



# Microvertebrates from the Wadhurst Clay Formation (Lower Cretaceous) of Ashdown Brickworks, East Sussex, UK

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## ABSTRACT

Ashdown Brickworks, near Bexhill, East Sussex, has produced a large number of vertebrate fossils from the Wadhurst Clay Formation, part of the Wealden Supergroup (Hastings Group; Valanginian; Lower Cretaceous). Here we describe the microvertebrate fauna of the 'conglomerate bed', representing a rich sample of taxa. While most of the recovered teeth and bones are abraded, some heavily, most can be identified to species level. The taxa include four species of hyodont sharks (*Egertonodus basanus*, *Planohyodus ensis*, *Polyacrodus parvidens*, *P. brevicostatus*), three taxa of bony fishes (an unidentified *Lepidotes*-like semionotiform, the pycnodontiform *Ocloedus*, and an albuliform), three taxa of crocodyliforms (the goniopholid *Hulkepholis*, a bernissartiid, and the atoposaurid *Theriosuchus*), and the theropod dinosaurs *Baryonyx* and an allosauroid. Sediments of the Wadhurst Clay Formation as a whole indicate freshwater to very slightly brackish-water environments of deposition, and the mainly aquatic time-averaged mixture of fishes and tetrapods recovered from the 'conglomerate bed', together with isolated terrestrial species, confirms this interpretation.

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## 1. Introduction

The Wealden Supergroup of south-east England has been one of the most productive continental Mesozoic units for fossil vertebrates, with the first reported finds dating back to before 1800 (Martill and Naish, 2001). The Wealden Supergroup, especially in Surrey, East and West Sussex and Kent, comprises many formations and members, characterized by diverse fluvial, lacustrine and terrestrial facies, that have been studied intensely by geologists and palaeontologists (e.g., Topley, 1975; Allen, 1975; Batten, 2011). Over 200 years, hundreds of skeletons of dinosaurs, crocodyliforms, turtles, and rare pterosaurs and plesiosaurs have been reported, with additional finds of fishes, lissamphibians, lizards and mammals based on microvertebrate remains (Allen, 1949; Martill and Sweetman, 2011). More recently, Steve Sweetman has conducted a series of investigations into microvertebrates

from bone-rich accumulations, especially on the Isle of Wight (e.g., Sweetman, 2011a, 2016; Sweetman and Evans, 2011a, 2011b; Sweetman et al., 2014). He reported a diverse vertebrate assemblage including chondrichthyan and osteichthyan fishes, lissamphibians, lizards, turtles, crocodyliforms, pterosaurs, non-avian dinosaurs, birds and mammals from the plant debris beds of the Wessex Formation (Barremian), and a sparser fauna of chondrichthyans and osteichthyans, and a small number of teeth of crocodyliforms, from the overlying Vectis Formation (late Barremian–early Aptian).

Microvertebrates had been reported from the Wealden of the Weald, particularly some important fossil mammals from Hastings, East Sussex, and other locations (Clemens and Lees, 1971). Intensive sampling efforts around Hastings through the 1960s and 1970s by Kenneth Kermack and his team from University College London revealed many new specimens, but only the mammals have been described. There are few accounts of the Wealden bone beds of the Weald Sub-basin since Allen (1949) and Cook (1995) described the sedimentology and taphonomy of numerous examples.

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The aim of this paper is to report the microvertebrate fauna from a unit that is older than the Isle of Wight Wealden fossil beds (Valanginian versus Barremian–early Aptian), but with many taxa in common. The location is the Ashdown Brickworks near Bexhill, East Sussex, where collecting since the 1990s has yielded abundant vertebrate fossils, initially larger remains, such as partial dinosaur skeletons, but also isolated teeth of a diversity of dinosaurs, crocodyliforms, and pterosaurs (Austen et al., 2010). We concentrate on the microvertebrate fauna from the ‘conglomerate bed’, one of five bone-bearing horizons at the site.

*Institutional abbreviation:* BEXHM, Bexhill Museum, 47 Egerton Rd, Bexhill-on-Sea, TN39 3HL, U.K.

## 2. Geological setting and previous work

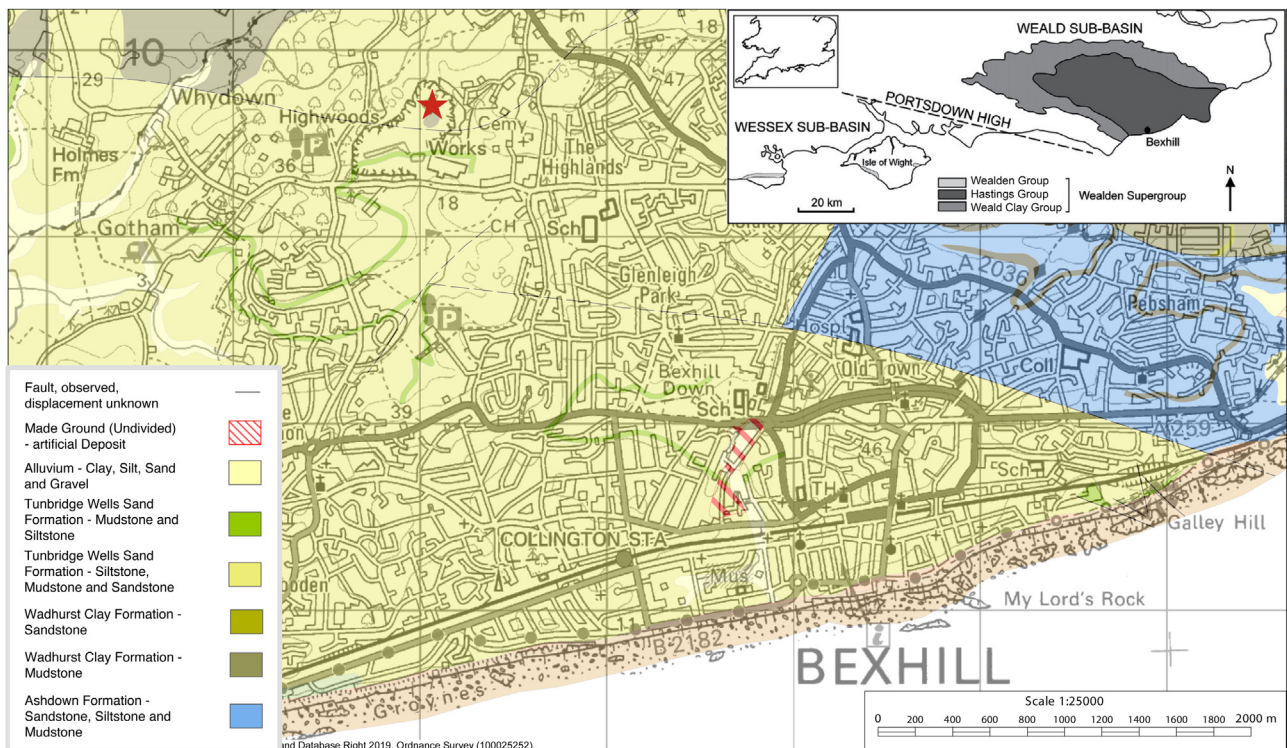
The Wealden sandstones around Hastings and Bexhill have long been a rich source of fossils, both from the inland stone quarries and from the coastal sections (Topley, 1875; Batten, 2011). Ashdown Brickworks (TQ 720095), on Turkey Road, near Bexhill, East Sussex (Fig. 1), has long been recognised as a prolific fossil locality (Batten and Austen, 2011; Austen and Batten, 2018). There are two pits, the southerly Crowborough Pit and the northerly Pevensy Pit, and they are separated by the Whydown Fault, which runs west–east (Figs. 1, 2). The pits expose two stratigraphic units, the Wadhurst Clay Formation overlain by the Lower Tunbridge Wells Sand Formation. The fossils described here come from the Wadhurst Clay Formation, which is exposed only in the Pevensy Pit.

A summary section through numerous sedimentary logs around the quarry shows the beds dipping at around 10° north (Fig. 2). The Wadhurst Clay Formation is divided into three units locally – a lower clay, some 30 m thick, a middle sandstone unit, the Northiam Sandstone, 2–3 m thick, and an upper clay, about 10 m thick.

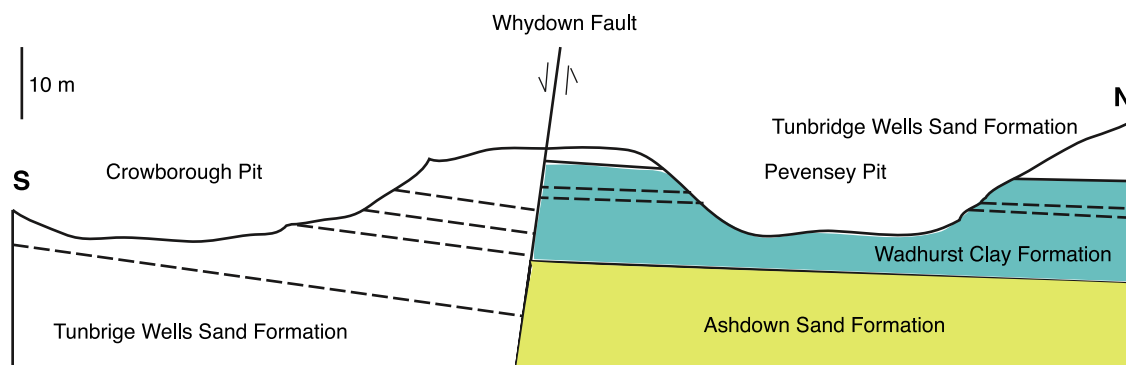
A brick works has operated continuously at this site since the 1890s. Formerly known as Lunsford Brickworks, and owned by the Sussex and Dorking Brick company, the site produced around 350,000 bricks per week, and was then taken over by Redland Brick in the 1970s. The site was redeveloped in 1978 to produce around 750,000 bricks per week and was then taken over by Ibstock Brick Ltd in 1996.

The Wadhurst Clay was named as a distinct rock unit by Drew (1861) and was later formally made the Wadhurst Clay Formation, a subdivision of the Wealden Group of Rawson (1992) and Hopson et al. (2008), and clarified by Batten (2011) as the Wadhurst Clay Formation within the Hastings Group of the Weald Sub-basin, a division of the Wealden Supergroup (Fig. 3A). It is part of what was formerly referred to as the ‘Hastings beds’, and ranges in thickness from 30 m at Rye to 70 m at Cuckfield and 78 m at Worth (Hopson et al., 2008, p. 10). The unit extends over most of the Weald Sub-basin, from Bexhill and Hastings on the coast, inland to Uckfield, Crowborough, Royal Tunbridge Wells, and Tenterden, and it is dated as early to early late Valanginian. The Wadhurst Clay Formation overlies the Ashdown Formation (Fig. 3A), and consists mainly of dark grey and soft shales and mudstones, with minor sandstones, conglomerates, calcareous gravels, ferrous clays and lignite, interpreted collectively as the deposits of freshwater to slightly brackish-water lagoon environments (Anderson et al., 1967; Allen, 1975; Lake and Young, 1978). The upper boundary is marked by a sharp change from siltstones to the fine-grained silty sandstones of the overlying Tunbridge Wells Sand Formation. The top of the Wadhurst Clay is commonly red-stained at this junction, marking the occurrence of pene-contemporaneous weathering.

The sediments at Ashdown Brickworks show many aspects of Allen’s (1975) classic environmental model for the Wealden of the Weald. He interpreted the overall environment as “a variable-salinity coastal mudplain with lagoons and sandy water-courses



**Fig. 1.** Geological map showing the region north of Bexhill-on-Sea (English Channel coast at bottom right), with the site of Ashdown Brickworks marked (red star), and the regional geology indicated. The Whydown Fault runs from west to east, through the middle of the works. Top right: Bexhill is indicated on the regional geological summary map of SE England. © Crown Copyright and Database Right 2017. Ordnance Survey (Digimap Licence). Regional map courtesy of Steve Sweetman. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 2.** Sketch cross section through the two pits at Ashdown Brickworks, showing the Whydown Fault between the two pits, and how this re-sets the observed successions (note that the orientation and throw of the fault are not exactly measured). Solid lines show formation boundaries, and dashed lines subordinate lithological units (e.g. Northiam Sandstone is indicated by dashed lines through the Wadhurst Clay Formation). Based on information in Hayward (1996).

loosely connected north-westwards with the East Anglian Sea.” The Wadhurst Clay represents slightly brackish and fresh shallow-water clays, which are punctuated by the Northiam Sandstone, marking a river channel that flowed at a time of increased rainfall or basin faulting, and transformed the slowly-accumulating muddy flood plain into a sandy braid plain. This kind of interruption of background sedimentation occurred at different times across the Weald Sub-basin (Fig. 3A), and the channel sands share many characters, including that they are often mature (abraded grains, well sorted) and packed with plant debris and bones, as in the case of the Cliff End bone bed at Hastings.

