocian (Maidment *et al.* 2021). Although Jurassic anklyosaurs exhibit low species diversity (Maidment *et al.* 2020), they do exhibit a large geographical range, including Europe (UK and Portugal), Morocco, the USA and China (Lydekker 1893; Galton 1980*a*; Dong 1993; Kirkland and Carpenter 1994; Kirkland *et al.* 1998; Maidment *et al.* 2021). Jurassic ankylosaurs also exhibit a wide range of armour morphologies, both between taxa and within individuals. An individual has different types of osteoderms in its head, neck, torso and tail regions (Dong 1993; Galton 1994; Kirkland and Carpenter 1994; Kirkland *et al.* 1998; Kilbourne and Carpenter 2005). The established definition of an osteoderm is any bone larger than 1 cm diameter situated within the dermis of an individual, while dermal bones smaller than 1 cm are termed ossicles (Arbour *et al.* 2014; Brown 2017).

The Oxford Clay Formation (Callovian–Oxfordian, Middle Jurassic) in the UK is important for understanding early ankylosaur evolution. Currently, only one ankylosaur taxon is confidently identified from the formation, *Sarcolestes leedsi* Lydekker 1893, known from a partial mandible with an attached osteoderm (Galton 1980*a*, 1983). Possible postcranial osteoderms have also been assigned to *Sarcolestes* but their isolated nature makes this assignment tentative and they could belong to a different taxon (Galton 1994; Lomax and Tamura 2014). *Sarcolestes* is stratigraphically the second oldest ankylosaur known, and phylogenetic analyses have resolved it as the most basally branching ankylosaur (Raven *et al.* 2023). *Scelidosaurus*, an earlier armoured dinosaur from the Sinemurian of Lyme Regis, UK, is a thyreophoran that pre-dates the stegosaur-ankylosaur split (Norman 2020*a*, *b*, *c*, 2021; Raven *et al.* 2023). The Oxford Clay was deposited in a shallow marine environment so terrestrial remains, including dinosaurs, are relatively rare (Martill 1991*a*; Martill *et al.* 1994; Lomax and Tamura 2014). Here, we describe an isolated osteoderm from the Oxford Clay that exhibits a type of morphology not previously found in Jurassic ankylosaurs.

Geological setting

NOTNH FS854 was discovered in 2015 at Pode Hole Quarry near Peterborough, Cambridgeshire (Fig. 1). The specimen was found *ex situ* so its exact stratigraphic age cannot be determined, but it has been tentatively identified as from the Stewartby Member based on the preservation and adjacent outcrops (R. Forrest pers. comm.). The Stewartby Member comprises intercalated silty, calcareous mudstones

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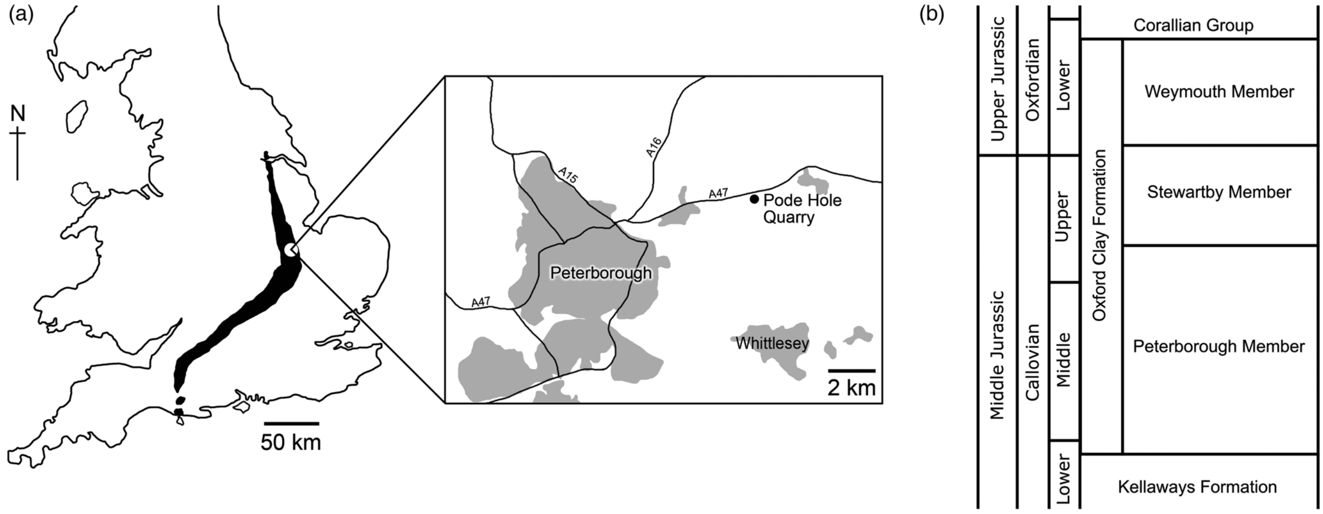

