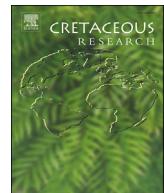




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# The wandering jaws of *Istiodactylus latidens* (Pterosauria, Istiodactylidae)



Alexander O. Averianov <sup>a,\*</sup>, Veniamin V. Kolchanov <sup>b</sup>, Nikolay G. Zverkov <sup>c</sup>,  
Galina N. Aleksandrova <sup>c</sup>, Olga P. Yaroshenko <sup>c</sup>

<sup>a</sup> Zoological Institute of the Russian Academy of Sciences, Universitetskaya Emb. 1, 199034 Saint Petersburg, Russia

<sup>b</sup> Vertebrate Zoology Department, Saint Petersburg State University, Universitetskaya Emb. 7/9, 199034 Saint Petersburg, Russia

<sup>c</sup> Geological Institute of the Russian Academy of Sciences, Pyzhevsky Lane 7, Bld. 1, 119017 Moscow, Russia

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## ABSTRACT

A new specimen of the Early Cretaceous pterodactyloid pterosaur *Istiodactylus latidens* is described. This specimen in the Moscow Vernadsky State Geological Museum represents the associated anterior ends of the rostrum and mandibular symphysis but lacks collection data. It likely comes from the Barremian-Aptian Vectis Formation of southern England based on pollen analysis of the matrix sample. This specimen could represent the missing jaws of the holotype of *I. latidens*. The specimen was studied using computer microtomography. It has an isodont dentition consisting of large lancet-like interlocking teeth, a mandibular odontoid process, and a palatal ridge. The palatal ridge, known previously for some istiodactylid taxa, is reported here for the first time for *Istiodactylus*.

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## 1. Introduction

In the first popular book on pterosaurs, Seeley (1901) described a new pterosaur, *Ornithodesmus latidens*, from the fresh-water Lower Cretaceous Wealden strata of the Isle of Wight in southern England, United Kingdom. The type species of *Ornithodesmus*, *O. cluniculus*, was based on a synsacrum from the Wealden strata at Brook, Isle of Wight, which Seeley (1887) initially referred to a bird. This specimen (NHMUK R187) was later reassigned to a maniraptoran theropod dinosaur (Howse and Milner, 1993) and the pterosaur species "*Ornithodesmus*" *latidens* was transferred to a new genus *Istiodactylus* (Howse et al., 2001).

In the original description of *Istiodactylus latidens*, Seeley (1901: p. 174) noted "the principal specimen" of this species found on the Isle of Wight and housed in the collection of reverend William Fox, a prominent private collector of that time (Blows, 1983). He described this specimen as having large and deep skull with large vacuities, short and wide teeth, and small braincase. Seeley briefly described also several postcranial elements of this "principal

specimen" (cervical, dorsal, and sacral vertebrae, sternum, and wing bones). Two postcranial bones, cervical vertebra and sternum, were figured (Seeley, 1901: figs. 66–68). The most striking feature of the new pterosaur was the structure of its teeth. Seeley (1901: p. 174) noted in this respect: "I have never seen any pterodactyle teeth so flattened and shaped like the end of a lancet." Because of this form of the teeth, W. Fox informally called this form "latidens." This epithet becomes part of the scientific name of the new pterosaur. After the death of W. Fox in 1881 his fossil collection was purchased by the London British Museum (now NHMUK) in 1882 (Blows, 1983).

The holotype of *I. latidens* received the collection number R176 and was described as a fragmentary and much crushed skeleton consisting of the posterior part of the cranium, as well as parts of the vertebral column and numerous portions of the wing bones (Lydekker, 1888: p. 24–25). The skull was sectioned and briefly described by Newton (1889). Surprisingly, no jaws or teeth, the most distinctive part of the skeleton, were preserved when the specimen was purchased by the British Museum. Hooley (1913) mentioned the rumor, that the jaws were lost before the collection came into the possession of the British Museum.

Two additional specimens of *I. latidens* (NHMUK R3877 and R3878) were described in detail by Hooley (1913). These specimens come from the Barremian-Aptian Vectis Formation of Atherfield,

\* Corresponding author.

