

Short communication

Pterosaur teeth from the Lower Cretaceous (Valanginian) Cliff End Bone Bed, Wadhurst Clay Formation, Wealden Supergroup of southern England, and their possible affinities



Steven C. Sweetman

School of the Environment, Geography and Geosciences, Burnaby Building, Burnaby Road, University of Portsmouth, Portsmouth, PO1 3QL, UK

ARTICLE INFO

Article history:

Received 20 October 2022

Received in revised form

10 June 2023

Accepted in revised form 10 June 2023

Available online 28 June 2023

Keywords:

Cliff End Bone Bed

Great Britain

Istiodactylidae

Pterosaur teeth

Valanginian

Wealden

ABSTRACT

Until now there have been no formal descriptions of pterosaur remains from the Cliff End Bone Bed of the Lower Cretaceous (Valanginian), Wadhurst Clay Formation, Wealden Supergroup, of south-east England. This horizon yields abundant vertebrate material representing both aquatic and terrestrial taxa and recent examination of a large collection of vertebrate remains obtained by a private collector has led to the discovery of two isolated pterosaur teeth, both referable to the same taxon. Tooth crown morphology differs from that of teeth informally reported from the Wadhurst Clay Formation and attributed to ornithocheirids in being triangular in lingual and labial view, labiolingually compressed with well-defined carinae on the mesial and distal margins and with a low basal cingulum. Their possible affinities are discussed, and they are tentatively, but with some uncertainty, attributed to an istiodactylid. If this attribution is correct, they represent the earliest record of Istiodactylidae to date.

© 2023 The Author(s). Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

1. Introduction

1.1. Petrology and mode of deposition of the Cliff End Bone Bed

The Cliff End Bone Bed crops out high in the cliff at Cliff End, East Sussex, south-east England, in the vicinity of British National Grid Reference TQ 886 127 (Figs. 1, 2), and cannot be accessed directly. Nevertheless, it can be seen to be lenticular in nature occurring approximately 2.9 m above the basal Cliff End Sandstone Member of the Lower Cretaceous (Valanginian) Wadhurst Clay Formation (Lake and Shephard-Thorn, 1987; Batten and Austen, 2011) of the Wealden Supergroup (Fig. 1B, C). While the bed in situ is inaccessible, coastal erosion causes frequent cliff falls and fallen blocks of the bone bed are commonly encountered on the foreshore. These are generally pale grey in colour and primarily comprise poorly sorted, very coarse quartz sand, individual grains being sub-angular to well-rounded. While approximately 95 percent of clasts are coarse extrabasinal 'vein quartz', some measuring as much as 20 mm × 11 mm × 5 mm (Radley and Allen, 2012) these occur with subsidiary finer sandstone, mudstone, and clay-ironstone clasts, some as much as 50 mm in length and probably representing rip-

up clasts. Also present are wood fragments and an abundance of mostly highly abraded vertebrate remains. All are bound by matrix of very fine quartz sand and clay cemented by calcite. The appearance of fallen blocks suggests that the bone bed was deposited in scours, runnels and gutters within the host mudstone (Allen, 1975; Lake and Shephard-Thorn, 1987; Cook, 1995; Batten and Austen, 2011). The Cliff End Bone Bed, and several others occurring in the Wealden Supergroup of south-east England, were initially deposited from high energy flows as winnowed, hydraulically sorted, channel-lags. These were subsequently reworked by a number of non-marine transgressions to form shoreline deposits (Allen, 1975; Cook, 1995). While much of the vertebrate material is moderately to highly abraded, reflecting several cycles of reworking, some, including one of the pterosaur teeth described here, show little abrasion suggesting that they were incorporated locally during final deposition of the bed.

1.2. Vertebrate palaeontology of the Cliff End Bone Bed

The Cliff End Bone Bed contains one of the richest accumulations of vertebrate remains in the Wealden Supergroup of southern England, the majority of which represent bony and cartilaginous fishes (Dineley and Metcalf, 1999). However, it is

E-mail address: steven.sweetman@port.ac.uk.