Fig. 1. (**a**) Map of England and Wales showing the location of the Oxford Clay Formation, with the location of Pode Hole Quarry highlighted and inset, the location of Pode Hole Quarry relative to Peterborough, Cambridgeshire; (**b**) Stratigraphic chart of the Oxford Clay Formation showing the inferred origin of NOTNH FS854. Both panels redrawn from Ewin and Thuy (2017).

and calcareous siltsone, and is poorly fossiliferous with very few vertebrate remains such as fish teeth (Cox *et al.* 1992; Martill *et al.* 1994; Phipps 2007). The Stewartby Member is from the upper Callovian (Phipps 2007) so if the osteoderm originated from this member it would be slightly younger than *Sarcolestes*, whose holotype specimen has been described from the middle Callovian Peterborough Member (Fig. 1; Galton 1980*a*, 1983). Dinosaurs found in the Oxford Clay Formation may have been washed out to sea where their bones were subsequently scattered and buried on the seafloor, known as the 'bloat-and-float' model (Martill 1985, 1991*c*; Mallon *et al.* 2018).

Methods

Institutional abbreviations

BMBG, Booth Museum of Natural History-Geology, Brighton, UK; **NOTNH**, Nottingham Natural History Museum, Wollaton Hall, Nottingham, UK; **NHMUK**, Natural History Museum, London, UK.

Photogrammetry

The osteoderm was recorded using manual photogrammetry, a reliable technique (Mallison and Wings 2014) for creating three-dimensional point clouds and meshes by taking overlapping photographs of a subject that are processed using specialist software. The technique can produce digital replicas with sub-millimetre resolutions, high degrees of reproducibility (Fahlke and Autenrieth 2016) and accuracies greater than models produced using a hand scanner (Díez Díez *et al.* 2021). A Fuji X10 mounted on a tripod was used to take the photographs and Agisoft Photoscan was used to process the photographic data. More detailed information can be found in Pond *et al.* (2023). An electronic version of the photogrammetric model (.obj format) is available in the Supplementary Material).

Systematic palaeontology

Dinosauria, Owen 1842
Ornithischia, Seeley 1887
Thyreophora, Nopcsa 1915 *sensu* Norman 1984
Ankylosauria, Osborn 1923
Ankylosauria indet. (Fig. 2)

Material

One dermal osteoderm (NOTNH FS854).

Description

NOTNH FS854 is an asymmetrical subrectangular osteoderm. It is 52.7 mm long along its inferred anteroposterior axis, 41.0 mm wide as measured transverse to the long axis, and 14.7 mm high. The inferred anteroposterior axis minus the posterior process is 43.2 mm long. An anteroposteriorly oriented low-lying keel runs along the top of the left side of the osteoderm and extends as a short posterior process that protrudes obliquely beyond the inferred posterior margin (Fig. 2a–c, g and 2h). The keel is rounded anteriorly but becomes sharper and more pronounced posteriorly, so the inferred right side of the posterior process has a steep, almost vertical edge (Fig. 2k–o). The left side of the posterior process is inclined at a shallow angle (Fig. 2m–o). The anterior margin is sharp and has a slightly concave notch (Fig. 2a–f). The right and posterior margins (excluding the posterior process) are convex and thicker than the anterior margin (Fig. 2i, j and m–o). The inferred left lateral margin of the osteoderm is slightly damaged and part has broken off, but the curvature of the adjacent finished bone suggests that not much is missing (Fig. 2c, f).