E-mail addresses: [dzharakuduk@mail.ru](mailto:dzharakuduk@mail.ru) (A.O. Averianov), [veniamin.kolchanov@mail.ru](mailto:veniamin.kolchanov@mail.ru) (V.V. Kolchanov), [zverkovnik@mail.ru](mailto:zverkovnik@mail.ru) (N.G. Zverkov), [dinoflag@mail.ru](mailto:dinoflag@mail.ru) (G.N. Aleksandrova).

Isle of Wight. The exact stratigraphic position of the holotype of *I. latidens* is uncertain. According to Sweetman and Martill (2010), it most likely comes from the Barremian Wessex Formation, which underlies the Vectis Formation. However, the mode of preservation of this specimen is more appropriate for the Vectis Formation (Howse et al., 2001; Martill et al., 2011). The fourth specimen of *I. latidens* (CAMMZ T706), comprising of almost complete rostrum and mandibles, was thought to be the lost jaws of the holotype (Howse et al., 2001). This specimen was never described or illustrated, but was included in the hypodigm of *I. latidens* by several authors (Howse et al., 2001; Unwin, 2003; Sweetman and Martill, 2010; Martill et al., 2011). The three dimensionally preserved wrist bones of *I. latidens* were used in the first functional analysis of pterodactyloid wrist by Hankin and Watson (1914). Apparently because of the presence of these better specimens, the holotype of *I. latidens* (NHMUK R176) has received little attention and was only partially illustrated (Hooley, 1913: pl. 37, fig. 3; pl. 39, fig. 1; Howse and Milner, 1993: fig. 3). The specimen in the online database of NHMUK (<https://data.nhm.ac.uk/>), identified as the holotype of *I. latidens* (NHMUK R176) is actually a dermal spine NHMUK R175 of an ankylosaur *Polacanthus foxii* illustrated by Hulke (1881: pl. 71, figs. 4–6, pl. 76, fig. 1), as written on the original label (see also Lydekker (1888: p. 190).

Here we describe an additional specimen of *I. latidens* consisting of associated anterior ends of the rostrum and mandible. This specimen (SGM 1810-01) is housed in the Vernadsky State Geological Museum of the Russian Academy of Sciences (Moscow) and likely comes from the Lower Cretaceous of England.

### 1.1. Institutional abbreviations

CAMMZ – Cambridge University Museum of Zoology, Cambridge, United Kingdom. IVPP – Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China. NGMC – National Geological Museum of China, Beijing, China. NHMUK – Natural History Museum of United Kingdom, London, United Kingdom. SGM – Vernadsky State Geological Museum, Russian Academy of Sciences, Moscow, Russia.

## 2. Material and methods

The core paleontological collection of Vernadsky State Geological Museum comes from the Geological Cabinet of the Moscow State University. The prominent Russian geologist Alexey P. Pavlov (1854–1929) was a curator of this Cabinet since 1880 and the head of the Cabinet in 1884–1929. Alexey Pavlov and his wife, paleontologist Maria V. Pavlova, assembled a large paleontological collection for the Cabinet. This cabinet became the Geological-Paleontological Museum named after A.P. Pavlov and M.V. Pavlova in 1926–1987 and later was transferred to the Vernadsky State Geological Museum.

Specimen SGM 1810-01 has no original label or records in the Museum database. Most likely, it belongs to the Paleontological collections assembled by A.P. Pavlov and M.V. Pavlova in the late 19 century. A.P. Pavlov and M.V. Pavlova visited England in 1888 to participate in the Geological Congress. They also visited England in 1891 on route to a Geological Congress in the USA (I.A. Starodubtseva, pers. comm.). A.P. Pavlov studied some Cretaceous outcrops in southern England, including the Isle of Wight, and northern France (Pavlow and Lamplugh, 1892). It is possible that A.P. Pavlov acquired SGM 1810-01 during his stay in England, although there is no direct evidence for this. It cannot be excluded that this specimen comes from the Fox collection and actually may represent the missing jaws of the *I. latidens* holotype.