In an unpublished BSc dissertation, Hayward (1996) presented detailed accounts of the sedimentology, geology and palaeontology, as well as measured sections from around the site. After the intensive fossil-collecting campaign from 1999 to 2010, D.B., P.A.A. and Joyce Austen (J.A.) visited the site in February 2010 to measure the section, and their measurements were used by Sweetman to construct a sedimentary log, published in Naish and Sweetman (2011, Fig. 3) and Sweetman (2013, Fig. 2). This additional work was required because borehole data from the quarry company showed that Hayward had not allowed for dip in making his thickness measurements, and so the overall thicknesses calculated by him were too great. The log here (Fig. 3B, C) is based on that of Naish and Sweetman (2011).

Horne (1988) reported ostracods from Ashdown Brickworks. Hayward (1996) recorded plant fossils (the horsetail *Equisetites*, the club moss *Lycopodites*, the alga *Chara*, and the fern *Weichselia*), as well as fossilised wood and rootlet traces in the laminated clays. He also noted specimens of freshwater molluscs and ostracods, generally from the laminated clays. Hayward (1996, pp. 98–103) may have been the first to report vertebrate remains from the various conglomerate beds in the quarry, including numerous sharks’ teeth, actinopterygian teeth and scales, including those of an unidentified semionotiform (*Lepidotes* or *Scheenstia*; López-Arbarello, 2012), and the teeth of the crocodyliforms *Hulkepholis* (formerly *Goniopholis*; Buscalioni et al., 2013) and a bernissartiid, and a putative piece of turtle carapace. Austen and Batten (2011) reported numerous sporophylls of the quillwort *Isoetites* sp. in the Northiam Sandstone (Austen and Batten, 2011, fig. 32.2D). Austen and Austen (2016b) recorded a rare find of more than 90 nodal diaphragms of the horsetail *Equisetites lyelli* in a gutter cast from the ‘iguanodont bed’ (see below) excavations.

The first fossil vertebrates were found in the Pevensey Pit in about 1990 by D.B., and he continued to find fossils and to collaborate with other geologists and palaeontologists to amass a large collection over succeeding years (Fig. 4). The vertebrate finds were reported piecemeal in print before 2010, in a series of newsletter reports. The first report (Anon., 1999) was of dinosaur

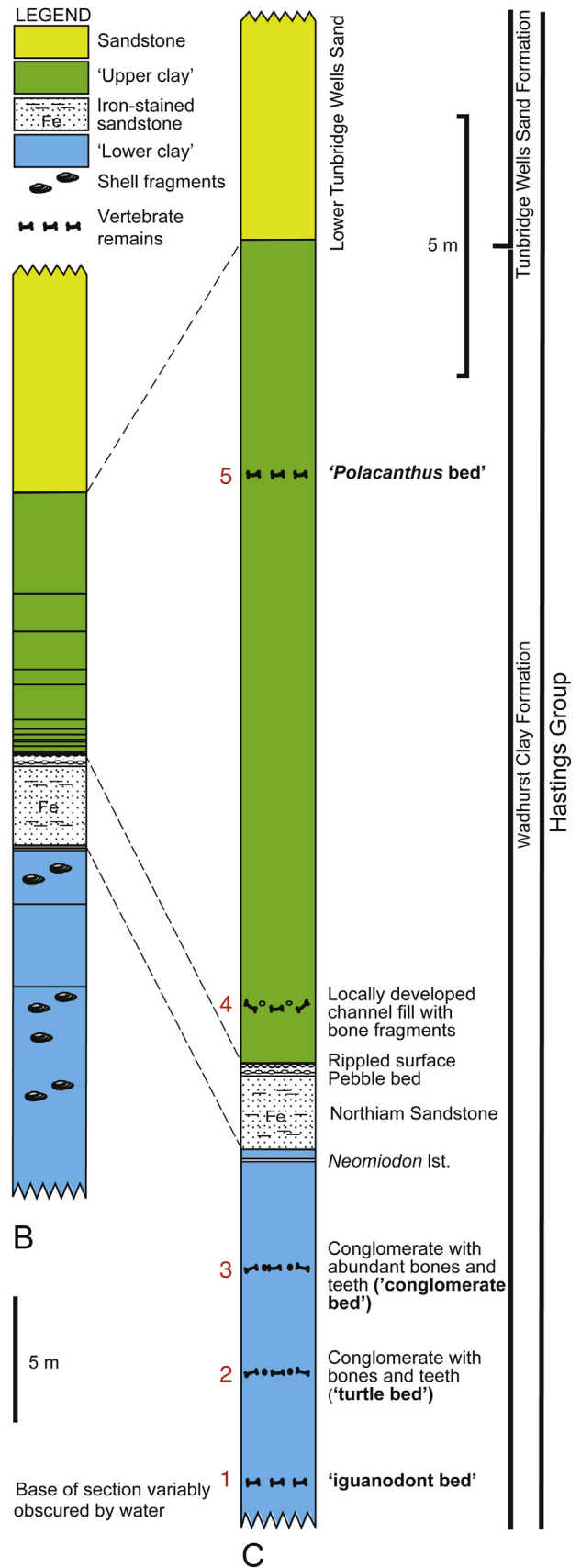
bones, identified as *Hylaeosaurus*, followed by a lizard jaw (Anon., 2001) from the same site. Day (1999) reported a piece of amber from the site. However, Ashdown Brickworks is most famous for the discovery of the so-called ‘Ashdown maniraptoran’, a contender for the world’s smallest adult dinosaur, represented in fact by a single posterior cervical vertebra of a maniraptoran theropod (Naish and Sweetman, 2011; Sweetman, 2011b). The find was also celebrated by the Royal Mail in 2013 in its special souvenir presentation pack to accompany the issue of ten first class ‘dinosaur’ stamps illustrated by John Sibbick (Austen, 2013).

Austen et al. (2010, p. 13) reported that the vertebrate material had “all been recovered from three main beds within the Wadhurst Clay of the Pevensey Pit.” In addition, since 2010, a further two bone-bearing beds have been identified, including the ‘iguanodont bed’ (Austen and Austen, 2013, 2014, 2015, 2016a, 2017, 2018). All five are summarised, from bottom to top (Figs. 3B, C, 4), as:

- 1 The ‘iguanodont bed’, a green clay up to 1 m thick, and the source of around 300 iguanodont bones representing two specimens of *Hypselospinus fittoni*, a juvenile and sub-adult (all accessioned in the collections at Bexhill Museum), occurring near the base of the Wadhurst Clay Formation.
- 2 The ‘turtle bed’, a bonebed normally 5–10 mm thick, but sometimes as much as 30 mm, and located 4 m above the ‘iguanodont bed’ and 8–9 m below the base of the Northiam Sandstone. Source mainly of the remains of turtles and crocodyliforms.
- 3 The ‘conglomerate bed’, a 50–60 mm thick bonebed, lying around 4 m below the base of the Northiam Sandstone. The bonebed is a matrix-supported conglomerate with clasts of clay ironstone and bone fragments, ranging in size from 2 to 40 mm, in a matrix of medium-grained mature quartz grains and grey clay. The bed is laterally continuous over 20 m or more, and its lower and upper margins are abrupt. In lithology it is similar to the Telham bonebed type described by Allen (1949). This bonebed is the main source of microvertebrate and larger remains, including sharks, bony fishes, salamanders, aigialosaurs, turtles, crocodyliforms, ornithischian dinosaurs including the iguanodont *Hypselospinus* and the ankylosaurs *Polacanthus* and *Hylaeosaurus*, and theropods. Austen et al. (2010, p. 13) reported more than 100 iguanodont teeth, as well as the teeth of a small bernissartiid crocodyliform. On an exposed surface at the same level, these authors reported lizard, plesiosaur, pterosaur, and theropod remains, and in a thin black band about 20 mm thick, located 30–40 cm above the conglomerate bed, some theropod teeth and vertebrae.
- 4 Bone-bearing horizon 2.3 m above the Northiam Sandstone (Hayward, 1996, p. 58).

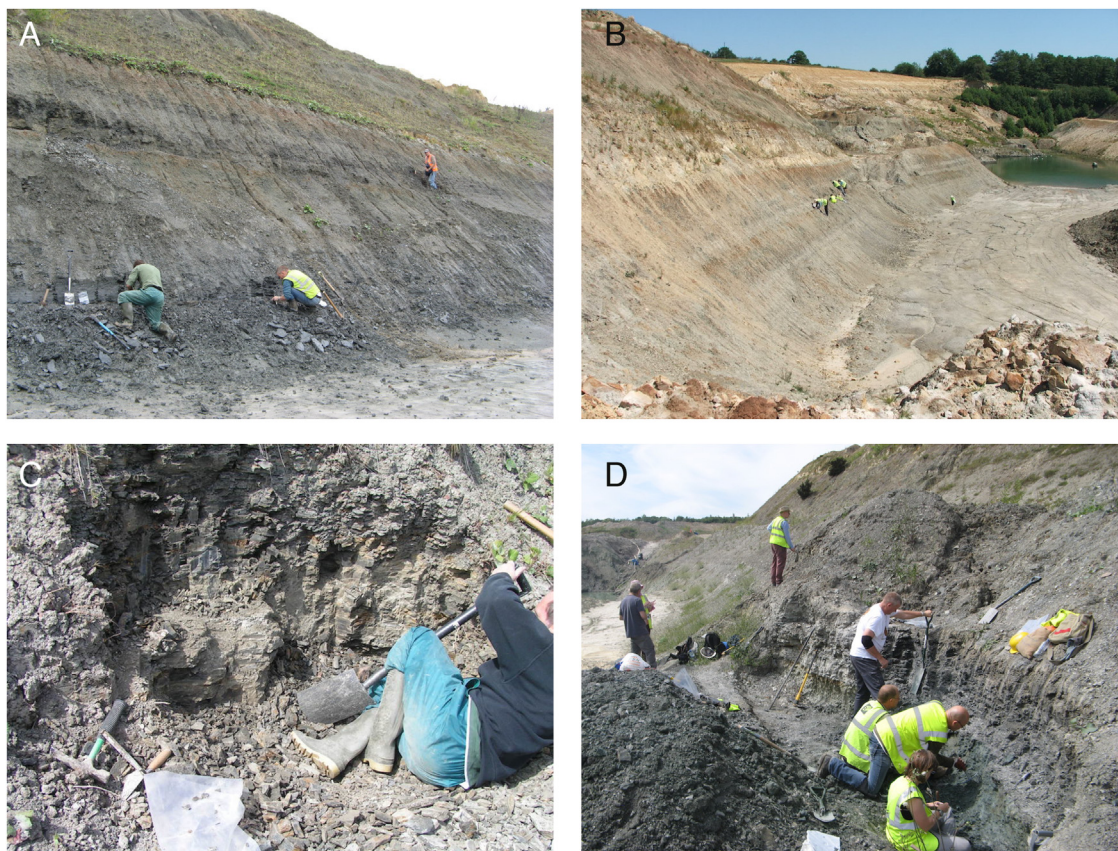
Age (Myr)	Stage	Lithostratigraphic divisions			
		Weald Sub-basin	Wessex Sub-basin		
125.0	Aptian (part)	Weald Clay Group		Vectis Formation	
	Barremian		Upper Weald Clay Formation	Wessex Formation	
129.4					
	Hauterivian		Lower Weald Clay Formation		
132.9		Hastings Group	Upper TWSF	Wealden Group	
	Valanginian		GCF		Wessex Formation (concealed)
			Lower TWSF		
			Wadhurst Clay Formation		
			Ashdown Formation		
139.8	Berriasian (part)			Purbeck Limestone Group	

A



**Fig. 3.** Wealden stratigraphy. (A) Stratigraphy of the Wealden Supergroup of southern England. Modified from [Batten \(2011\)](#). (B, C) Schematic lithological logs at Pevensey Pit, Ashdown Brickworks, showing information from a borehole at the site (B), and a log measured in the field by D.B., P.A.A. and Joyce Austen in February 2010 (C). The five vertebrate-bearing horizons are numbered 1–5. Modified from [Naish and Sweetman \(2011\)](#). Abbreviations: GCF, Grinstead Clay Formation; TWSF, Tunbridge Wells Sand Formation.