The dorsal surface on the right side of the keel has a distinct rugose texture, with parallel grooves oriented transverse to the keel (Fig. 2b, c, e and f). The main grooves are connected by short connecting channels (Fig. 2c, f). There are shallow pits on the surface of the keel and between the grooves and channels (Fig. 2c, f).

The ventral surface of the bone is gently concave, with a smooth bone surface in the middle, surrounded by rough and irregular rugose texture around the edges (Fig. 2d–f).

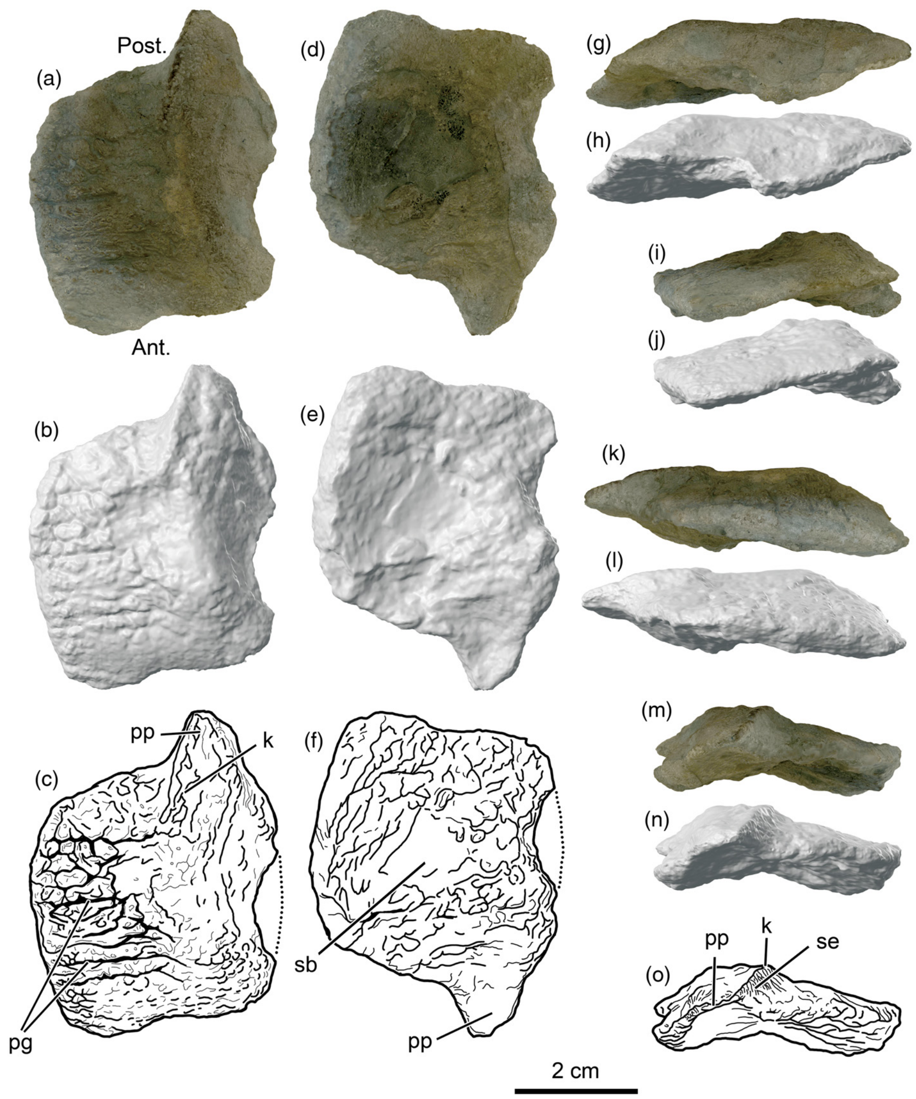

Fig. 2. Photographs, photogrammetric models and interpretive illustrations of Ankylosauria indet., NOTNH FS854. Orientation presumed. (**a–c**) dorsal view. (**a**) photograph; (**b**) photogrammetric model; (**c**) interpretive illustration with dotted line inferring broken edge; (**d–f**) ventral view. (**d**) photograph; (**e**) photogrammetric model; (**f**) interpretive illustration with dotted line inferring broken edge. (**g–h**) left lateral view. (**g**) photograph; (**h**) photogrammetric model. (**i–j**) anterior view. (**l**) photograph; (**j**) photogrammetric model. (**k–l**) right lateral view. (**k**) photograph; (**l**) photogrammetric model. (**m–o**) posterior view. (**m**) photograph; (**n**) photogrammetric model; (**o**) interpretive illustration. Abbreviations: k, keel; pg, parallel grooves; pp, posterior process; sb, smooth bone; se, steep edge.

Comparisons

NOTNH FS854 is morphologically very different to all currently described Oxford Clay osteoderms. The osteoderm attached to the *Sarcolestes* mandible (NHMUK PV R 2682) is broken in places, which prevents identification of its original shape, and has rugose texture only on its ventral surface and has shallow, suboval and tear-drop shaped depressions on its dorsal surface (Galton 1983). The isolated osteoderms that are tentatively identified as postcranial *Sarcolestes* osteoderms exhibit strongly convex dorsal margins with smooth apices, no keels or posterior processes and mostly flat ventral surfaces (Galton 1983, 1994).