The Moscow specimen was CT-scanned at 200 kV and 250 mA, generating a resolution of 46.883 μm of voxel size and output of 2024×2024 pixels per slice (2400 slices) at the Skoltech Center for Hydrocarbon Recovery (Moscow, Russia) using CT phoenix v|tome| x L 240/300 and L 450. CT scan data were imported to the software Amira 6.3.0 (FEI-VSG Company), where the model was reconstructed and segmented.

An assemblage of gymnosperm pollen, bryophyte and pteridophyte spores, as well as rare dinocysts, was extracted from the sample of matrix of SGM 1810-01. Palynological maceration was performed according to the methodology of Aleksandrova et al. (2012). The study and photography of the palynomorphs was performed under in an optical microscope Axiostar plus (Carl Zeiss), with a magnification of ×400 and × 600. All palynomorphs (spores and pollen of plants, microphytoplankton) were identified. The minimal value per sample was 200 palynomorphs, following which the slide was reanalysed to detect rare taxa. When calculating in palynological spectra, the sum of all palynomorphs, i.e. spores, pollen and microphytoplankton was considered as 100%. The studied palynological slides are housed in the Geological Institute of the Russian Academy of Sciences, Moscow.

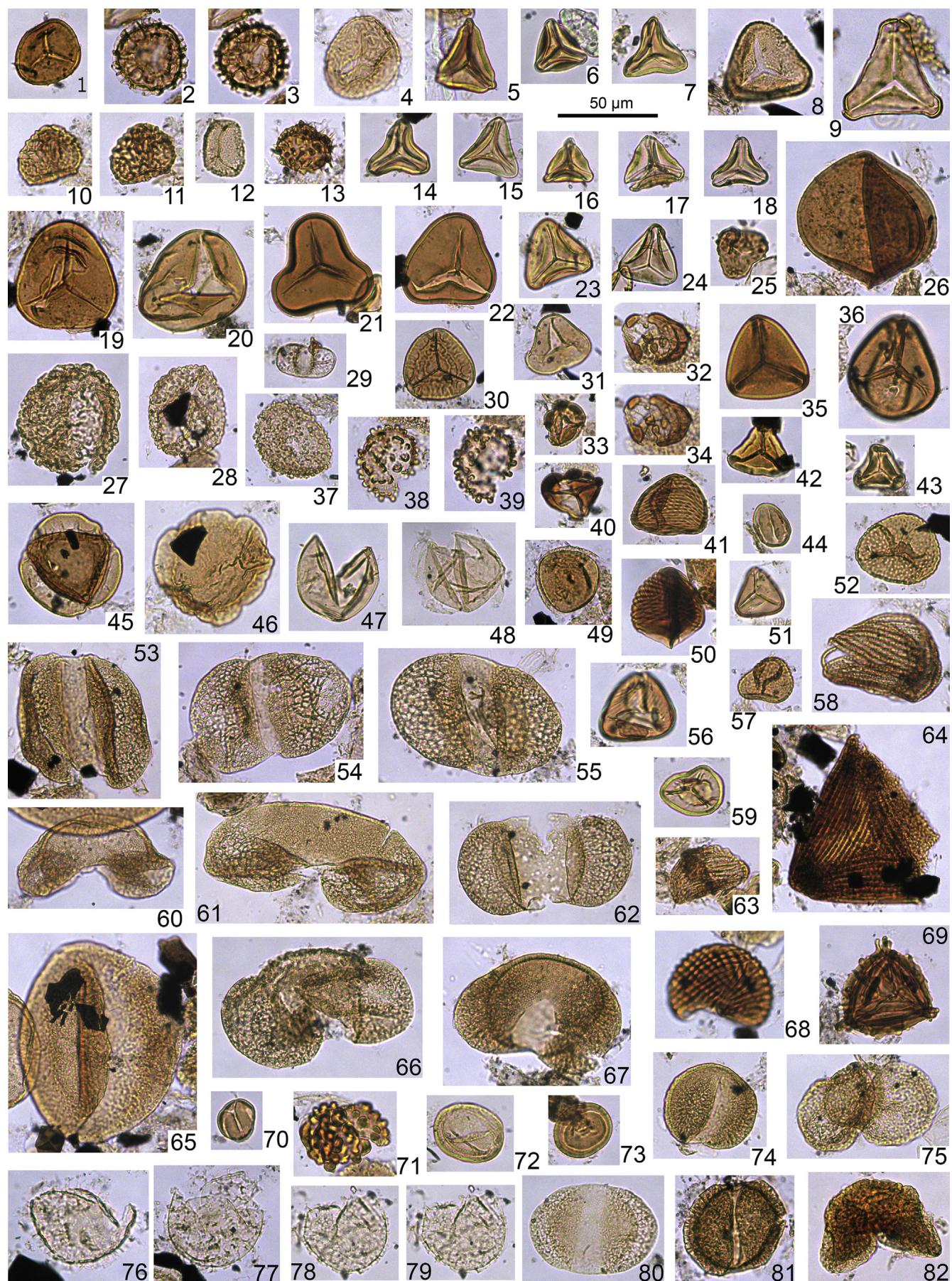
## 3. Palynology

The pollen of gymnosperms prevail in the sample (Fig. 1). These are largely represented by the fragments of indeterminate bisaccate pollen *Disaccites* (20%). Among the identifiable morphs are *Parvisaccites radiatus* (13.5%), *Taxodiaceapollenites hiatus* (8%), *Podo-carpidites* spp. (*P. minusculus*, *P. bifloris*, *P. cf. herbstii*, *Podocarpidites* sp.) (5%), *Classopollis* spp. (4%); less common are *Alisporites* spp. (including *A. bilateralis* and *A. grandis*) (3%), *Cerebropollenites mesozoicus* and *Sciadopityspollenites* spp. (2.6%), *Perinopollenites elatoides* (2%), and *Cedripites canadensis* (1.3%). The pollen of *Piceapollenites* sp., *Vitreisporites pallidus*, *Eucommiidites troedssonii*, *Callialasporites dampieri*, and *C. trilobatus* constitute less than 1%.