**Fig. 4.** Field photographs of the fossiliferous beds in Pevensy Pit, Ashdown Brickworks, near Bexhill-on-Sea. (A) People working on the 'turtle bed', below, and 'conglomerate bed', above in 2010. (B) Wider views of the quarry, and people working on the 'conglomerate bed' in 2006. (C) The 'Polacanthus bed' being exposed in 2009. (D) The 'iguanodont bed' being excavated about 2015, when the iguanodont bones were recovered. Photographs: A, B, D by P.A.A.; C by D.B.

5 The '*Polacanthus* bed', 45–60 cm thick and located 11–12 m above the top of the Northiam Sandstone, produced substantial portions of the skeleton of the ankylosaur *Polacanthus* (five vertebrae, a partial ilium, an armour spine, several scutes, four toe phalanges), as well as portions of a *Hypselospinus* skeleton (21 vertebrae, six chevrons, four phalanges, rib fragments), and teeth from two theropod taxa. Austen and Austen (2017) reported new excavations of this bone-rich horizon.

Austen et al. (2010, p. 14) note that the measurements set out above are from the north-west face of the Pevensy Pit, and that the measurements are very variable in different parts of the site. Naish and Sweetman (2011) provide a faunal list and details of the site.

A partial iguanodont skeleton was presented in some detail by Austen and Austen (2013), with a report of additional remains the year after (Austen and Austen, 2014), then amounting to over 100 individual bones. They also gave a report of further finds and a detailed site map of the distribution of the bones (Austen and Austen, 2015). This was followed by a further report of more finds (Austen and Austen, 2016a) and its identification as the Wealden iguanodontid *Hypselospinus fittoni*. At the completion of the excavations in 2016 around 300 bones had been recovered, representing at least two individuals.

Some of the Ashdown Brickworks fossils have been published already: Naish and Sweetman (2011) on an abraded cervical vertebra of a small theropod; Sweetman and Evans (2011a) on two forms of frog ilia and four forms of salamander vertebrae and other remains; Sweetman and Evans (2011b) on

two types of scincomorph lizard dentaries and other remains; Sweetman (2013) on numerous isolated durophagous teeth of an albuliform bony fish; and Blows and Honeysett (2014a) on three nodosaurid ankylosaur teeth, all from the 'conglomerate bed'. Further, Blows and Honeysett (2014b) reported the partial *Polacanthus* specimen from the 'Polacanthus bed'.

### 3. Materials and methods

#### 3.1. Sampling and processing of fossils

All the fossils described here were collected by D.B. between 1995 and 2017, and they are all accessioned in the collections of Bexhill Museum.

Many fossils were identified by picking over the exposures in the field, and simply washed clean of clay. In some cases, sediment samples were treated with hydrogen peroxide to aid disaggregation. Identifiable fossils were retained.

#### 3.2. Fossil identification and faunal composition

Fossil specimens were isolated from the sediment under a binocular microscope. The most complete and well preserved of these were digitally photographed using image stacking software and a Leica DFC425 C camera mounted on an optical microscope with multiple image stacking software. Typically, 20 digital images were taken and then fused, to minimise depth-of-field effects. Digital images were then processed using GIMP 2.10.8 software to remove backgrounds and adjust colour balance to be as realistic as possible.

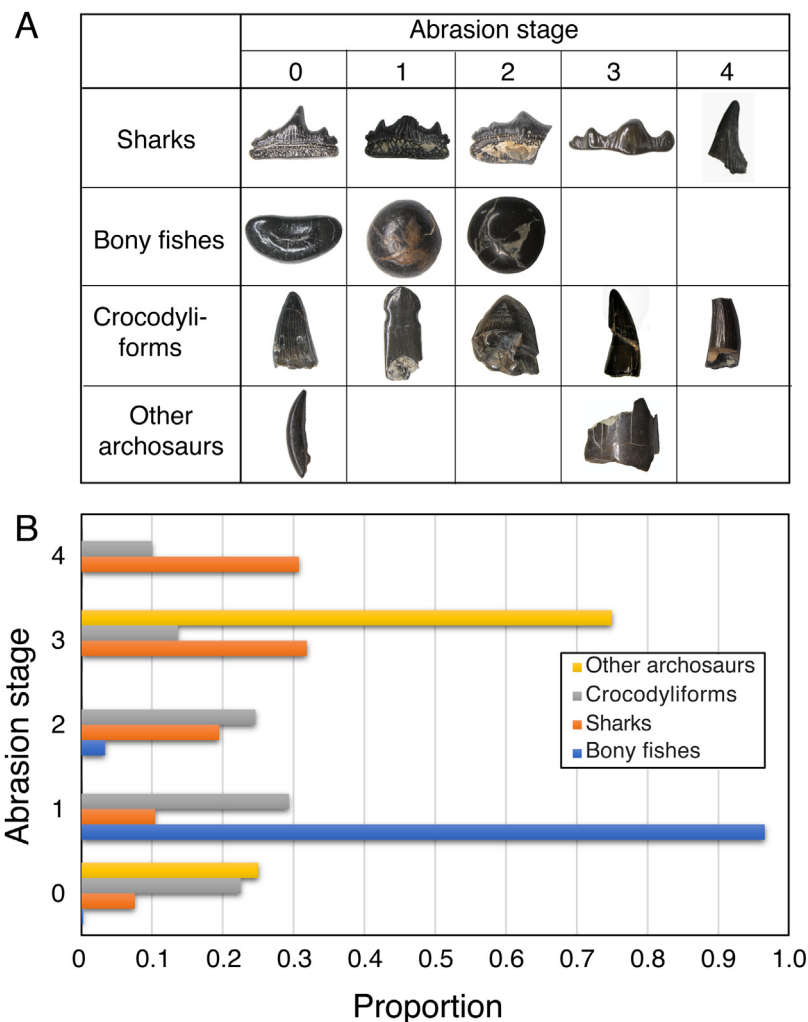
The average size of the microvertebrate fossils is small (<5 mm); the teeth are quite variable in size, ranging from a few millimetres for the smallest species, up to 30 mm for the largest. In sharks, tooth sizes are generally constant for each species, although those of the smallest shark, *Polyacrodus brevicostatus*, range from 1 to 10 mm. The largest shark teeth are those of *Polyacrodus* sp. which exceed 25 mm.

We provide some ecological information, including counts of fossils of each taxon, relative body sizes and possible positions in the food web. Evidence concerning body size and likely diets comes from more complete examples of the same taxa from other locations, as specified in the systematic descriptions. For the fishes, it is difficult to determine the full body size using only the teeth, particularly in the unidentified semionotiform where tooth size varies according to position in the jaw. The same goes for albuliforms which also have very variable tooth sizes. The fishes ranged from small to medium size, with body lengths of perhaps 10 cm to 3 m. For the crocodyliforms the total body lengths are known from complete specimens from elsewhere: the genus *Hulkepholis* (formerly *Goniopholis*) is the largest found at Ashdown Brickworks, being more than 4 m long, whereas bernissartiids did not exceed 1 m in length.

#### 4. Taphonomy

The specimens are generally moderately to heavily abraded, and many of the shark teeth lack roots. Actinopterygian and reptile teeth are also usually represented by shed crowns. During transport, the teeth would also frequently break up, losing their roots and/ or lateral cusps, in the case of multicusped shark teeth. Some specimens are in good condition, and these were used for identification and illustration. Altogether, we picked 2972 specimens, and of these, 2899 are teeth, excluding those on tooth plates of the unidentified semionotiform. More than half of the teeth allow positive identification to species level, which is important in attempting to work out a food web and providing some information on the palaeoenvironment.

The most abraded teeth are those of the sharks, including many in which all sculpture and cusp sharpness has been lost, although some examples are well preserved. The bony fish teeth are all very well preserved, especially those of the unidentified semionotiform. On the other hand, some albuliform teeth show cracked surfaces. The crocodyliform teeth are generally in good condition, and the only trace of abrasion is the removal of ornamentation or enamel.



**Fig. 5.** Taphonomic records of abrasion and completeness of specimens. (A) The standard scheme of numbered abrasion stages (Cook, 1995), from excellent condition (stage 0) to incomplete or heavily abraded (stage 4), showing examples of the Ashdown Brickworks fossils in each class. (B) Proportions of Ashdown Brickworks specimens in each of the five abrasion stages.

Bones are generally very well preserved. Many are broken, but along sharp edges with no trace of abrasion, and their structure and surface features are clearly visible. Breakage probably occurred at the time of collection; when larger bones are seen in situ, many have cracks and are recovered as fragments whether collected manually or using bulk screening techniques. As incomplete elements, it is difficult to determine the species, or even the part of the skeleton, represented. Larger bones are generally well preserved, exhibiting less abrasion and suggesting shorter transport distances than many of the smaller specimens such as teeth.

We summarise the condition of all specimens using standard abrasion stage indices, as documented by Cook (1995) for the Wealden. The five abrasion-completeness stages (Fig. 5A) range from essentially undamaged (stage 0) to heavily broken and/or abraded (stage 4). The abrasion indices, showing proportions of each taxon in each category (Fig. 5B) discriminate between an assemblage of forms with robust teeth (sharks, crocodyliforms) that show equivalent numbers in all abrasion stages, and those with small teeth and delicate scales (bony fishes), mainly in abrasion stage 1. The 'other archosaurs', including dinosaurs and a possible pterosaur, mainly occur in the rather damaged abrasion stage 3, which could indicate extra transport distances or subaerial weathering prior to transport.

The varying degrees of abrasion of different elements within the 'conglomerate bed' suggests a mixed history of transport. Those showing a high average degree of abrasion were almost certainly subject to numerous cycles of reworking as well as turbulent river transport (Cook, 1995). On the other hand, those showing a lower degree of abrasion represent material that has undergone fewer cycles of reworking, and those showing little or no abrasion were probably derived locally and have not been reworked. Allen (1949, 1975) suggested that the Ashdown and Cliff End bone beds were not only similar in age, but also in sedimentary provenance. Certainly, both were deposited under high-energy regimes, producing winnowed lag deposits. However, clast composition in the Ashdown Brickworks 'conglomerate bed' contrasts with that of the Cliff End bone bed. The lithology of the former suggests reworking of fluvial lags (which may have incorporated earlier shoreline lags) rather than shoreline lags (*pers. comm.*, Steve Sweetman, 2019). This could have occurred following an unusually high precipitation event, probably of short duration. It does not suggest reworking of lags by a non-marine transgression across the

Wealden flood plain, as suggested by Allen (1975). These contrasting hypotheses should be tested by further study of the Ashdown Brickworks and Cliff End bone beds.

## 5. Faunal descriptions

The remains found in the Ashdown Brickworks conglomerate bed are mainly teeth, more or less fragmentary or abraded, but for the most part identifiable to some extent. We present the fossils in sequence, describing the sharks, bony fishes, crocodyliforms, and dinosaurs. We include here only those previously undescribed fossils collected over the years by D.B. from the conglomerate bed, and do not repeat published descriptions of durophagous teeth of an albuliform bony fish (Sweetman, 2013), two forms of frog ilia and four forms of salamander vertebrae (Sweetman and Evans, 2011a), two types of scincomorph lizard dentaries and other remains (Sweetman and Evans, 2011b), the abraded cervical vertebra of a small theropod (Naish and Sweetman, 2011), and three nodosaurid ankylosaur teeth (Blows and Honeysett, 2014a). We note that additional specimens from the conglomerate bed are figured by Austen et al. (2010): *Bernissartia* tooth (fig. 33), *Theriosuchus* teeth (fig. 36), *Theriosuchus* maxilla (fig. 37), *Lepidotes* (= the unidentified semionotiform) teeth (fig. 44), and an unidentified fish or reptile jaw (fig. 45). These materials are, however, included in our later discussions of the food web.