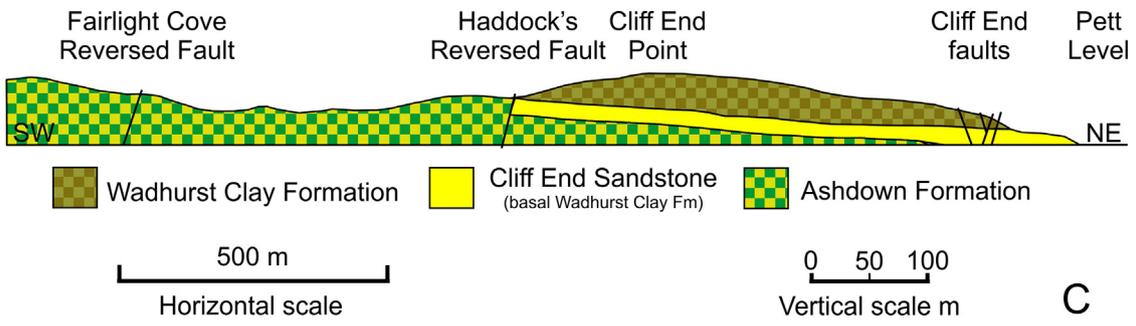
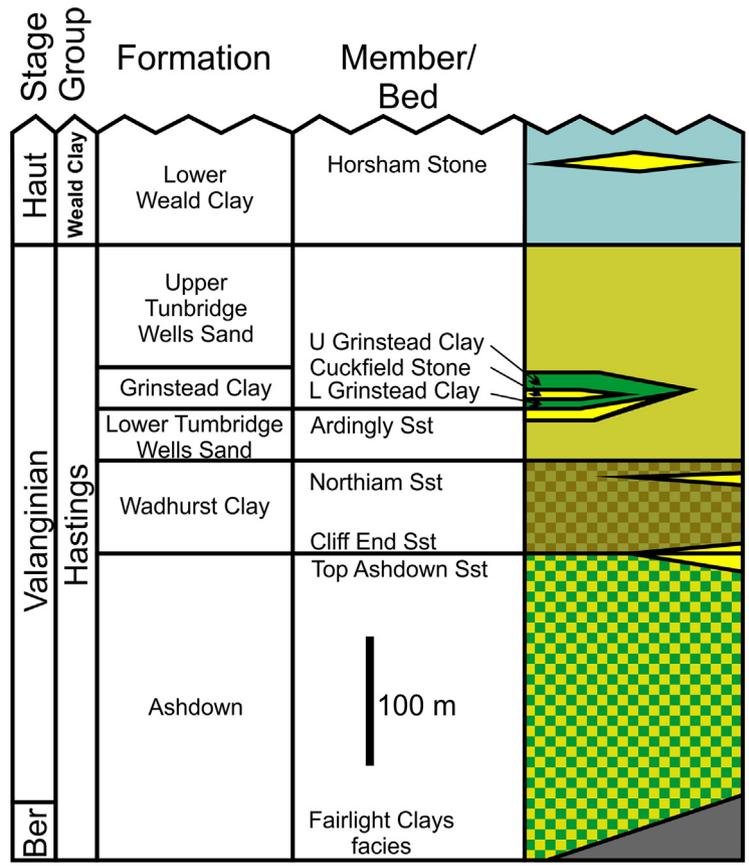
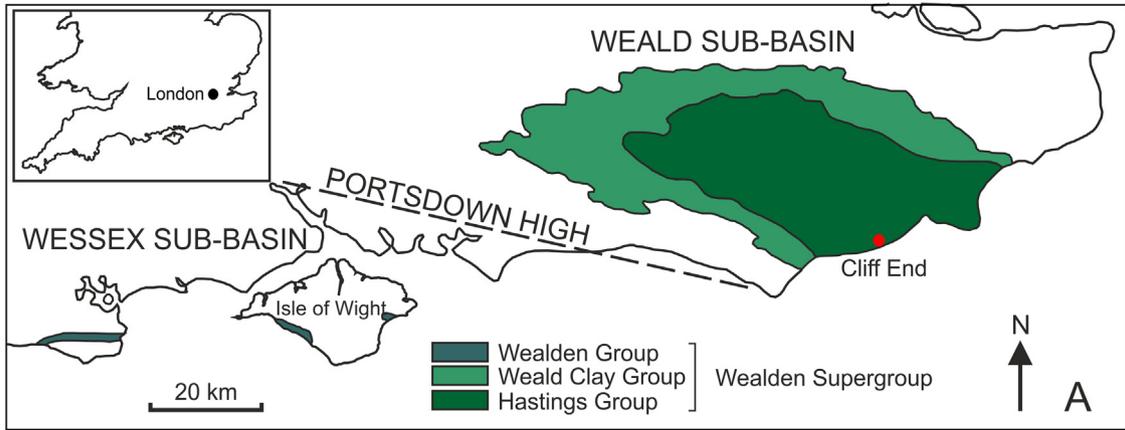


Fig. 1. A, location maps and outline geology of the Wealden Supergroup of southern England. B, simplified stratigraphy of the lower part of the Wealden Supergroup of Sussex, south-east England (modified from [Batten and Austen, 2011](#)). C, schematic cliff section of the area shown in [Fig. 2](#) (based on [Booth, 2005](#), fig. 1). Abbreviations: Ber, Berriasian; Haut, Hauterivian.

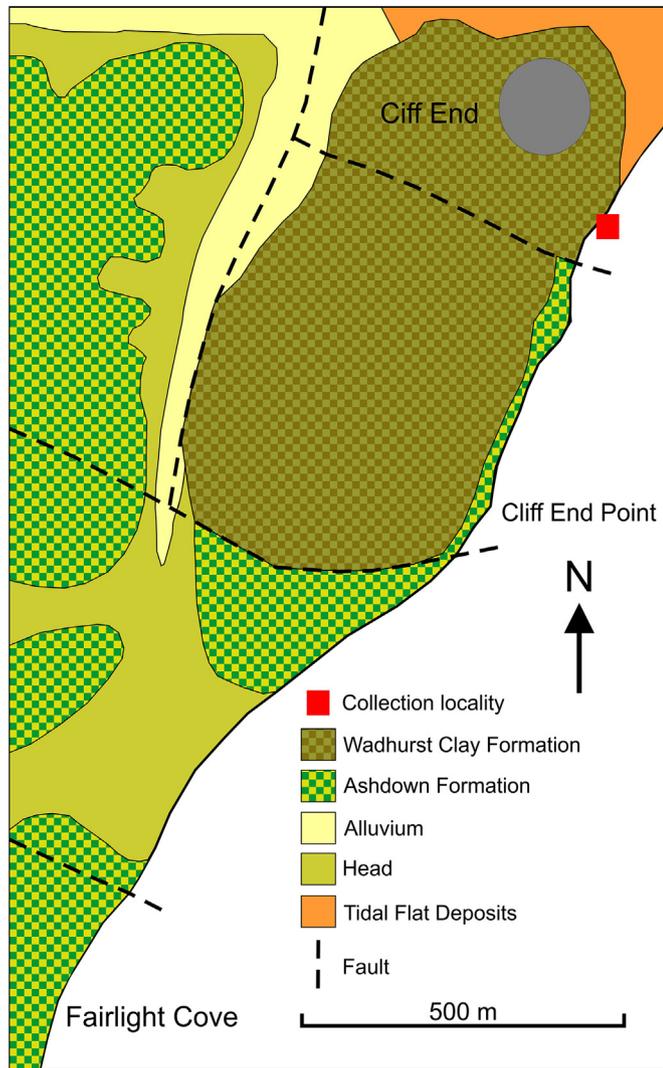


Fig. 2. Outline geological map of the area in the vicinity of, and to the south-west of Cliff End, East Sussex, southern England, showing the collection locality of the described specimens, BEXHM: 2022.109.1 and BEXHM: 2022.109.2 (simplified and redrawn from British Geological Survey (1980) sheet 320/321).