The spores are diverse. Characteristic is a dominance of the spores of the Gleicheniaceae (22%), represented by *Gleicheniidites* sp., *G. senonicus*, *G. laetus*, *G. cf. umbonatus*, *G. stellatus*, *Clavifera* sp., and *Ornamentifera* sp. In approximately equal amounts are spores of the Cyatheaceae (6.5%) and Schizaeaceae (7.5%). The Cyatheaceae include *Cyathidites* sp., *C. minor*, and *C. asper*. Spores of the Schizaeaceae are varied, although they are poorly preserved, but most can be identified as *Cicatricosporites* sp. Other identifiable schizaeacean taxa include *Appendicisporites spinosus*, *Cicatricosporites venustus*, *C. augustus*, *C. baconicus*, and *C. perforatus*.

*Matonisporites* sp., *M. minor*, *Collarisporites aequatorialis*, *Dicytophyllidites* sp., and *Distaltriangulisporites* sp. are found in the amount of 3–2%; 1% or less is represented by *Stereisporites* sp., *S. cf. antiquasporites*, *Todisporites* sp., *Acanthotriletes varispinosus*, *Lycopodiumsporites* sp., *Tigrisporites* sp., *Coronatispora valdensis*, *Concavissimisporites* sp., *C. punctatus*, *Microreticulatisporites* sp., *M. cf. uniformis*, *Sestrosporites pseudoalveolatus*, *Concavisporites jurienensis*, cf. *Leptolepidites* sp., *Foraminisporis wonthaggiensis*, and some others. Rare dinocysts are represented solely by a form similar to *Valensiella parvula*.

The taxonomic composition of the palynomorph assemblage and their relative abundance indicates an Aptian age (Bolkhovitina, 1953, 1968; Couper, 1958; Deák, 1964, 1965; Kemp, 1970; Bolkhovitina and Fokina, 1971; Shirokova, 1972; Khlonova, 1988; Strepetilova, 1994; Herngreen et al., 1996; Vajda, 2001). The assemblage resembles the Aptian pollen spectra of different regions of Eurasia in the high amount and variety of Gleicheniaceae along with *Cicatricosporites* spp., *Sestrosporites pseudoalveolatus*, *Parvisaccites radiatus*, *Taxodiaceapollenites hiatus*, and also in the



absence of taxa characteristic of the stratigraphically older Lower Cretaceous units (e.g. *Trilobosporites*, *Pilosisporites*, *Impardecispora*).