### 5.1. Sharks

The most common vertebrates represented in the fauna are the sharks (chondrichthyans); all recorded species belong to the Family Hybodontidae, with *Egertonodus basanus* and *Planohybodus ensis*, and various species of the genus *Polyacrodus*, such as *Polyacrodus* sp., *P. parvidens* and *P. brevicostatus* (Duffin and Sweetman, 2011; Cappetta, 2012). Sharks today are generally the top predators in their food chains (Nelson et al., 2016), although the hybodonts may not have been, as they were small but agile predators whose diet was mainly soft-bodied animals (Cuny et al., 2001). A guide to the descriptive terminology used for hybodont teeth is provided in Figure 6.

#### 5.1.1. Hybodont cephalic spines

Despite the large number of hybodontid teeth from Ashdown Brickworks, only two complete cephalic spines have been found, as

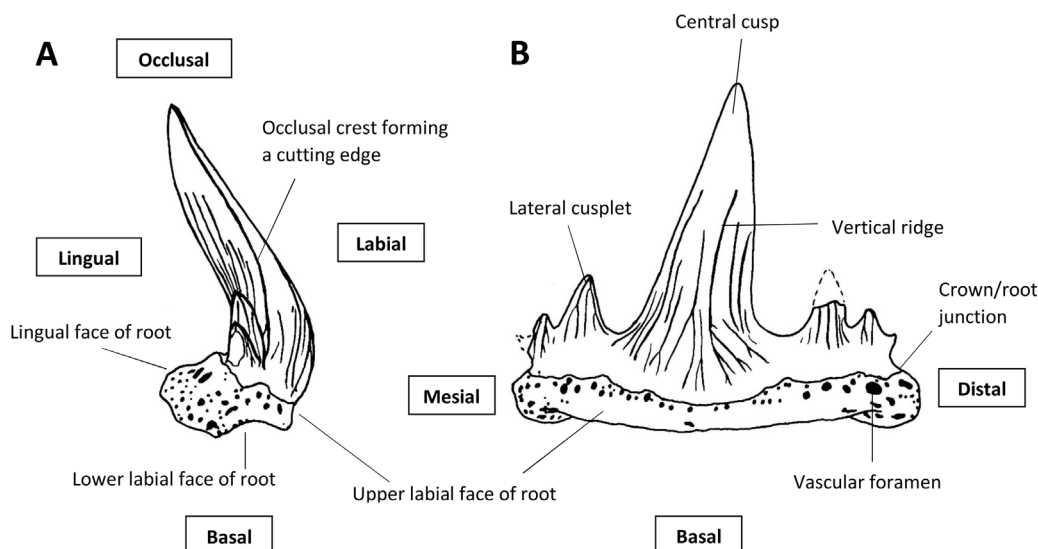
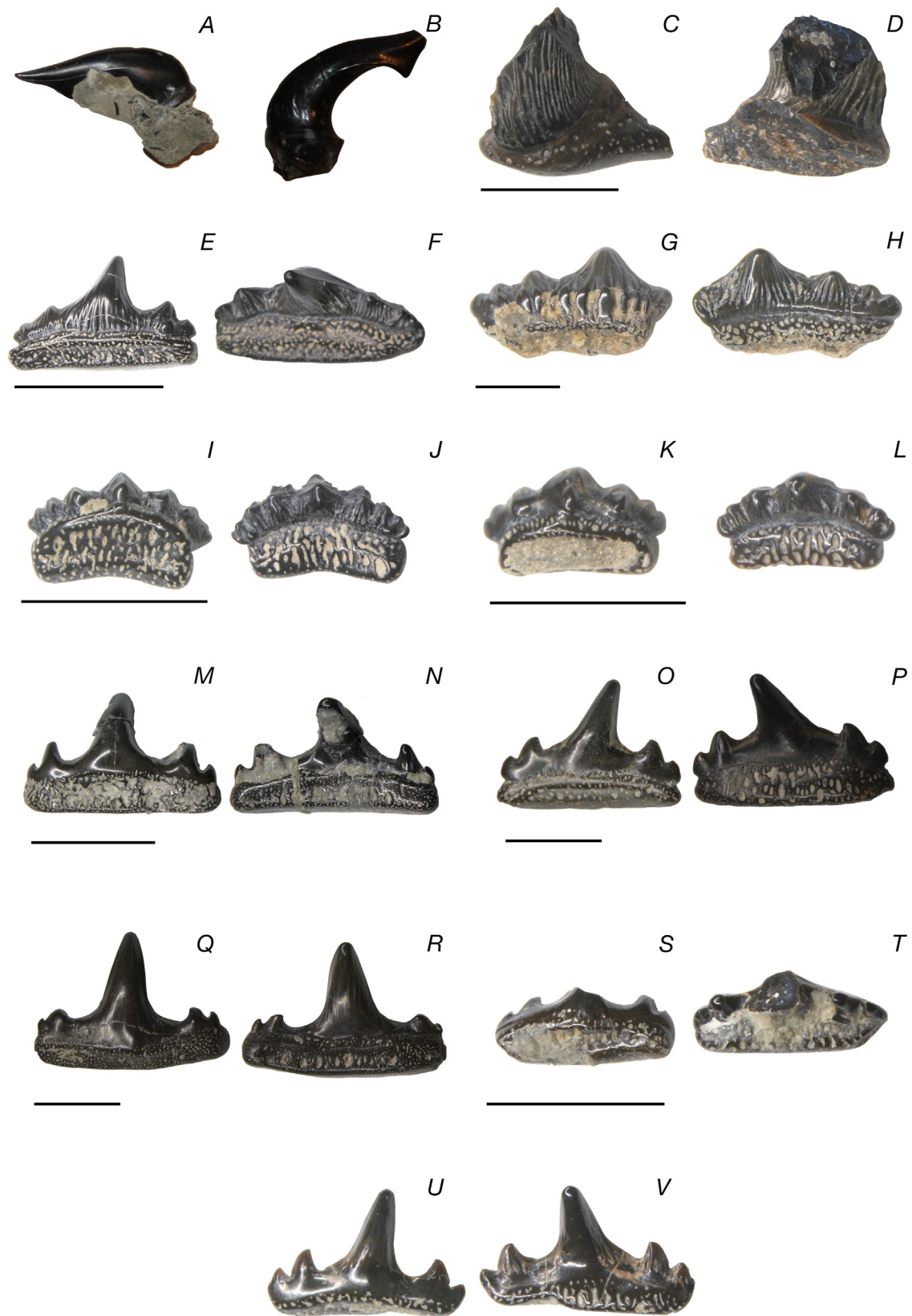


Fig. 6. Anatomical terms used in the description of hybodontid teeth in mesial (A) and lingual (B) views.





**Fig. 7.** Cephalic spines and teeth of hybodontiform sharks. (A–D) Cephalic spines of hybodonts (A, BEXHM 2019.49.2965; B, BEXHM 2019.49.2966; C, D, BEXHM 2019.49.1), in lateral (A, B), anterior (C) and posterior (D) views. (E, F) Tooth of *Polyacrodus parvidens*, BEXHM 2019.49.2, in labial (E) and apicolingual (F) views. (G–L) Teeth of *Polyacrodus brevicostatus* (G, H, BEXHM 2019.49.3; I, J, BEXHM 2019.49.4; K, L, BEXHM 2019.49.5) in labial (G, I, K) and lingual (H, J, L) views. (M–R) Teeth of *Planohybodus ensis* (M, N, BEXHM 2019.49.14; O, P, BEXHM 2019.49.40; Q, R, BEXHM 2019.49.16.) in labial (M, O, Q) and lingual (N, P, R) views. (S–V) Teeth of *Egertonodus basanus* (S, T, BEXHM 2019.49.37; U, V, BEXHM 2019.49.39) in labial (S, U) and lingual (T, V) views. The scale bars are 10 mm (A–D) and 5 mm (E–V).



well as a spine base. The two complete cephalic spines (Fig. 7A–B) each belong to a different hybodont taxon, both are smooth, unornamented, rather gracile, and the lateral crest seems to be longer than in *E. basanus*. In the latter, the crest dies out more quickly and encroaches onto the anterior surface forming an anterior ridge. One spine (Fig. 7A) terminates in a sharp point, the tip being roughly circular in cross section, whereas the other (Fig. 7B) terminates in a hook. We do not name these cephalic spines, although the hooked spine (Fig. 7B) is similar to that of *Asteracanthus ornatissimus* from the Oxford Clay (Maisey, 1982, fig. 16A–C) in the curve and shape of the terminal hook, although our specimen lacks the basal plate.

The cephalic spine base (Fig. 7C–D) shows part of the tripartite basal plate that was embedded in the skin, bearing deep pores, capped by the crown, bearing irregular longitudinal ridges. This specimen, although incomplete, compares well with that described for *Egertonodus basanus* (Maisey, 1983, fig. 24; Duffin and Sweetman, 2011, fig. 17.6A) in terms of its size, robust attachment to the basal plate, and heavily ridged ornamentation.

The cephalic spines of Hybodontidae are generally described as having a hook-like morphology, and one, or sometimes two pairs were located on the postorbital part of the skull. In some species, the spines are supported by a cartilaginous boss. Cephalic spines are specific to male specimens, and they were used during breeding to allow males to cling to females (Maisey, 1982, 1983).

#### 5.1.2. *Polyacrodus parvidens* (Woodward, 1916)

The teeth are multicuspid, possessing one main central cusp and two pairs of lateral cusplets (Fig. 7E–F). They measure 6–8 mm long mesiodistally, and the crown of the central cusp is 1.5–3.5 mm high. The first pair of lateral cusplets are around half the height of the central cusp, and the height of the second pair of lateral cusplets is slightly lower. The cusps are all inclined lingually from the crown/root junction but are not sigmoid or significantly curved in lateral view. The specimen (Fig. 7E–F) is an anterolateral tooth; the central cusp is slightly inclined distally. Main cusp height to root width has a 1:4 ratio on the measurable specimen, and the root is slightly longer than the crown mesiodistally. The crowns are strongly striated, with discrete vertical ridges running up the central and lateral cusplets from the crown/root junction. The ridges are more densely packed on the lingual face of the crown than on the labial face. Some attain the cusp apices, especially labially, and there are a few examples of ridge bifurcation basally. A labial node is developed at the base of the first distal lateral cusplet.

The moderately deep root makes up one third of the total tooth height at the position of the central cusp and projects lingually from the crown underside. The crown/root junction is clearly demarcated and relatively deeply incised. Labially, the root face is divided into a shallow upper portion and a deeper lower face which is concave in lateral view. The basal face of the root is flat. All faces of the root are punctuated with small, circular and occasional elongate vascular foramina without any special organisation (anaulacorhize vascularisation).

The taxonomy of hybodontoid sharks has become clearer in recent years, but some genera, including *Polyacrodus*, still require close attention and further clarification. We follow the generally accepted composition of the genus here (see Duffin and Sweetman, 2011; Cappetta, 2012, p. 66).

*Polyacrodus parvidens* is a well-established member of the Wealden chondrichthyan fauna, also being recorded from the Ashdown and Grinstead Clay Formations, and the Weald Clay in Sussex, and the Wessex and Vectis Formations on the Isle of Wight (Duffin and Sweetman, 2011, p. 209). Teeth and spines have been recorded from the Middle and Upper Purbeck Limestone Group of Dorset, and possibly also from the Lower Cretaceous of north-central Texas and Spain. Reworked examples have also been

recorded from the Aptian (Lower Cretaceous) Hythe Formation of Surrey (Patterson, 1966, p. 296; Thurmond, 1971; Winkler et al., 1989, p. 10; Bermúdez-Rochas, 2009, p. 676; Duffin and Sweetman, 2011, p. 209).

It has proved difficult to determine the habitats of hybodontoids because they could seemingly tolerate significant variations in salinity which allowed them to inhabit freshwater, brackish and marine habitats (Underwood and Rees, 2002). *Polyacrodus parvidens* has a dentition with both durophagous and gripping adaptations, allowing it to feed on both shellfish and bony fish. It is not certain whether each individual maintained a broad range of habitats and diets throughout its life, or switched during ontogeny, or whether different individuals were specialised (Landemaine, 1991; Underwood and Rees, 2002).