The specimen shares more morphological similarities to osteoderms from other Jurassic ankylosaurs than to the *Sarcolestes* type material and to the postcranial osteoderms tentatively assigned to this taxon, but there are still several important differences. For example, the ventral margins of many Jurassic ankylosaur osteoderms exhibit some degree of ventral concavity but none have been described with a posteriorly protruding process (Galton 1980*b*; Dong 1993; Kirkland and Carpenter 1994; Kirkland *et al.* 1998; Kilbourne and Carpenter 2005; Russo and Mateus 2021). Most of these osteoderms are broadly subcircular, oval or lunate (e.g. *Dracopelta zbyszewskii, Mymoorapelta maysi*, *Tianchisaurus nedegoapeferima*), except for some *Gargoyleosaurus parkpinorum* osteoderms which are subrectangular but do not possess a keel (Galton 1980*b*; Dong 1993; Kirkland and Carpenter 1994; Kirkland *et al.* 1998; Kilbourne and Carpenter 2005; Russo and Mateus 2021). *Mymoorapelta*, *Tianchisaurus* and ovate *Gargoyleosaurus* osteoderms possess keels but these keels are either much taller (*Mymoorapelta*), or have much sharper edges (*Gargoyleosaurus*, *Tianchisaurus*), than NOTNH FS854 (Galton 1980*b*; Dong 1993; Kirkland and Carpenter 1994; Kirkland *et al.* 1998; Kilbourne and Carpenter 2005; Russo and Mateus 2021). *Dracopelta* osteoderms are broadly symmetrical with slightly convex dorsal centres instead of keels (Galton 1980*b*; Russo and Mateus 2021).

Other osteoderm-bearing reptiles that NOTNH FS854 could plausibly belong to, such as the Early Jurassic non-eurypodan thyreophorans *Scelidosaurus harrisonii* and *Scutellosaurus lawleri*, can be confidently ruled out. *Scelidosaurus* postcranial osteoderms are generally ovate and transversely narrow with shallow to tall steep ridges along the midline and flat ventral surfaces (Norman 2020*c*). *Scutellosaurus* exhibits several distinct morphologies that bear very little resemblance to NOTNH FS854 (Breeden and Rowe 2020). These include (but are not limited to): symmetrical ovate osteoderms with sharp-edged narrow keels; asymmetrical osteoderms with very tall, almost vertically sloping keels; and flat osteoderms with a longitudinal ridge on either side of the midline (Breeden and Rowe 2020).