The spectrum is very similar to the palytomorph complexes from the Barremian-Aptian strata of southern England (Couper, 1958; Kemp, 1970) and is most similar to the complexes from the stratigraphic interval spanning the Vectis Formation (Wealden Group) to Atherfield Clay Formation (lower part of the Lower Greensand Group) in the dominance of gymnosperm pollen over spores with abundance of *Parvisaccites radiatus* and *Gleicheniidites senonicus*, occurrence of *Collarisporites aequatorialis*, *Sestrosporites pseudoalveolatus*, and very rare dinocysts. It is important to note that the dinocysts are most similar to *Valensiella parvula*, a taxon originally described from the fresh-to brackish-water deposits of the Vectis Formation (Barremian-Aptian) of the Isle of Wight, England (Batten and Lister, 1988). This supports an origin of the specimen from Western Europe. Similar complexes are also reported from the Aptian of Southern Baltic states (Vasileva, 1973), Moscow Region (Bolkhovitina, 1953, 1968), Eastern Ustyurt (Shevtsova, 1973), and Eastern Ciscaucasia (Danilenko, 1973). However, the absence of detailed data on taxic distribution within stratigraphic sections, and the use of different taxonomic frameworks by those authors complicate any comparison with these regions. Therefore, the region of occurrence of similar palytomorph complexes is restricted to the European Province of the Euro-Sinian phytogeographic region (Vakhrameev, 1964, 1988).

#### 4. Systematic paleontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Istiodactylidae Howse, Milner and Martill (2001)

*Istiodactylus* Howse, Milner and Martill (2001)

*Istiodactylus latidens* (Seeley, 1901)

Referred specimen. SGM 1810-01, anterior parts of associated rostrum and mandibular symphysis (Figs. 2–4).

Locality and horizon. Unknown. Probably Isle of Wight, England, United Kingdom; Lower Cretaceous (Barremian-Aptian) Vectis Formation, Wealden Group.

#### 5. Description

The specimen SGM 1810-01 comprise a partial rostrum and a partial mandible with dentition. The rostrum consists of the fused premaxillae. The rostrum and mandibular symphysis have similar shape and width (Figs. 3–4), with rounded anterior margin. Both jaw fragments are mostly hollow, with few trabeculae concentrated mainly between the labial and lingual alveolar borders. The upper and lower teeth are similar in size and morphology. The tooth crowns are lanceolate, greatly compressed labiolingually. Some teeth have a “medial carina” on the labial surface, which is merely a facet between the two slightly differently oriented planes of the

labial crown side. The roots mirror the shape of the crown, but somewhat smaller. They are similarly compressed labiolingually and have a pointed apex.

On the rostrum, there are eleven teeth preserved on the right side and ten on the left side. The widest part of the rostrum is at the seventh tooth. The width at the preserved posterior end (at the eleventh tooth) is similar with that at the third tooth. In lateral view, the alveolar border is slightly convex. The dorsal border of the rostrum gently rises posteriorly between the fourth – ninth teeth. Posterior to the embrasure between the ninth – tenth teeth the angle of elevation is slightly greater. This increase in elevation angle marks beginning of a premaxillary crest, which is accentuated by slight lateral depressions. Anterior to the fourth tooth the dorsal profile of the rostrum steeply decreases attaining its minimum height at the first tooth. The anterior part of the palatal side, anterior to the seventh-eighth teeth, is depressed, with a similar concavity in both anteroposterior and mediolateral planes. At the level posterior to the eighth tooth there is a pronounced median ridge. The median ridge gradually increases in height between the anterior end and the level of eleventh tooth. Posteriorly the ridge is almost horizontal. The height of the median ridge is less than half of the opposite tooth crowns. The median ridge is flanked by lateral depressions, which extend anterolaterally beyond the anterior end of the ridge to the level of the seventh tooth. Between the anterior ends of these depressions and the anterior end of the median ridge, there is a flat palatal surface with a triangular outline, pointed posteriorly.

The left and right upper mesial teeth are separated by a gap greater than the crown width. The gaps between the first three mesial teeth is similar in width with the crown width. The third-ninth teeth are separated by distinctly smaller gaps. The gap increases posteriorly to the ninth tooth.