perhaps best known for its Lower Cretaceous mammal fauna (Clemens and Lees, 1971). At the time work commenced to recover and record this, Lower Cretaceous mammals had only been found at two other localities worldwide. Isolated mammal teeth and fragments thereof, are extremely rare components among vertebrate remains whereas, apart from fish remains, those of crocodyliforms and dinosaurs are relatively common, mostly comprising isolated teeth and small bone fragments (SCS pers. obs.). Pterosaur remains have also been reported (e.g., Austen et al., 2013; Austen and Austen, 2017) but not described or figured. An indeterminate ornithocheirid tooth and bone have been reported and figured from an approximately coeval horizon at Ashdown Brickworks, near Bexhill-on Sea, East Sussex (Austen et al., 2010) and this material is now accessioned in the collections of Bexhill Museum. Other indeterminate pterosaur teeth with broad similarity to the anterior teeth of ornithocheirids in being tall relative to their basal width, conical and with a broadly circular or oval basal profile have also been reported from the Cliff End Bone Bed by private collectors. Some have also been illustrated on websites and in online forums. However, until this account no pterosaur specimens from this horizon have been formally described and figured in the scientific literature.

1.3. Institutional abbreviation

BEXHM, Bexhill Museum, Bexhill-on-Sea, East Sussex.

2. Material and methods

Fallen blocks of the bone bed were collected from the foreshore and broken up using a hammer at the collector's residence. In the case of BEXHM: 2022.109.1 (Fig. 3), it was observed in a rock fragment which was trimmed using a small, diamond trim saw. The specimen was then partially prepared under a binocular microscope using a ZOIC PalaeoTech Tr air scribe. The somewhat abraded specimen, BEXHM: 2022.109.2 (Fig. 4), was completely released

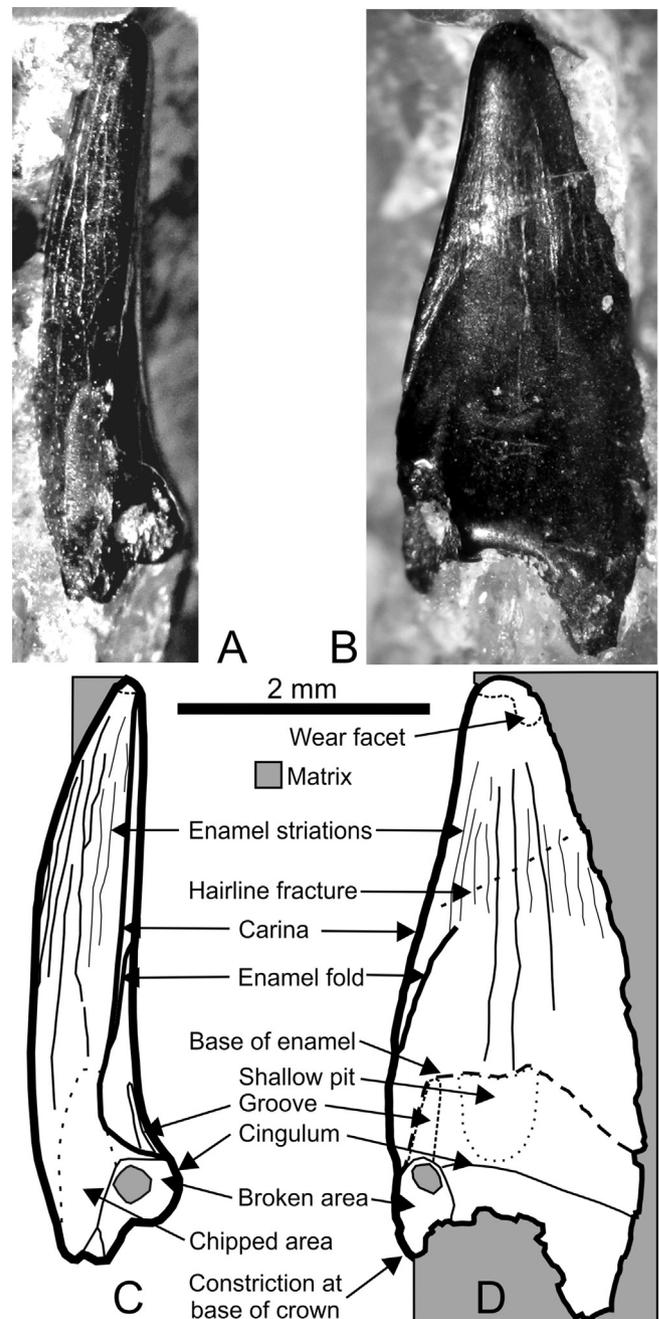


Fig. 3. BEXHM: 2022.109.1 in: A, distal view; B, lingual view. C, D, annotated line drawings in: C, distal and; D, lingual views.