#### 5.1.3. *Polyacrodus brevicostatus* (Patterson, 1966)

The teeth are multicuspid, fairly symmetrical and relatively low-crowned, possessing one main central cusp and three pairs of lateral cusplets (Fig. 7G–L). The crowns measure 3.5–10 mm long mesiodistally and 1–4 mm high at the main cusp. The varying tooth shapes, variously symmetrical about the central cusp, reflect the position in the jaw. The first lateral cusplet pair is about half as long and high as the central cusp, with each subsequent mesial and distal cusplet being about half as wide and 80 percent as tall as the last. The cusps project lingually away from the crown/root junction. The ratio of the central cusp height to mesiodistal length for the whole tooth varies from 1:2.5 to 1:4.5. The teeth are heavily ornamented with a series of coarse vertical striations. These are distributed over the whole tooth, arising from the crown/root junction and ascending the crown to attain the cusp apices both labially and lingually. The ridges may bifurcate basally; bifurcations tend to occur most often at the crown shoulder and half way up the cusps. A series of strongly developed labial nodes is developed at the cusp bases on the labial face of the crown, the most prominent being found at the base of the central cusp.

The root forms approximately half the total tooth height at the central cusp, and its mesiodistal length is less than that of the crown; the mesial and distal margins of the crown project beyond the limits of the root. Small, circular vascular foramina are arranged in a single row along the very shallow upper labial face of the root, while the concave lower labial face of the root is much deeper possessing loosely organised elongate foramina. The basal face of the root is flat, while the lingual face is convex with strongly elongate vascular foramina.

*P. brevicostatus* has also been recorded from the Ashdown, Wadhurst Clay and Grinstead Clay formations (Hastings Group) and Weald Clay Group in Sussex, the Weald Clay Group in Surrey, and the Vectis Formation (Wealden Group) on the Isle of Wight (Patterson, 1966, p. 301; Duffin and Sweetman, 2011, p. 211).

*Polyacrodus brevicostatus*, in common with other species of the genus, has been found in brackish and freshwater environments (Vullo, 2005), and its sharp teeth suggest it fed on smaller fishes (Underwood and Rees, 2002).

#### 5.1.4. *Planohybodus ensis* (Woodward, 1916)

The multicuspid crown is fairly symmetrical with a labio-lingually compressed central cusp flanked by up to two pairs of lateral cusplets (Fig. 7M–R). These tooth crowns range in size from 4.5 to 16 mm long mesiodistally and 2–10 mm high at the central cusp. The inner lateral cusplet ranges from half to a quarter of the height of the central cusp, while the outermost cusplet is half to a quarter the height of the inner lateral cusplet. The cusps project lingually away from the base and the tooth height at the central cusp to mesiodistal length of the tooth has a ratio of 1:1.4 to 1:2.5. The crowns are striated, with mostly non-bifurcating vertical

ridges restricted to the base of the labial face and the flanks of the lateral cusplets.

The root forms up to one third of the total tooth height at the central cusp, clearly separated from the crown by an incised crown/root junction, and the same length as the crown mesiodistally. The basal face of the root is flat, and the labial face is divided into a shallow upper labial root face and a deeper lower face. The lingual face of the root is convex. The vascularisation is anaulacorhize with small circular and larger elongate vascular foramina organised into rough longitudinal rows.

The genus *Planohybodus* was established by Rees and Underwood (2008) for three species of hybodonts mainly from southern England, *P. peterboroughensis* from the Oxford Clay (Callovian), *P. grossiconus* from the Stonesfield Slate and other horizons (Bathonian), and *P. ensis* from the Berriasian–Barremian. *Planohybodus* teeth are characterised by high and wide, somewhat flattened central cusps with well-developed cutting edges formed by the occlusal crest running through the cusp apices from the mesial to the distal ends of the crown, and bearing an ornamentation of short, simple folds.

The Ashdown Brickworks teeth are somewhat worn, and do not show the occasional serrations on the cutting edges recorded in other specimens of *P. ensis* (Rees and Underwood, 2008, p. 230; Bermúdez-Rochas, 2009, p. 679). *P. ensis* has been recorded from the Purbeck Beds of Dorset, the Ashdown, Wadhurst Clay and Grinstead Clay formations (Hastings Group) in Sussex, the Wadhurst Clay Formation in Kent, and the Lower Cretaceous of northern Spain (Patterson, 1966, p. 293; Bermúdez-Rochas, 2009, p. 679; Duffin and Sweetman, 2011, p. 211).

*Planohybodus ensis* has a dentition which is close to the cutting type, and with some species measuring 2–3 m long, this suggests that it fed on larger prey, snatching smaller prey whole or tearing flesh from larger fishes and reptiles (Cappetta, 1986, 2012; Rees and Underwood, 2008, p. 141; Bermúdez-Rochas, 2009, p. 684).

#### 5.1.5. *Egertonodus basanus* (Egerton, 1845)

These teeth are multicuspid, with the lingually inclined central cusp being flanked by either two or three lateral cusplets (Fig. 7S–V). The central cusp shows consistent proportional length at the base but varying between a straight or concave edge from the base to the tip. The tooth crowns vary in mesiodistal length from 6 to 11 mm and from 3 to 8 mm high at the central cusp. The exact proportions of the lateral cusplets to the central cusp cannot be determined because of wear to the specimens. Similarly, the lack of complete teeth in the collection makes the tooth height to mesiodistal length ratio impossible to calculate. The tooth crowns are striated on the lower quarter to two thirds of the labial face, slightly extending onto the base, while the lingual face of the cusps is striated for its full height. The vertical ridges commonly bifurcate basally, and occasionally apically as well.

*Egertonodus* was established by Maisey (1987) for *Hybodus basanus* from the Early Cretaceous of the Isle of Wight (or possibly from near Hastings; Rees and Underwood, 2008, p. 122) and possibly also *Hybodus fraasi* from the Late Jurassic of southern Germany. The genus was first diagnosed by cranial characters. Rees and Underwood (2008, p. 122) established four dental characters unique to *Egertonodus*, and which discriminate *E. basanus* from *Hybodus reticulatus*, namely sigmoidally curved cusps in anterior teeth, labially displaced and strong cutting edges that provide a flattened labial surface of the central cusp, high slender lateral cusplets, and moderate ornamentation.

The teeth of *E. basanus* are distinguished from those of *P. ensis* in having a more slender central cusp with a longer base at its contact with the remainder of the crown, a less flattened labial face, and an ornament that comprises more extensive, more commonly bifurcating vertical ridges. Vertical ridges ascending the central

cusp in teeth of *P. ensis* are generally restricted to the lower third of the cusp.

*Egertonodus basanus* may have fed on softer prey than other hybodonts (Rees and Underwood, 2008, p. 144), using its high, slender teeth to pierce cephalopod skin or thin scales of smaller sharks and actinopterygians. The species is most often found in sediments from former lagoon and fluvial environments, and it may have been migratory (Duffin and Sigogneau-Russell, 1993).

### 5.2. Bony fishes

Actinopterygians are represented by the largest number of teeth in the collection. The most abundant teeth are those of a *Lepidotes*-like member of the Family Semionotidae. The second most common teeth are those of an albuliform.

#### 5.2.1. Undetermined semionotiform

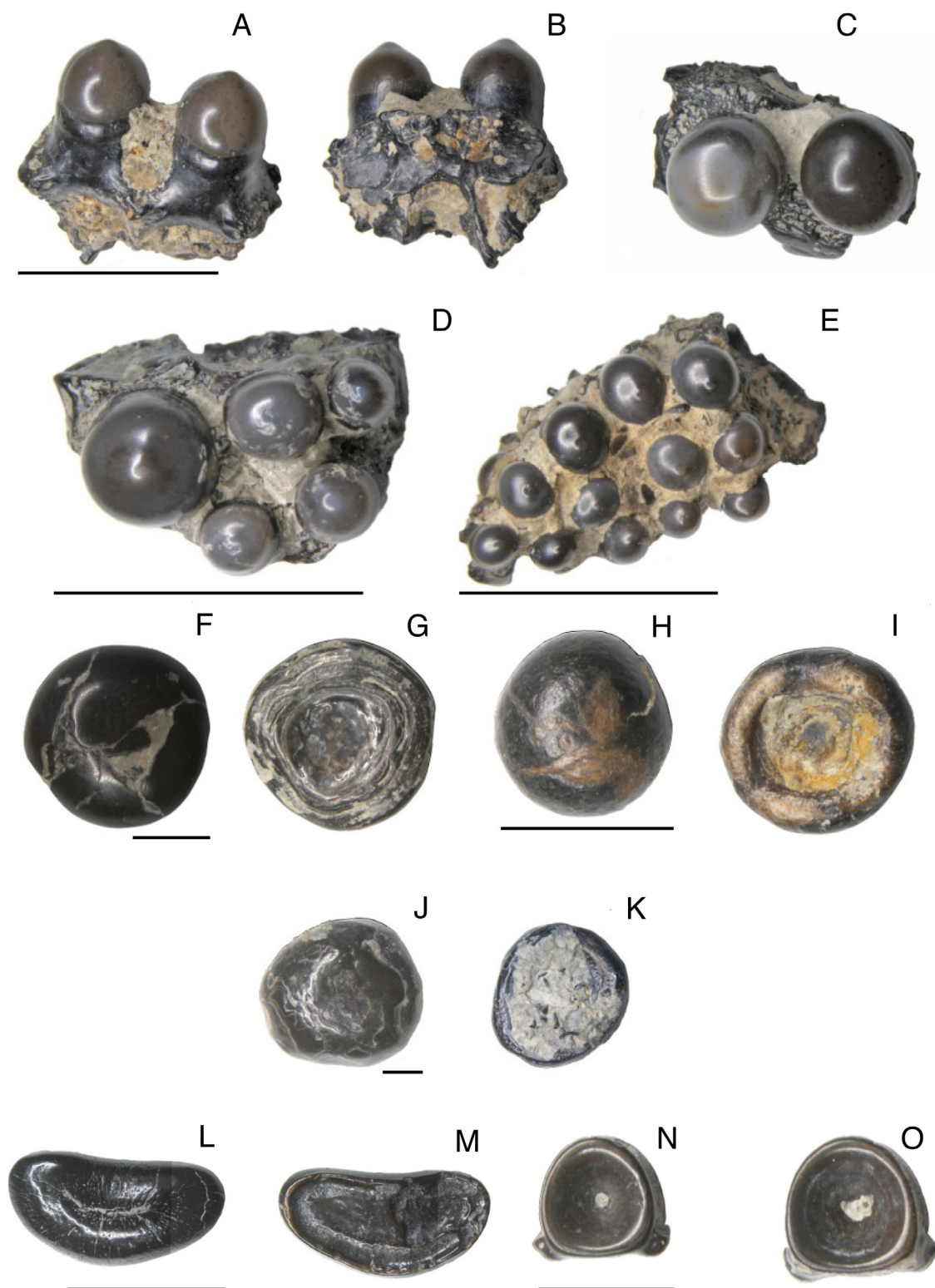
Teeth of a currently undetermined semionotiform include both isolated crowns and clusters of closely-packed unornamented teeth still embedded in their bones of attachment (Fig. 8A–E). Individual teeth are quite small, 0.3–0.9 mm maximum dimension in occlusal view, and circular to oval in occlusal view, usually tumid and dome-shaped with a central tubercle at the crest of the crown. The bases are more-or-less constricted, with a very short pedicle anchoring the tooth to the bone. In more complete specimens (Fig. 8D–E), teeth are arranged in a series of parallel lines, with the smaller teeth located toward the presumed labial margin of the bone.

Hemispherical to rather obtuse conical teeth from the Mesozoic in general, and the Wealden in particular, have generally been ascribed to the genus *Lepidotes*, which has become something of a wastebasket taxon. The genus *Scheenstia* was erected for specimens of a basal semionotiform neopterygian from the Late Jurassic of southern Germany (López-Arbarello and Sferco, 2011). It subsequently became clear that several species originally included in *Lepidotes* should be transferred to *Scheenstia*, based upon a suite of shared characters (López-Arbarello, 2012, p. 35). The well-established *Lepidotes mantelli*, relatively common in Wealden deposits, was one such species. It should be noted that there is currently no means of distinguishing between the teeth and fragmentary tooth plates of *Scheenstia* and *Lepidotes*. Because of this absence of taxonomically useful characters in isolated tritoral teeth and tooth-bearing bone fragments, we prefer to record the Ashdown Brickworks material as an as yet unidentified semionotiform, accepting that subsequent revision might result in them being allocated to *Lepidotes* and/or *Scheenstia*.