On the mandibular symphysis there are eleven teeth preserved on the left side and nine on the right side. The widest part of the mandibular symphysis is at the fourth and fifth teeth. Posterior to this point, the mandibular symphysis is slightly constricted laterally, with the deepest point of the concavity at the ninth tooth. In lateral view, the alveolar border is slightly concave. The ventral profile of the mandibular symphysis steeply decreases between the second and third teeth. Posterior to the third teeth the ventral profile is gently convex with the deepest point at the seventh and eighth teeth. This deepest part of the mandibular symphysis could be considered as a low mandibular crest, similar to the maxillary crest, which is accentuated by a slight lateral depression. The dorsal surface of the mandibular symphysis is depressed with the concave profile of the mediolateral section. The deepest point of this depression is at the level of the third tooth. Posterior to this point, there is a shallow median ridge flanked by slight depressions laterally. This ridge is lower and mediolaterally much wider than the palatal median ridge. Its height slightly decrease posteriorly.

At the mesial end of the mandibular symphysis there is a well preserved odontoid process of triangular outline with pointed apex. Its height is about one third of the crown height of the lower mesial

**Fig. 1.** Spores, pollen and dinocysts from the matrix sample of SGM 1810-01. All figures are in the same magnification. 1, *Stereisporites* sp.; 2–3, *Lycopodiumsporites crassatus*; 4, *Reticulispores* sp. (cf. *Camarozonosporites insignis*); 5, *Clavifera* sp. (cf. *C. triplex*); 6, 16, *Gleicheniidites cf. umbonatus*; 7, 14, 15, 18, *Gleicheniidites senonicus*; 8, *Concavissimispores* sp.; 9, gen et species indet.; 10–11, *Microreticulispores* sp.; 12, *Foraminispores* wonthaggiensis; 13, *Acanthotriletes varispinosus*; 17, *Gleicheniidites* sp.; 19, *Deltoidospora diaphana*; 20, 36, *Cyathidites* sp.; 21, *Matonisporites* sp.; 22, *Matonisporites equiexinus*; 23, 24, *Gleicheniidites stellatus*; 25, *Ornamentifera echinata*; 26, *Leiotriletes* sp.; 27, *Sciadopityspollenites multiverrucosus*; 28, 37, *Cerebropollenites mesozoicus*; 29, *Vitreisporites pallidus*; 30, *Coronatispora vallensis*; 31, *Cyathidites minor*; 32, 33, 34, 40, *Collarisporites aequatorialis*; 35, *Dicotyphlidites* sp. (cf. *Matonia pectinataeformis*); 38–39, *Sciadopityspollenites* sp.; 41, *Cicatricosporites baconicus*; 42, cf. *Distaltriangulisporites* sp.; 43, *Concavispores jurienensis*; 44, 70, *Eucommiidites troedssonii*; 45, *Callialaspores trilobatus*; 46, *Callialaspores dampieri*; 47, 48, *Taxodiaceapollenites hiatus*; 49, *Perinopollenites elatoides*; 50, *Cicatricosporites* cf. *hallei*; 51, *Deltoidospora* sp.; 52, *Sestrosporites pseudoalveolatus*; 53, *Alisporites bilateralis*; 54, 55, *Alisporites aequalis*; 56, *Cicatricosporites venustus*; 57, *Microreticulispores* cf. *uniformis*; 58, *Costatoperforosporites* sp.; 59, *Stereisporites* cf. *antiquasporites*; 60, 61, *Piceapollenites* sp.; 62, 66, *Alisporites* sp.; 63, 64, 68, *Cicatricosporites* spp.; 65, *Cedripites canadensis*; 67, 74, 81, *Parvisaccites radiatus*; 69, *Appendicisporites spinosus*; 71, cf. *Leptolepidites* sp.; 72, *Classopollis classoides*; 73, *Classopollis torosus*; 75, *Podocarpidites multesimus*; 76, 77, 78–79, cf. *Valensiella parvula*; 80, *Alisporites similis*; 82, *Rugubivesculites* sp.