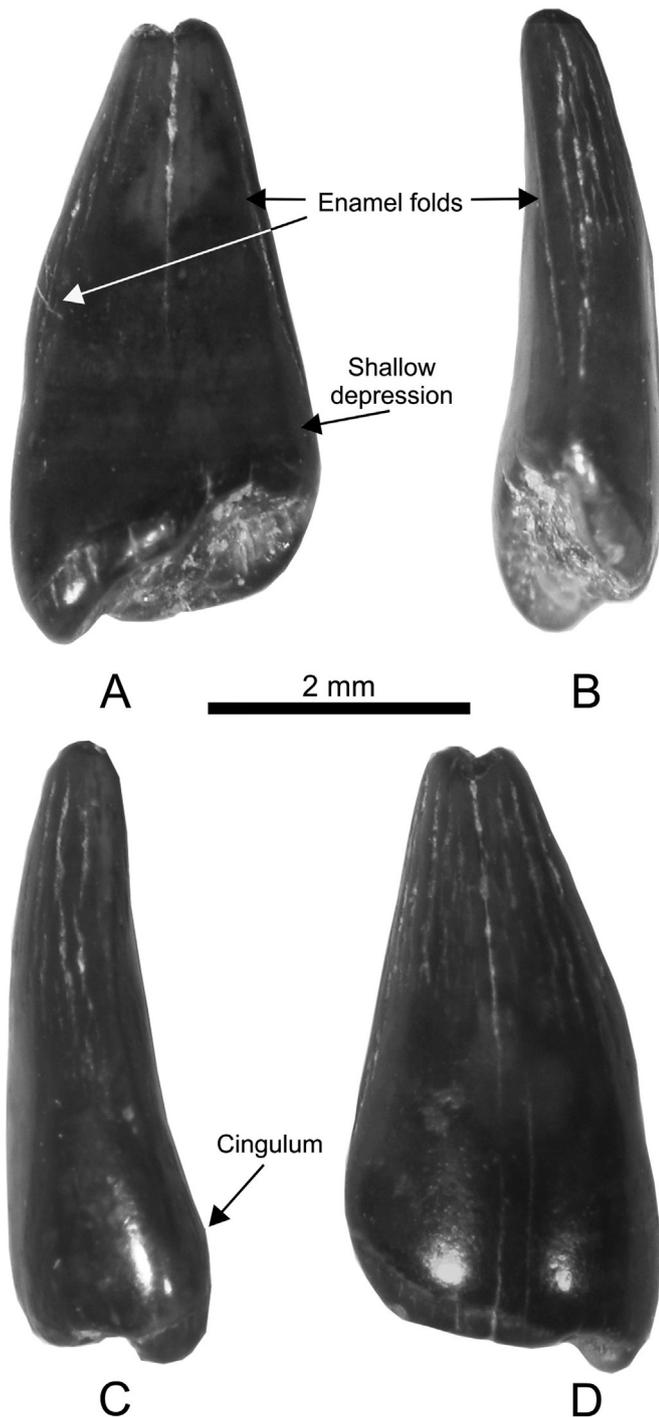


Fig. 4. BEXHM: 2022.109.2 in: A, lingual view; B, distal view; C, mesial view; D, labial view.

from the matrix facilitating examination of tooth morphology as a whole. Images were obtained using a Canon G12 digital camera and measurements were taken manually using digital callipers under a Nikon SMZ800 binocular microscope.

3. Taxonomic assignment

The tooth crowns described below are triangular in outline and strongly labiolingually compressed, characters typical of the teeth of istiodactylid pterosaurs (Witton, 2013). They also bear a low

lingual cingulum and pronounced mesial and distal carinae, also characters observed in at least part of the dentition of most istiodactylids. The constriction between the root and crown of the described specimens is a further character observed in the teeth of some istiodactylids, e.g. *Nurhachius ignaciobrito* (Wang et al., 2005). However, the constriction between the root and crown and the presence of well-defined carinae are not seen in all taxa, e.g. *Hongshanopterus lacustris* which lacks both (Wang et al., 2008). See Xu et al. (2022) for discussion and their fig. 6 for illustration of istiodactylid teeth from the Aptian Jiufotang Formation of China. They differ from the anterior teeth of ornithocheirids in their pronounced labiolingual compression. They also differ from most posterior ornithocheirid teeth, including those of taxa from the Lower Cretaceous Santana Formation of Brazil illustrated by Wellnhofer (1985 Abb. 7), and resemble teeth of istiodactylids in greater labiolingual compression, lack of pronounced lingual curvature and in the presence of a basal constriction at the crown–root junction. The teeth are therefore tentatively, but with some uncertainty, assigned to an indeterminate member of Istiodactylidae.

3.1. Systematic palaeontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

?Istiodactyliformes Kellner et al., 2019

?Istiodactylidae Howse, Milner & Martill, 2001

?Istiodactylidae indet.

Material. Two isolated tooth crowns, BEXHM: 2022.109.1 (Fig. 3) and BEXHM: 2022.109.2 (Fig. 4)

Horizon and locality. The Lower Cretaceous (Valanginian), Cliff End Bone Bed of the Wadhurst Clay Formation, Cliff End, East Sussex, UK. Fallen blocks collected from the foreshore at approximately British National Grid Reference TQ 8876 1299 (Fig. 2).

4. Descriptions

Note. Following Vullo et al. (2009) and based on observation of istiodactylid teeth figured in the literature (e.g., Zhou et al., 2019, fig. 4A, B; Xu et al., 2022, fig. 4C), the convex carina seen in BEXHM: 2022.109.2 (Fig. 4A, D) is taken to be the mesial one and that being the case the exposed carina seen in BEXHM: 2022.109.1 (Fig. 3) is the distal one. These orientations are used in the descriptions below.