The Oxford Clay also contains teleosaurid crocodyliform osteoderms (Martill 1991*a*, *b*). However, they have a distinctive ornamentation on their dorsal surfaces comprising large ovate, elongate pits that often radiate outwards from the keel (Johnson *et al.* 2018). Teleosaurid and ankylosaur osteoderms are therefore easy to differentiate from each other.

The subrectangular shape and posteriorly-protruding, low-lying spine of NOTNH FS854 is most similar to the thoracic osteoderms of Cretaceous ankylosaurs such as *Borealopelta markmitchelli* (Brown 2017). There are still a few differences however, such as the keel of the NOTNH FS854 osteoderm is slightly laterally located, while the keels of *Borealopelta* thoracic osteoderms are centrally or near-centrally located (Brown 2017). The dorsal surfaces of the thoracic osteoderms also exhibit less rugose textures than NOTNH FS854 but this may be due to the *Borealopelta* osteoderms having at least some epidermal covering preserved on these surfaces (Brown 2017).

NOTNH FS854 also shares some similarities to isolated osteoderms from the Cambridge Greensand, UK (early Cenomanian), tentatively identified as cervical osteoderms from an indeterminate nodosaur (*sensu* Coombs 1978, e.g. BMBG 020531; Blows 2014). These specimens are similarly subrectangular with concave ventral margins and posteriorly pointing lip-like protrusions, although the Greensand osteoderms are more symmetrical with much taller, sharp-edged keels in their centre (Blows 2014).

Because the specimen was found *ex situ*, and because ankylosaur osteoderms generally exhibit great morphological variation within individuals, Ankylosauria indet. is the most precise taxonomic assignment possible.

Discussion

The presence of NOTNH FS854 does not imply that a more derived ankylosaurian, or even a second ankylosaurian species (third if the osteoderms described by Galton (1994) do not belong to *Sarcolestes*), inhabited the Oxford Clay due to poor phylogenetic signals known from ankylosaur osteoderms (Raven *et al.* 2023). The specimen could represent a previously unknown *Sarcolestes* morphology and be from a different body location and/or from an individual at a different ontogenetic stage to currently known Oxford Clay osteoderms. However, there is no way to be certain without additional discoveries. Moreover, due to high intra-individual variation in osteoderm morphologies, we are unable to determine where on the body the specimen was located in life, although a cranial osteoderm is less likely.

Despite the taxonomic and morphological limitations of the specimen, this newly described osteoderm is an important contribution to early ankylosaur evolution. The specimen increases the known morphological diversity of Jurassic ankylosaur osteoderms and indicates that osteoderm morphologies, thought to be exclusive to Cretaceous taxa, evolved much earlier, both in stratigraphic time and in ankylosaur evolution. It is possible that examination of currently undescribed Oxford Clay material in museum collections may reveal further morphological diversity in the earliest ankylosaurs.

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Author contributions **JB**: formal analysis (lead), investigation (lead), project administration (lead), writing – original draft (lead), writing – review & editing (lead); **SP**: investigation (supporting), software (lead), visualization (equal), writing – original draft (supporting), writing – review & editing (supporting); **CLO**: investigation (supporting), writing – original draft (supporting), writing – review & editing (supporting); **MN**: investigation (supporting), writing – original draft (supporting), writing – review & editing (supporting); **ASS**: conceptualization (lead), formal analysis (supporting), investigation (supporting), visualization (equal), writing – original draft (supporting), writing – review & editing (supporting).

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Data availability The photogrammetric model of the osteoderm in .obj format is available in the Supplementary Material.

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