The most common fish tooth specimens obtained from the conglomerate bed at Ashdown Brickworks are those of the semionotiform, whose numbers far exceed all other species (53% of all specimens and 93% of all actinopterygian specimens). The morphology of the teeth suggests a diverse durophagous diet, matching the diversity of their environments. The semionotiform was not at the top of its food chain since it was likely the prey of predators such as crocodyliforms, sharks and piscivorous dinosaurs such as *Baryonyx walkeri*.

#### 5.2.2. Unidentified albuliform

The teeth we have tentatively assigned to an unidentified albuliform (Fig. 8F–K), although possessing a circular to sub-circular outline in occlusal view, are much thinner and flatter than those of the semionotiform described above. Our specimens have smooth crowns, whereas those described by Sweetman (2013) have rugose crowns, but the crown undersides (Fig. 8G, I) are very similar to those figured by Sweetman (2013, Fig. 3R).



**Fig. 8.** Teeth of bony fishes. (A–E) Teeth of an unidentified semionotiform, traditionally assigned to *Lepidotes*, forming partial tooth plates (A, B, BEXHM 2019.49.41; C, BEXHM 2019.49.42; D, BEXHM 2019.49.43; E, BEXHM 2019.49.44.) in lateral (A, B) and occlusal (C–E) views. (F–K) Teeth of an albuliform (F, G, BEXHM 2019.49.91; H, I, BEXHM 2019.49.92; J, K, BEXHM 2019.49.93) in occlusal (F, H, J) and basal (G, I, K) views. (L, M) Tooth of *Ocloedus* sp. (BEXHM 2019.49.176) in occlusal (L) and basal (M) views. (N, O) Actinopterygian vertebra (BEXHM 2019.49.177) in anterior (N) and posterior (O) views. The scale bars are 10 mm (D–E, L–M) and 5 mm (A–C, F–K, N–O).

Sweetman (2013) described numerous circular albuliform teeth from the Wadhurst Clay conglomerate bed at Ashdown Brickworks, ranging in diameter from 0.8 to 5.9 mm, but mostly in the 2–3 mm range. In that the teeth are circular, and with replacement teeth stacked directly below functional teeth, they can be assigned

to Phyllodontidae and possibly to the Subfamily Phyllodontinae, as discussed by Sweetman (2013). Like the unidentified *Lepidotes*-like semionotiform, albuliforms have teeth embedded in the jaw bones and palate. These teeth are circular in shape, fairly flat and thin (Sweetman, 2013; Cavin, 2018).



The Albuliformes are a living order, comprising 11 species in three genera of bonefishes, and 30 extinct genera, dating from the Cretaceous and Cenozoic. The Ashdown Brickworks specimens are the oldest representatives of the clade. Extant bonefishes are 40–100 cm long, have their mouth under the tip of the snout and they can breathe with a modified swim bladder. They are adapted to life in the brackish waters of tropical coastal areas, and they feed in the shallow sand and mud flats on benthic organisms, including animals with carapaces, vertebrates, invertebrates, such as worms, molluscs, shrimp and crabs. In addition to the dentition, fossils from elsewhere indicate that the albuliforms had a fairly low snout, suitable for digging in the river bed (Michaut, 2017).

### 5.2.3. *Ocloedus* sp

The teeth of *Ocloedus* sp. (formerly *Coelodus* sp.; Poyato-Ariza and Wenz, 2002) are mesiodistally longer than wide (typically, 17 mm long and 7.5 mm wide). The teeth are domed, reflecting a durophagous diet, showing a characteristic arched oval shape in occlusal view (Fig. 8L–M). The occlusal dome exhibits a central longitudinal depression, and the crown sits low on the bone. The enamel shows radiating wrinkles in the rough and depressed central area (Fig. 8L).

*Ocloedus* is a pycnodont with palatal teeth that are low-crowned and adapted to durophagy (Vullo, 2005). They also possess incisiform anterior marginal teeth on the dentary and premaxilla. Pycnodonts were benthic foragers that could bite or nip their prey and use suction to draw in food fragments (Kriwet, 2001). They have been recorded in freshwaters, such as lakes and some streams, but also in coastal marine environments such as estuaries (Vullo, 2005). In freshwater, their diet was probably mainly small organisms such as bivalves, gastropods and some aquatic plants (Poyato-Ariza, 2005). Collectively, pycnodonts were omnivorous with a broad range of prey, but individual specimens show specialisation in that individual specimens show gut contents of single species, such as spines of echinoderms or shells of bivalves. The flat-sided, tall body morphologies of pycnodonts were not adapted to strong currents or even pelagic environments, but they are reported from a wide range of marine, brackish and freshwater environments (Poyato-Ariza, 2005). Despite the large number of teeth, only a single pycnodont vertebra has been found, and identification to species level is therefore problematic.

## 5.3. Crocodyliforms

We have identified three species of crocodyliforms in the collection, the goniopholidid *Hulkepholis* sp., the atoposaurid *Theriosuchus pusillus*, and a bernissartiid. These species are represented by teeth but also some fragments of bone, mainly from the skull. The atoposaurid and bernissartiid were quite small, between 0.5 and 2 m in length, whereas *Hulkepholis* could reach 4 m. They were excellent swimmers but also agile and well adapted to terrestrial and underwater movements (Mojon, 2006).

Most extant crocodiles are at the top of their food chains, despite evidence of interactions between marine crocodiles and bull sharks (some of the only extant euryhaline sharks) and alligators killed by jaguars. Furthermore, it is quite possible that the smaller of the Wealden crocodyliforms were prey for larger predators including *Hulkepholis* and dinosaurs.

### 5.3.1. *Hulkepholis* sp

The teeth of *Hulkepholis* are very similar to those of extant alligators. They are variable in size, with crown height ranging from 15 to 40 mm. They are conical, broad labio-lingually and slightly curved labially (Fig. 9A–E), with a circular cross section. Crowns are ornamented with grooves and ridges extending from the base to close to the apex, and which are more elongated on the

lingual surface. Individual grooves are spaced regularly about 0.3–0.5 mm apart.

*Hulkepholis* is widely found in non-marine facies in Western Europe, from the Late Jurassic to Early Cretaceous (Salisbury et al., 1999). It occurs mainly in fluvial, lagoonal and lacustrine deposits, relating to their assumed amphibious lifestyle (Buscalioni et al., 2013). It has been suggested that this crocodyliform was a large durophage, not a carnivore (Pictet, 1845).

### 5.3.2. *Theriosuchus* sp. indet. (Owen, 1879)

The dentition is heterodont, and teeth show pseudocaniniform morphology, including lanceolate teeth with low crowns that are more or less symmetrical. Anterior teeth are slender with slightly labio-lingually flattened conical shapes (Fig. 9F–G), and they bear weak mesial and distal carinae that lie lingual to the mesiodistal plane. The labial surface of the crown is convex whereas the lingual side is almost flat to slightly convex. In cross section, all teeth are longer than wide. Posterior teeth are much smaller in height (Fig. 9H–K), with a marked constriction between crown and root, labio-lingual compression of the crown and radial distribution of lingual striations and mesial and distal carinae (Tennant et al., 2016). The base is narrowed with an ornamentation of parallel flutes. The enamel ornamentation on the surface of the teeth gives a false impression of serration (Young et al., 2016).

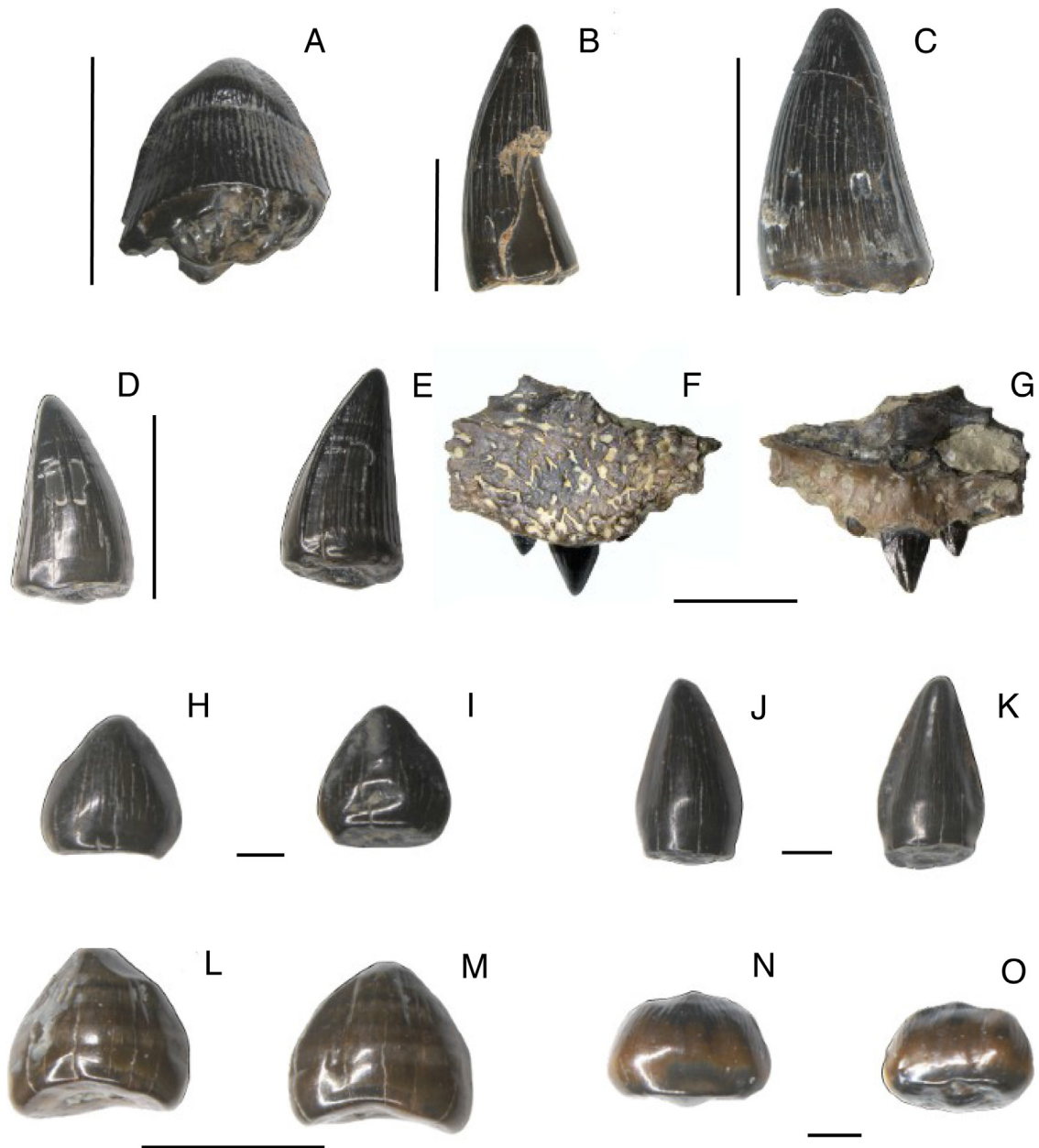
Some of the specimens from Ashdown Brickworks occur in fragments of jaw bone (Fig. 9F–G), and in these, there is a progressive reduction in size of the alveoli from 4th to 6th (Tennant et al., 2016). Complete specimens of *Theriosuchus* from elsewhere show several tooth morphotypes, these being, from front to back of the jaws, slender and conical teeth, lanceolate teeth, labiolingually compressed teeth, and low-crowned teeth (Salisbury and Naish, 2011; Tennant et al., 2016). Our examples appear to represent the middle two categories.

The atoposaurids have long been considered to have been exclusively terrestrial (Buscalioni and Sanz, 1990), although Buffetaut (1975) suggested that *Theriosuchus* might have had an amphibious mode of life, similar to that of extant crocodilians. The remarkable degree of heterodonty suggests that *Theriosuchus* was able to exploit a wide range of trophic resources, including small mammals, insects, eggs, fishes, and plants (Tennant et al., 2016, p. 889), providing support for Buffetaut's (1975) suggestion.