4.1. BEXHM: 2022.109.1

BEXHM: 2022.109.1 (Fig. 3), has been partially prepared from the matrix. A substantial part of the lingual surface is visible. All of the distal margin and part of the labial surface are also visible. A hairline fracture, extending from the lingual to labial sides of the crown (Fig. 3B, D) renders complete release from the matrix inadvisable as there is a risk of serious damage to or destruction of the specimen. It comprises a substantially complete tooth crown. Lack of any trace of the root suggests that it is a shed tooth. It displays minor abrasion basally on the lingual side but is otherwise well preserved. However, a small area at the base of the left side as seen in lingual view (Fig. 3D) was broken post-mortem and pre burial, and a small area close to this was chipped during collection and preparation (Fig. 3A, C).

The tooth crown measures 5.1 mm apicobasally. It is 2.3 mm wide mesiodistally at its widest point but part of the base of the crown at this position, visible in lingual view, is obscured by matrix. It narrows at the basal extremity where it is 1.8 mm wide. In distal

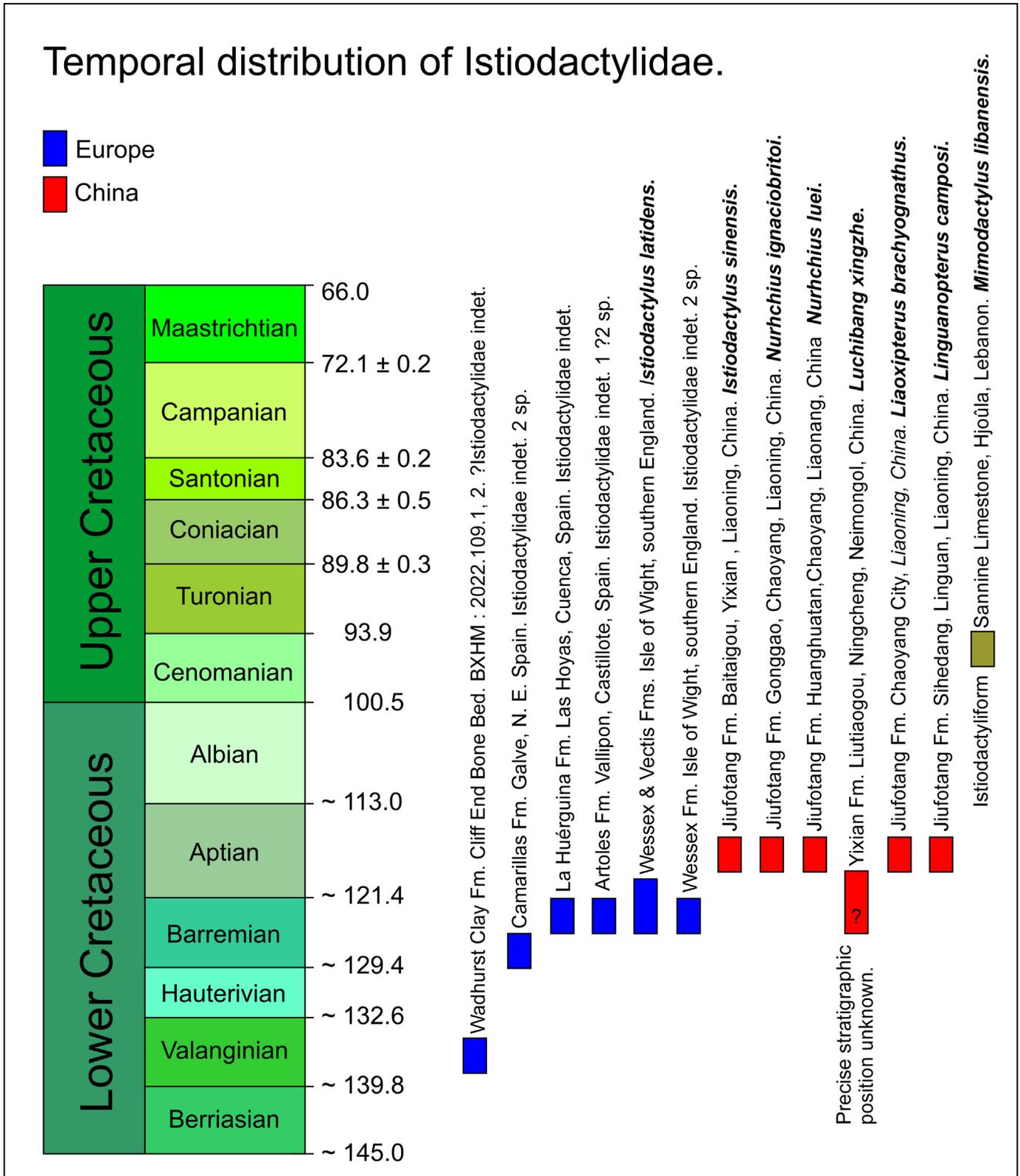


Fig. 5. Temporal distribution of taxa currently assigned to Istiodactylidae with *Mimodactylus libanensis* shown as the latest occurrence of the more inclusive clade, Istiodactyliformes (see section 5 for discussion). Stage ages, Ma, from the International Commission on Stratigraphy's International Chronographic Chart v2022/02.

view the maximum labiolingual width is 1.2 mm gently tapering above the cingulum (Fig. 3A, C) to 0.4 mm at the apex.

In lingual view the crown is triangular in outline. It bears a pronounced enamel fold lingually on the left side at its mid-point

apparently providing support for the distal carina (Fig. 3B, D). The latter is very well defined and narrow but polished and somewhat rounded rather than sharp at its lateral extremity (Fig. 3A, C). The rounding appears to represent minor post-mortem abrasion. As

exposed, a similar fold is not present on the right side in lingual view. Orientation of the apex of the crown and the crown root junction suggests that the tooth may have been somewhat distally reclined. There is a groove extending from the apex of the broken surface at the base of the crown on the left side. This appears to be a primary feature and not a product of abrasion (Fig. 3C, D). There is also a very shallow pit in the lower central part of the lingual surface, also appearing to be a primary feature (Fig. 3D). Below this the base of the crown is expanded lingually to form a pronounced but low cingulum (Fig. 3C, D). This is somewhat polished by abrasion. Apicobasally, above the cingulum, the lingual surface is almost planar, but it is slightly lingually convex mesiodistally. The labial surface is labially convex apicobasally and mesiodistally.

Lingually, enamel does not cover the entire surface of the crown (Fig. 3D). It is smooth basally, but this may reflect minor abrasion. Apically, where unaffected by dietary attrition, it is ornamented by fine striations a small number of which extend to the base of the enamel. Dietary attrition is mostly confined to the apex, as commonly seen in the teeth of pterosaurs (Witton, 2013), but it extends to form a small wear facet lingually on the mesial side (Fig. 3D). Enamel on the labial side, as exposed, covers the entire surface of the crown except at the extreme apex where it has been removed by dietary attrition. Striations on the labial surface are more pronounced than those on the lingual side. While striations are more basally extensive than those on the lingual side, only a small number approach the base of the crown (Fig. 3C).

4.2. BEXHM: 2022.109.2

BEXHM: 2022.109.2, (Fig. 4), is very similar in most respects to that described above but is from the opposite side of the dentition. The crown has been fully released from the matrix permitting examination of it as a whole. However, it is considerably more abraded than BEXHM: 2022.109.1, especially on the lingual side (Fig. 4A). Parts of the apex and base of the crown have also been removed by abrasion. As preserved it has an apicobasal height of 5.2 mm. It is 2.5 mm wide mesiodistally at its widest point. It also narrows at the basal extremity where it is 2.3 mm wide, but abrasion here does not permit an accurate determination of the basal width. In lateral view the maximum labiolingual width is 1.4 mm gently tapering to 0.6 mm at the apex as preserved. The cingulum has been diminished by abrasion but is still a discernible feature (Fig. 4C). The distal enamel fold observed in BEXHM: 2022.109.1 (Fig. 3C, D) has been partially removed by abrasion but is also clearly visible (Fig. 4A, B). There is a somewhat broader but low fold on the mesiolingual margin (Fig. 4A) confirming the presence of mesial as well as distal lingual reinforcement of the carinae. This area is obscured by matrix in BEXHM: 2022.109.1. A shallow depression (Fig. 4C) occurring in the same area as the lingual groove seen in BEXHM: 2022.109.1 (Fig. 3C, D) may represent the abraded remnants of a similar groove in BEXHM: 2022.109.2. The carinae, while slightly abraded, are similar on both the mesial and distal margins of the crown but that on the mesial margin is slightly labiolingually wider than that on the distal margin. As in BEXHM: 2022.109.1, the lateral margins of the carinae are rounded as a result of abrasion. Precise determination of the extent of enamel cover on the lingual side is not possible due to abrasion. It occupies the apical half of the crown but has been partially removed basally. Enamel covers the entire labial surface, but it is highly polished basally (Fig. 4C, D). The degree of dietary attrition in BEXHM: 2022.109.2 cannot be determined as the apex of the crown is missing and abrasion on the lingual side has erased any facet that may have been present. Apically, striations on the labial side (Fig. 4A) are very similar to those observed in BEXHM: 2022.109.1. Striations on the lingual side have mostly

been removed by abrasion but are apparent apically on the mesial extremity (Fig. 4B).

5. Discussion

As discussed above, teeth with the morphology described here are seen in the dentitions of istiodactylids. However, labiolingually compressed teeth also occur in the posterior part of the dentitions of some ornithocheirids and attribution to an indeterminate ornithocheirid cannot be precluded. Until now, isolated teeth recovered from the lower Barremian, Camarillas Formation at Galve, north-east Spain, morphotype 4 of Sánchez-Hernández et al. (2007, fig. 5d), comprised the earliest potential occurrence of Istiodactylidae and, therefore, of the more inclusive clade Istiodactyliformes (Kellner et al., 2019). Elsewhere in Europe istiodactylids were hitherto restricted to the upper Barremian and lower Aptian. The Lower Cretaceous, Las Hoyas Lagerstätte of the La Huérguina Formation, eastern Spain, is upper Barremian and has yielded two teeth referred to Istiodactylidae by Vullo et al. (2009). These authors consider both teeth to represent a single taxon and that this may be conspecific with the taxon represented by some of the small pterodactylid teeth from the upper Barremian part of the Artoles Formation of Vallipón, Teruel Province, north-east Spain, described by Ruiz-Omeñaca et al. (1998, figs. 1, 2a–i). Other teeth from this locality, also referred to Istiodactylidae may represent a second species. Vullo et al. (2009) also suggest that the species represented by teeth from Las Hoyas may be conspecific with the taxon from Galve, also in the Teruel Province of north-east Spain, represented by ‘morphotype 3’ teeth described and figured by Sánchez-Hernández et al. (2007, fig. 5c), although these authors attribute their morphotype 3 teeth to an indeterminate ornithocheirid. None of these authors appear to have considered the possibility that the triangular, labiolingually compressed teeth they describe might be the posterior teeth of ornithocheirids.