### 5.3.3. Bernissartiid crocodyliform

The molariform tooth crowns (Fig. 9L–O), from 2 to 5 mm tall, take the form of globular buds and are small, with longitudinal ridges from the base of the crown to the apex (Buffetaut and Ford, 1979; Buscalioni and Sanz, 1990; Vullo, 2005). The Ashdown Brickworks specimens are abraded, so the ridges are partly worn away, especially from the apex; this represents dietary attrition as well as abrasion.

Until recently, teeth of this kind would have been assigned to the species *Bernissartia fagesii*, but Sweetman et al. (2015) described a new genus of bernissartiid crocodyliform from the Wessex Formation and demonstrated that isolated teeth are only diagnostic at family level. Bernissartiids were small crocodyliforms, from 0.5 m to 1 m in length, and with the peculiarity of having a short (brevirostral) snout. They were heterodont, with anteriorly located caniniform teeth, which are pointed and procumbent, and posteriorly located labio-lingually compressed molariform teeth bearing mesial and distal carinae. We have identified only molariform teeth. *Bernissartia* possessed a dorsal dermal armour comprising two rows of rectangular scutes, and a ventral armour of several nested rows but not linked together (Buffetaut, 1975). The globular posterior teeth of bernissartiids facilitated the grinding of shells of freshwater molluscs, including bivalves and gastropods (Buffetaut and Ford, 1979).



**Fig. 9.** Teeth of crocodyliforms. (A–E) Teeth of *Hulkepholis* sp. (A, BEXHM 2019.49.178; B, BEXHM 2019.49.179; C, BEXHM 2019.49.184; D, E, BEXHM 2019.49.185) in labial (A, C, D), and lingual (B, E) views. (F–K) Teeth of *Theriosuchus* sp.: mid-series teeth in a jaw (probably maxilla) fragment (F, G, BEXHM 2019.49.229), posterior teeth (H, I, BEXHM 2019.49.231), and anterior teeth (J, K, BEXHM 2019.49.232) in labial (F, H, J) and lingual (G, I, K) views. (L–O) Teeth of a bernissartiid crocodyliform (L, M, BEXHM 2019.49.239; N, O, BEXHM 2019.49.240) in labial (L, N) and lingual (M, O) views. The scale bars are 10 mm (A–C, F–G), 5 mm (D–E, L–M) and 1 mm (H–K, N–O).

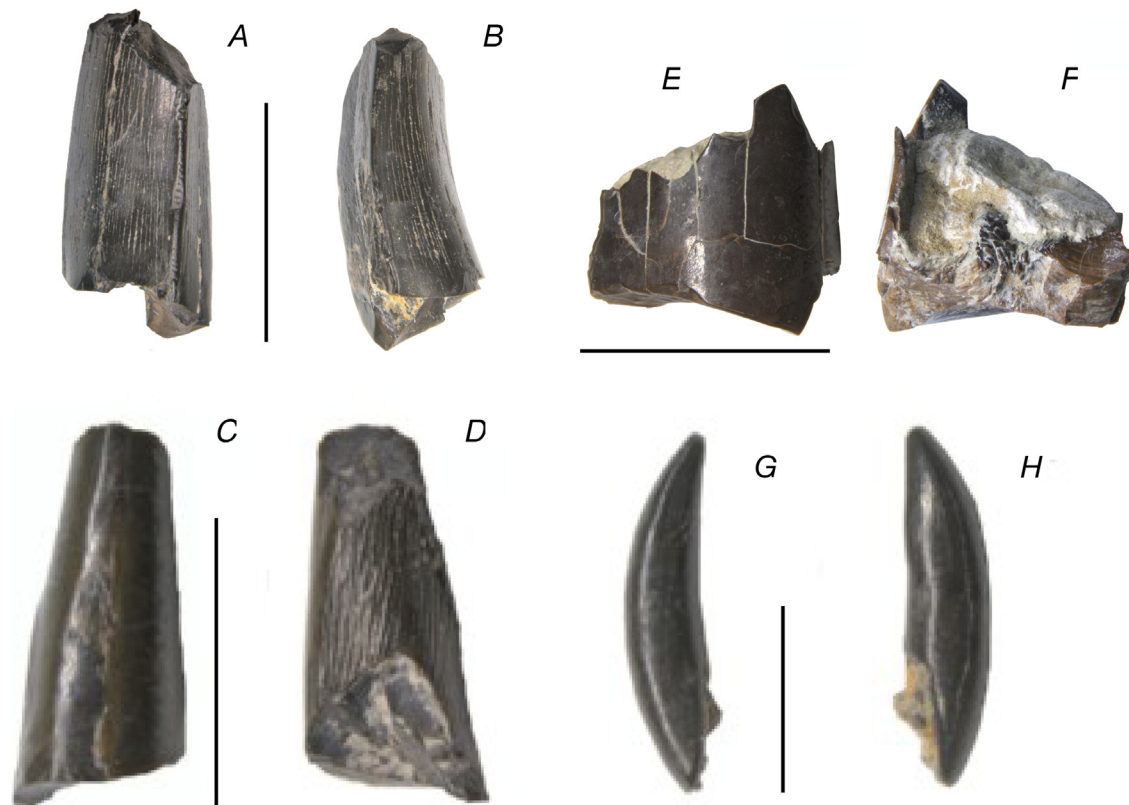
#### 5.4. Other archosaurs

Other archosaurs represented in the 'conglomerate bed' at Ashdown Brickworks include teeth belonging to theropod dinosaurs (*Baryonyx*, allosauroid) and possibly pterosaurs.

The teeth of spinosaurids assumed to be those of *Baryonyx walkeri* are commonly found in the Wealden of Britain, and coeval deposits such as the Early Cretaceous of several countries in North Africa. BEXHM 2019.49.251 (Fig. 10A–B) is incomplete but shows the characteristic sub-rounded cross section (anterior and posterior margins less well defined than in teeth of other large theropods), and the slightly wrinkled enamel. Another partial tooth, likely from a dinosaur, shows wrinkled enamel (Fig. 10C–D), and so might also come from a spinosaurid such as *Baryonyx*.

Another large theropod is represented by broken tooth fragments (Fig. 10E–F), and it is identified as an unnamed allosauroid, simply because of its size, typical theropod shape, and geological age.

*Baryonyx* is a spinosaurid, known from reasonably complete skeletal remains from the Barremian Upper Weald Clay Formation of Surrey (Charig and Milner, 1986, 1997). The mode of life of spinosaurids has been debated since the first specimens were collected in north Africa in 1912. Current views (Arden et al., 2019; Lakin and Longrich, 2019) and oxygen isotope data (Amiot et al., 2010) confirm that they were semi-aquatic and primarily piscivorous, with elevated nostrils and orbits, as well as long, slender snouts like those of crocodiles, lined with teeth capable of piercing fish (Cuff and Rayfield, 2013). Direct evidence from earlier



**Fig. 10.** Teeth of dinosaurs and a possible pterosaur. (A, B) Tooth of *Baryonyx* sp. (BEXHM 2019.49.251) in two side views. (C, D) Possible tooth of *Baryonyx* sp. (BEXHM 2019.49.253) in labial (C) and lingual (D) views. (E, F) Tooth of allosauroid theropod (BEXHM 2019.49.252) in two lateral views. (G, H) Elongate tooth of possible pterosaur (BEXHM 2019.49.254) in labial (G) and lingual (H) views. The scale bars are 10 mm (B–C) and 5 mm (A, D–G).

discoveries of *Scheenstia* in the gut contents of *Baryonyx* (Charig and Milner, 1997), and the morphology of the claws that were perhaps adapted to dealing with slippery prey, indicates that it fed on fishes, including the largest, 2–3 m long specimens.

One slender, curved, 19 mm long tooth (Fig. 10G–H) could belong to a large pterosaur. It resembles the tooth from Ashdown Brickworks illustrated by Austen et al. (2010, fig. 27) and identified as the tooth of an unidentified ornithocheirid pterosaur. It is also similar to the tooth of the ornithocheirid *Caulkicephalus* illustrated by Sweetman and Martill (2010, Fig. 8).

## 6. Discussion

### 6.1. Wealden environment and climate

There have been many studies of the sedimentology and inferred climates of the English Wealden (Allen, 1975; Allen et al., 1998; Haywood et al., 2004; Radley and Allen, 2012). Allen (1975, p. 389) memorably summarised the Wealden environments as “Large expanses of alluvial plain were bare of trees and bushes, but supported rich growths of herbaceous pteridophytes where deposition and erosion became inactive temporarily. Herds of dinosaur travelled freely across the basin and maintained themselves in it. The climate was warm, with marked wet and dry seasons and, possibly, diurnal rhythms in precipitation.” During the Early Cretaceous Pangaea had split, with the opening of the Atlantic and the breakup of Gondwana. Southern England lay at a latitude of 30–35°N, equivalent to that of north Africa today.

The Ashdown Brickworks succession indicates a climate that was close to that of present subtropical regions, which is true of the English Wealden in general. Summers were times of

high aridity and temperatures of up to 40 °C, alternating with milder periods during the spring and autumn (12 to 16 °C) and a gentle winter, when temperatures might have descended to 4–8 °C (Allen et al., 1998). These relatively large seasonal temperature changes between winter and summer involved heavy rainfall during periods of transition. From March to May, there may have been a precipitation rate of 4–8 mm per day, and then from December to February perhaps 16 mm per day at most. During arid periods, the rate of evaporation was sufficient to cause powerful fires (Haywood et al., 2004).

This climate model is supported by the Wealden fossil flora, which is similar to that of modern ecosystems adapted to the risk of fires. Indeed, the Wealden plant groups match those found in tropical areas today (Camus et al., 1991). In addition, Wealden plants likely combined rapid reproductive rates with the production of large quantities of spores, leading to high rates of generation turnover and reproductive capacity. Germination of spores at the beginning of the wet season would have compensated for possible losses during dry periods (Klekowski, 1979). Growth rings in trees confirm the alternation between dry and wet periods (Watson and Alvin, 1996). The fossil insects of the Wealden also provide a test of the environmental model. In particular, insect groups such as Isoptera (termites) and Blattodea (cockroaches) occur in the Wealden (Jarzembowski, 1995), and today these proliferate in tropical zones.

The Ashdown Brickworks conglomerate was deposited in a rapidly flowing river, one of those that punctuated the slower deposition of mudstones and siltstones, according to Allen's (1975) environmental model. Variations of sedimentation through the Wadhurst Clay Formation shows the advance and retreat of small fan-deltas into a freshwater to low salinity lake, with reworking of sediment along pebble shorefaces and strandlines, generating



bone beds in some instances, and incorporating sedimentary and plant debris from a range of settings. Weak marine influence was widespread in the Wadhurst Clay, but not so much from the proximity of a nearby coast, which in fact lay many tens of kilometres north, but because the Weald Sub-basin was open and allowed occasional marine influxes from one or more sources at some distance. Among the fishes and reptiles, we have identified taxa that indicate two environments, lagoonal/ lacustrine and freshwater fluvial zones. The fishes and crocodyliforms are all typical of fresh and brackish waters, with no marine species. The dinosaurs confirm this, with the allosauroid, and other Ashdown dinosaurs such as *Iguanodon* and *Polacanthus*, being primarily terrestrial, and *Baryonyx* also recognised as a freshwater piscivore. The Ashdown lissamphibians also demonstrate freshwater habitats and the scincomorph lizards terrestrial habitats (Sweetman and Evans, 2011a,b).