Elsewhere in Europe istiodactylids are only known from the Wealden Supergroup of southern England (Sweetman and Martill, 2010). Istiodactylidae was originally erected by Howse et al. (2001) as a then monospecific family to accommodate *Istiodactylus latidens* (originally named *Ornithodesmus latidens* by Seeley, 1901). The type material of *I. latidens* was thought to be derived from the upper Barremian–lower Aptian Vectis Formation exposed on the south-west coast of the Isle of Wight, southern England. However, Sweetman and Martill (2010) did not preclude the possibility of its derivation from the underlying Barremian, Wessex Formation. Additional specimens of *I. latidens* were later recovered from the Vectis Formation (see Averianov et al., 2021 for a review), and an *I. latidens* specimen held in the collections of Moscow Vernadsky State Geological Museum may represent the missing jaws of the holotype. Palynological analysis of matrix associated with this specimen supports its, and possibly, therefore, the holotype's, derivation from the Vectis Formation (Averianov et al., 2021). Nevertheless, isolated teeth very similar to those of *I. latidens* were recovered from close to the top of the Wessex Formation exposed on the south-east coast of the Isle of Wight confirming the presence of *Istiodactylus* sp. if not *I. latidens* in the upper Barremian there (Sweetman and Martill, 2010). Also recovered from the same horizon were other teeth representing two additional istiodactylid species (Sweetman and Martill, 2010).

Outside of Europe members of Istiodactylidae have only been recorded from north-east China. A recent study (Xu et al., 2022) concludes that there are currently five valid genera and six species (Fig. 5). All but one of these are derived from the Aptian Jiufotang Formation, the other, *Luchibang xingzhe*, having been recovered from the underlying Barremian–Aptian Yixian Formation (Hone et al., 2020). Unfortunately, the exact stratigraphic

placement of the holotype and only known specimen is unknown and it is uncertain whether it comes from the upper Barremian or Aptian part of the Formation.

6. Concluding remarks

Referring to previous studies and, with the exception of *Istiodactylus latidens*, based only on isolated teeth, at least six istiodactylid species have been recorded from the Lower Cretaceous of Europe. If identification of these isolated teeth is correct, and none represent posterior teeth of ornithocheirids, this reflects a similar diversity to that observed in the Lower Cretaceous of China, based on substantial remains. The recovery of isolated teeth from the Valanginian of southern Britain with istiodactylid-like morphology is notable. Both are referred to the same taxon based on close morphological similarities and if, as tentatively proposed, assignment to Istiodactylidae is correct this Valanginian record predates any previous record (lower Barremian) and adds a seventh record of Istiodactylidae in Europe. It would also represent the earliest record of Istiodactyliformes, the last representatives of which, members of Lonchodectidae (Unwin, 2001; Xu et al., 2022) and Mimodactylidae (Kellner et al., 2019), are recorded from the Cenomanian of Europe (*Lonchodraco giganteus*, is considered to be from the Cenomanian rather than the Turonian of Britain by Martill et al., 2021), and Lebanon (*Mimodactylus libanensis* Kellner et al., 2019, Fig. 5).

Acknowledgements

The collector and preparator of the described specimens, Mr David Jenkins of Rye East Sussex, is sincerely thanked for making available his collection for study and generously agreeing to donate the specimens described here to the collections of Bexhill Museum, thus rendering them available for scientific description. Mr Julian Porter, Bexhill Museum, is thanked for curatorial assistance. Valuable discussions were held with, and assistance provided by Prof. David Martill, University of Portsmouth. His help and support are gratefully acknowledged. Mr Peter Austen is thanked for insightful discussions concerning the Cliff End locality and for providing access to an image forming the basis of Fig. 1B shown here. The helpful comments of the reviewers and Editor are gratefully acknowledged.