## 6.2. Relative abundances of species

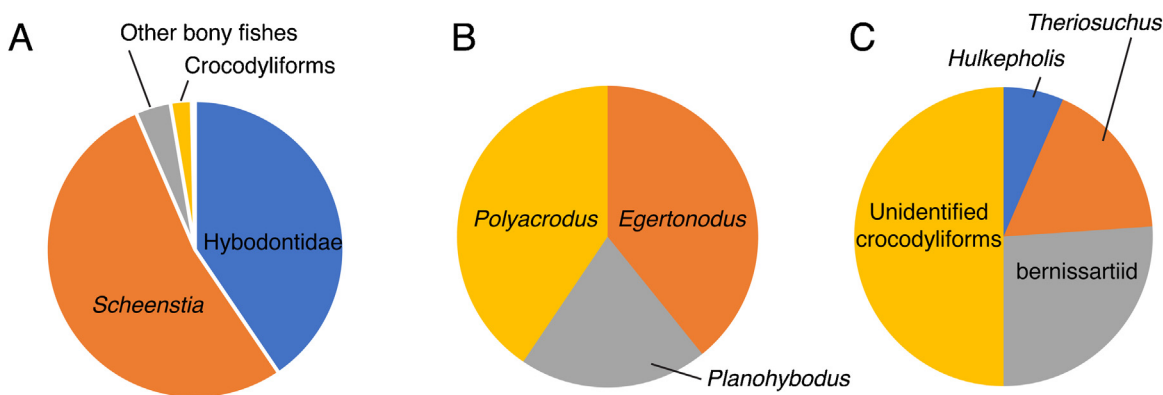
In estimating relative abundances of fossil species, it is important to take care when counting teeth because specimens can break or become difficult to identify. Furthermore, each fish or crocodile might shed multiple sets of teeth during the course of its lifetime, and then contribute its final set of teeth to the deposit after it has died. Further uncertainties arise from taphonomic damage to more delicate specimens, and any selective collecting by palaeontologists. The proportions we count could then represent a largely geological signal (specimens sorted by energy of current and winnowing during transport) or a biological signal (representing roughly the proportions of the animals when alive), or a mix of both.

In the case of Ashdown Brickworks, the sample (full details in Supplementary data) is dominated by the durophagous teeth of the unidentified semionotiform actinopterygian and by the various species of hybodont sharks (Fig. 11A). The other taxa, including 'other species of bony fishes' and crocodyliforms are present in relatively low proportions, and other archosaurs are so rare they do not show in the pie chart. Among the identified hybodont sharks (Fig. 11B), teeth of *Polyacrodus* and *Egertonodus* are about equally common, with *Planohybodus* less abundant. Among the crocodyliforms (Fig. 11C), most teeth could not be identified to genus, but among those that could, bernissartiids are most abundant, then *Theriosuchus*, and then *Hulkepholis*.

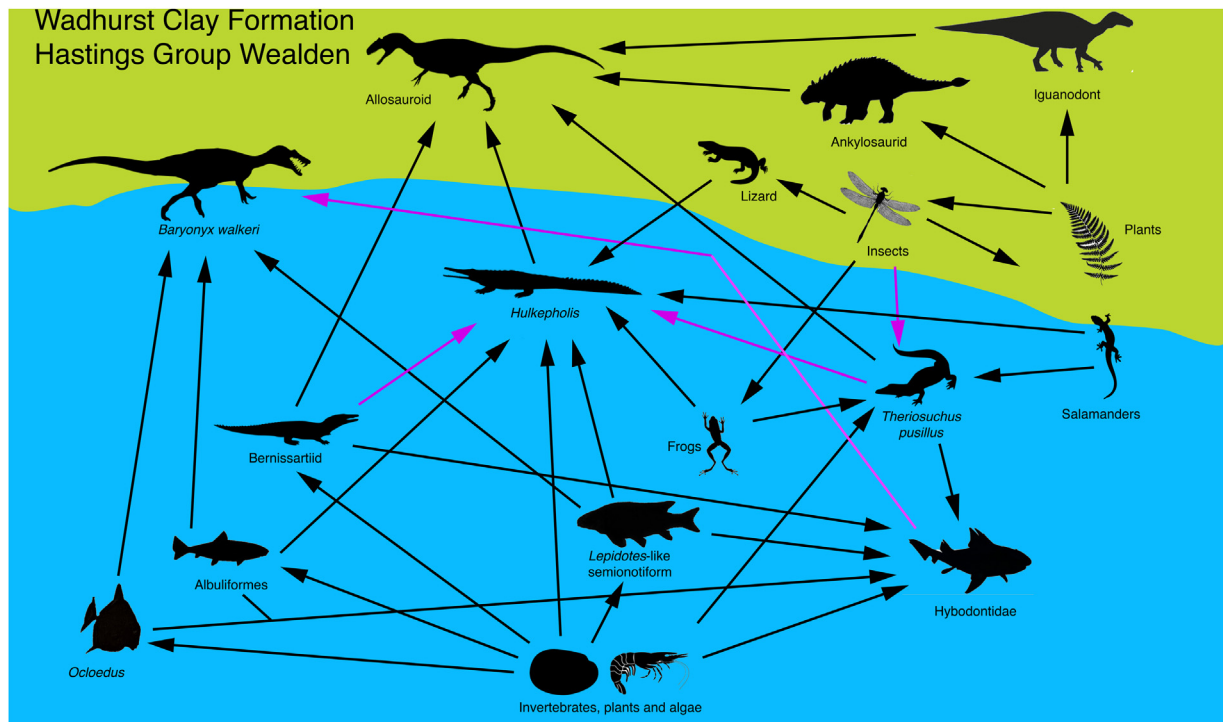
## 6.3. The Wealden food web at Ashdown Brickworks

Establishing a food web based on fossil evidence is problematic. However, where there are large samples of teeth and other elements, and where plant and invertebrate fossils have been found nearby, it is possible to make some reasonable suggestions (Fig. 12). Many of the taxa, such as the crocodyliforms and dinosaurs have been extensively studied in terms of the functional morphology of their teeth and skeletal elements, while others, such as some of the fishes, lissamphibians and lizards have living relatives whose dietary preferences can inform the reconstruction. It should be noted that, although we focus on the fossils from the conglomerate bed, we are combining information from all five bone bed levels at Ashdown Brickworks. We believe this to be justifiable because they are likely close to each other in age. What cannot be determined, however, is whether all these animals encountered each other, or whether the different bone beds are sampling organisms from different ecological zones, and which never interacted.

In the case of the Ashdown Brickworks vertebrate assemblage, we can base inferences about paths of energy flow through the food web on information from the study of the dental adaptations and inferred body sizes of the various species represented. Coprolites can also provide unique information on dietary elements in a food chain. Although we have not studied the coprolites from Ashdown Brickworks, specimens from other Wealden localities can inform discussion (Goldring et al., 2005; Pollard and Radley, 2011). Heteropolar spiral coprolites contain inclusions of fin rays and other bony fish remains (Goldring et al., 2005, p. 679). They indicate the presence of a valvular intestine and are generally identified as having been produced by piscivorous sharks, primarily members of the Hybodontidae. It is likely that some or all of our hybodont sharks fed on bony fishes and on each other. Other coprolites with amphipolar spiral morphology contain large scales of *Scheenstia* sp. and other fish debris (Goldring et al., 2005, p. 679). These are probably also produced by some species of larger hybodont sharks. The third type of Wealden coprolite, elongate irregular forms, lack inclusions, and consist of a fine-grained phosphatic matrix. Residues from the 'conglomerate bed' yield small, 2–4 mm well rounded/ polished coprolites of this type (S. Sweetman, pers. comm., 2019). This composition is peculiar to predators, especially those that digest bone remains with the use of stomach acids, and synaeresis cracks on the surface suggest that some of these coprolites were first deposited on land (Goldring et al., 2005, pp. 679–681). The sizes (80–120 mm) of these latter



**Fig. 11.** Pie charts showing relative abundances of specimens of the major taxa, based on a total of 2972 identified specimens. (A) Proportions of the whole sample, comprising the *Lepidotes*-like semionotiform (53.0%), Hybodontidae (40.4%), Other bony fishes (3.8%), Crocodyliforms (2.3%), and other archosaurs (0.3%; not shown). (B) Proportions of the 74 identifiable shark teeth, comprising *Egertonodus* (38.7%), *Polyacrodus* (40%), and *Planohybodus* (20%). (C) Proportions of the 92 identifiable reptile teeth, comprising Other crocodyliforms (50%), bernissartiid (26%), *Theriosuchus* (17.4%), and *Hulkepholis* (6.5%).



**Fig. 12.** Hypothetical food web for the Wadhurst Clay Formation (Valanginian), of the Hasting Group, Wealden Supergroup, exposed at Ashdown Brickworks, based on the microvertebrates described here, and data available elsewhere in the literature (plants, invertebrates, frogs, salamanders, ankylosaurid, iguanodont). Arrows point from food to consumer. Black arrows indicate inferred trophic pathways, purple arrows those based on direct evidence from coprolites from other Wealden localities and tooth morphology. Silhouettes from Phylopic.com (plants by greengrass from depositphotos.com, insects by Kathy Gold from fr.123rf.com, allosauroid from shareicon.net, *Baryonyx* from onlinewebfronts.com, and crustacean from aliexpress.com; others drafted by P.J.). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

coprolites suggest that their producers were crocodyliforms or small theropods. Goldring et al. (2005, pp. 680–681) note that these three coprolite types cover all the main groups of vertebrates, except for herbivorous dinosaurs such as the iguanodonts and ankylosaurs. However, their excrement probably consisted of partly digested, coarse plant material, and so would have been rapidly consumed by insects and/or decay processes as well as disaggregating during transport in water.

Surprising numbers of Wealden fishes and reptiles were durophages. At this site, the preponderance of the unidentified semionotiform, which represents more than half of the total number of specimens, together with an albuliform and the bernissartiid, demonstrates the importance of durophagous feeding here. This diet implies the existence of abundant hard-shelled animals such as gastropods and bivalves, or animals with carapaces such as crustaceans. Bivalves are abundant in certain horizons at Ashdown Brickworks (Fig. 3A), and all these invertebrates are abundant in coeval strata elsewhere in the Wealden (Batten, 2011).

Some sharks from Ashdown Brickworks have small, sharp-pointed teeth like the bony fishes, which suggests there might have been competition for food. However, most of the shark species have teeth adapted to a fairly varied diet, ranging from hard-shelled invertebrates to small vertebrates. Based on the size of the teeth but also some other skeletal remains make it possible to determine that the aquatic animals populating this environment were generally of medium size (about 1 m long).

The bernissartiid crocodyliform was also a durophage, even though its front teeth were perfect for catching slippery prey or dislodging prey items from soft substrates. The large crocodyliform *Hulkepholis* sp. also had a dentition adapted to durophagy but because of its size, this animal could very well have had a more

varied diet, perhaps relying on ambush predation. Other smaller tetrapods include frogs and salamanders in and around the water's edge, as well as some rare lizards, but these are not represented in our fossil samples. These all likely fed on insects.

The dominant predators of this food chain are the theropods, the unnamed allosauroid and *Baryonyx*. The Allosauroidae had no food preferences other than requiring a great deal of meat. They may have preyed on all other tetrapods from Ashdown Brickworks, as well as dinosaurs such as the iguanodonts. *Baryonyx*, as noted, was likely a piscivore, so it could well have represented the top of the aquatic food chain, being capable of even eating the larger predatory fishes.

Large herbivores, such as *Hypselospinus* and ankylosaurids have been found in other fossiliferous beds at Ashdown Brickworks, as well as widely in the English Wealden at other localities. These herbivorous animals fed mainly on ferns and gymnosperms (Martill and Naish, 2001). Ankylosaurids and iguanodonts are terrestrial dinosaurs, their only contact with water being to drink from fresh waters of rivers or lakes (Butler and Barrett, 2008). It is assumed that these dinosaurs weighing several tonnes formed part of the diet of the allosauroid.

## 7. Conclusion

Ashdown Brickworks has yielded a diversity of hybodont sharks, durophagous actinopterygians, crocodyliforms, dinosaurs, and pterosaurs that is typical of the Early Cretaceous in general, and the Wealden in particular. The sedimentology indicates a water body characterized by fluctuating but overall low salinity, and perhaps flanked by gravelly shorelines. In such a setting, vertebrate material from a variety of terrestrial and aquatic settings was reworked and concentrated. In the reconstructed food

web, which is probably typical for many Wealden, and coeval Early Cretaceous localities in Europe and North Africa, a complex aquatic (freshwater to brackish) community is topped by various crocodyliforms, as well as the semi-aquatic theropod dinosaur *Baryonyx*. On land, we assume that plants, insects and lizards provided food for the amphibious crocodyliforms, as well as for a network of dinosaurs of various sizes, as at other Wealden sites. Mammals and birds existed during these times but have not been reported from Ashdown Brickworks.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.pgeola.2019.08.003>.

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