References

- Allen, P., 1975. Wealden of the Weald: a new model. *Proceedings of the Geologists' Association* 86, 389–437.
- Austen, P.A., Austen, J., 2017. June 20th – Cliff End – Geology and fossils of Hastings III [2017]. *The Seaford Naturalist* 184, 7–9.
- Austen, P.A., Brockhurst, D., Honeyset, K., 2010. Vertebrate fauna from Ashdown brickworks, Bexhill, East Sussex. *Wealden News* 8, 13–23.
- Austen, P.A., Broos, K., Jarzembowski, E., 2013. HDGS/GA field meeting: Cliff End to Fairlight Saturday, 20th July 2013. *Hastings & District Geological Society Journal* 19, 34–35.
- Averianov, A.O., Kolchanov, V.V., Zverkov, N.G., Aleksandrova, G.N., Yaroshenko, O.P., 2021. The wandering jaws of *Istiodactylus latidens* (Pterosauria, Istiodactylidae). *Cretaceous Research* 126, 104887. <https://doi.org/10.1016/j.cretres.2021.104887>.
- Batten, D.J., Austen, P.A., 2011. The Wealden of south-east England, 15–51. In: Batten, D.J. (Ed.), *Palaeontological Association Field Guide to Fossils*, 14. English Wealden Fossils. The Palaeontological Association, London, p. 769.
- Booth, K.A., 2005. Geological Investigation of the Ashdown Beds at Fairlight, East Sussex. British Geological Survey Commercial Report, CR/05/040N, p. 32.
- Clemens, W.A., Lees, P.M., 1971. A review of English Early Cretaceous mammals, 117–130. In: Kermack, D.M., Kermack, K.A. (Eds.), *Early Mammals*. Zoological Journal of the Linnean Society 50. Academic Press, London, p. 203.
- Cook, E., 1995. Taphonomy of two non-marine Lower Cretaceous bone accumulations from southeastern England. *Palaeogeography, Palaeoclimatology, Palaeoecology* 116, 263–270.
- Dineley, D.L., Metcalf, S.J., 1999. British Cretaceous fossil Fishes, 417–479. In: Dineley, D.L., Metcalf, S.J. (Eds.), *Fossil Fishes of Great Britain*. Geological Conservation Review Series, 16. Joint Nature Conservation Committee, Peterborough. xxi + 675 pp.
- Hone, D.W.E., Fitch, A.J., Ma, F., Xu, X., 2020. An unusual new genus of istiodactylid pterosaur from China based on a near complete specimen. *Palaeontologia Electronica* 23 (1), a09. <https://doi.org/10.26879/1015>.
- Howse, S.C.B., Milner, A.R., Martill, D.M., 2001. Pterosaurs, 324–335. In: Martill, D.M., Naish, D. (Eds.), *Dinosaurs of the Isle of Wight*. The Palaeontological Association, London, p. 433.
- Kaup, S.S., 1834. Versuch einer Eintheilung der Säugethiere in 6 Stämme und der Amphibien in 6 Ordnungen. *Isis von Oken* 1834, 311–315.
- Kellner, A.W.A., Caldwell, M.W., Holgado, B., Vecchia, F.M.D., Nohra, R., Sayão, J.M., Currie, P.J., 2019. First complete pterosaur from the Afro-Arabian continent: insight into pterodactyloid diversity. *Scientific Reports* 9 (1), 1–9. <https://doi.org/10.1038/s41598-019-54042-z>.
- Lake, R.D., Shephard-Thorn, E.R., 1987. *Geology of the Country Around Hastings and Dungeness*. Memoir for 1:50,000 Geological Sheets 320 and 321 (England and Wales). HMSO, London viii + 81 pp.
- Martill, D.M., Smith, R.E., Longrich, N., Brown, J., 2021. Evidence for tactile foraging in pterosaurs: a sensitive tip to the beak of *Lonchodraco giganteus* (Pterosauria, Lonchodectidae) from the Upper Cretaceous of southern England. *Cretaceous Research* 117. <https://doi.org/10.1016/j.cretres.2020.104637>.
- Plieninger, F., 1901. Beiträge zur Kenntniss der Flugsaurier. *Palaeontographica* 48, 65–90.
- Radley, J.D., Allen, P., 2012. The Wealden (non-marine Lower Cretaceous) of the Weald Sub-basin, southern England. *Proceedings of the Geologists' Association* 123, 245–318. <https://doi.org/10.1016/j.pgeola.2012.01.003>.
- Ruiz-Omeñaca, J.L., Canudo, J.L., Cuenca-Bescós, G., 1998. Primeros restos de reptiles voladores (Pterosauria: Pterodactyloidea) en el Barremiense superior (Cretácico inferior) de Vallipón (Castellote, Teruel). *Mas de las Matas* 17, 225–249.
- Sánchez-Hernández, B., Benton, M.J., Naish, D., 2007. Dinosaurs and other fossil vertebrates from the Late Jurassic and Early Cretaceous of the Galve area, NE Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 249 (1–2), 180–215. <https://doi.org/10.1016/j.palaeo.2007.01.009>.
- Seeley, H.G., 1901. *Dragons of the Air: an Account of Extinct Flying Reptiles*. Methuen & Company, London.
- Sweetman, S.C., Martill, D.M., 2010. Pterosaurs of the Wessex Formation (Early Cretaceous, Barremian) of the Isle of Wight, southern England: a review with new data. *Journal of Iberian Geology* 36 (2), 225–242. https://doi.org/10.5209/rev_JIGE.2010.v36.n2.9.
- Unwin, D.M., 2001. An overview of the pterosaur assemblage from the Cambridge Greensand (Cretaceous) of Eastern England. *Geowissenschaftliche Reihe* 4 (1), 189–221.
- Vullo, R., Buscalioni, Á.D., Marugán-Lobón, J., Moratalla, J.J., 2009. First pterosaur remains from the Early Cretaceous Lagerstätte of Las Hoyas, Spain: palaeoecological significance. *Geological Magazine* 146 (6), 931–936. <https://doi.org/10.1017/S0016756809990525>.
- Wang, X., Kellner, A.W.A., Zhou, Z., de Almeida Campos, D., 2005. Pterosaur diversity and faunal turnover in Cretaceous terrestrial ecosystems in China. *Nature* 437, 875–879. <https://doi.org/10.1038/nature03982>.
- Wang, X., de Almeida Campos, D., Zhou, Z., Kellner, A.W.A., 2008. A primitive istiodactylid pterosaur (Pterodactyloidea) from the Jiufotang Formation (Early Cretaceous), northeast China. *Zootaxa* 1813, 1–18.
- Wellnhofer, P., 1985. Neue Pterosaurier aus der Santana Formation (Apt) der Chapada do Araripe, Brasilien. *Palaeontographica Abteilung A* 187, 105–182.
- Witton, M.P., 2013. *Pterosaurs: Natural History, Evolution, Anatomy*. Princeton University Press, Princeton.
- Xu, Y., Jiang, S., Wang, X., 2022. A new istiodactylid pterosaur, *Lingyuanopterus camposi* gen. et sp. nov., from the Jiufotang Formation of western Liaoning, China. *PeerJ* 10, e13819. <https://doi.org/10.7717/peerj.13819>.
- Zhou, X., Pêgas, R.V., Leal, M.E.C., Bonde, N., 2019. *Nurhachius luei*, a new istiodactylid pterosaur (Pterosauria, Pterodactyloidea) from the Early Cretaceous Jiufotang Formation of Chaoyang City, Liaoning Province (China) and comments on the Istiodactylidae. *PeerJ* 7, e7688. <https://doi.org/10.7717/peerj.7688>.