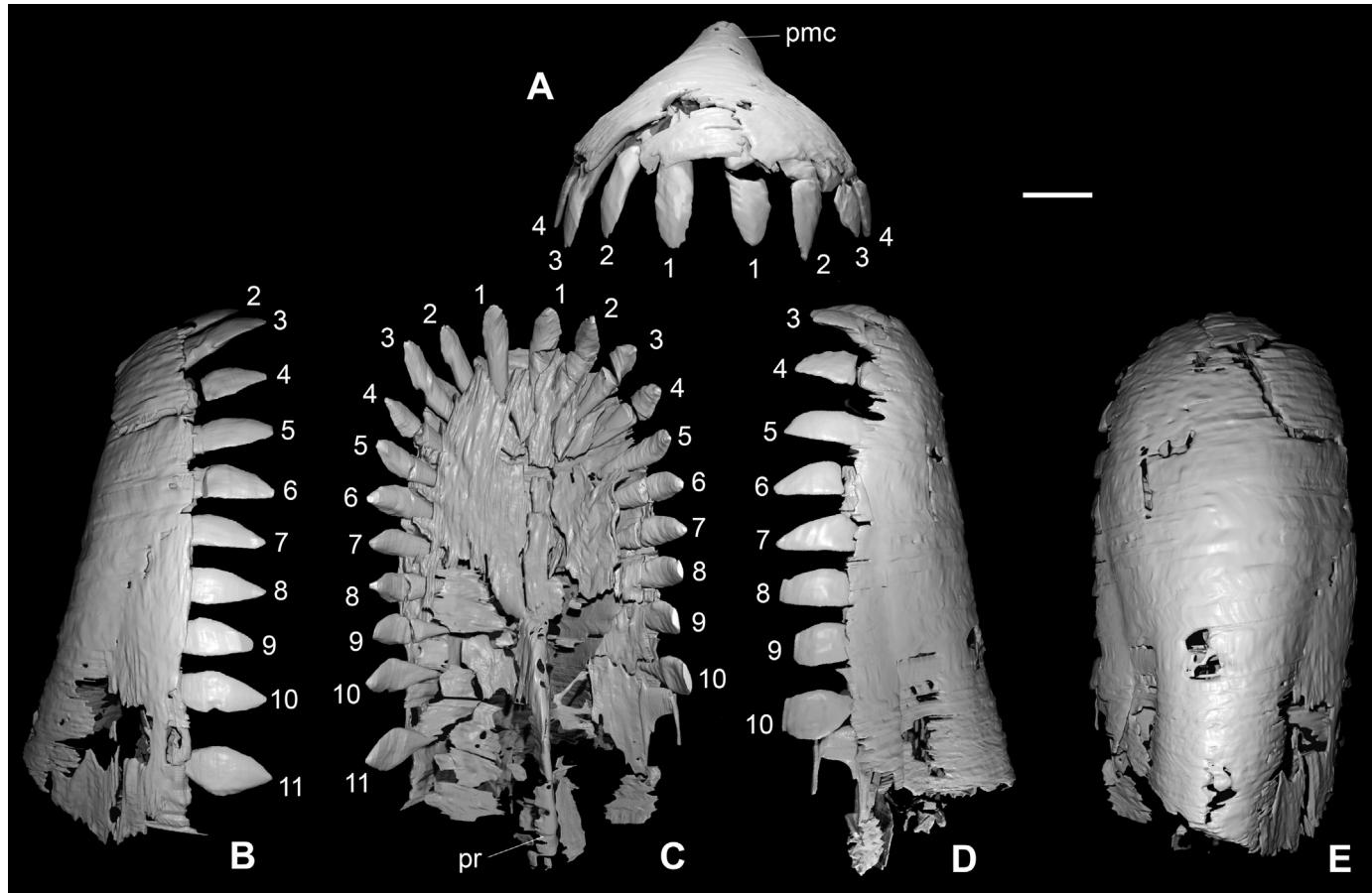


**Fig. 2.** *Istiodactylus latidens*, SGM 1810-01, associated rostrum and mandibular symphysis, in anterior (A), dorsal (B), right lateral (C), ventral (D), and left lateral (E) views. Possible Vectis Formation (Barremian-Aptian), England. Abbreviations: ms, mandibular symphysis; r, rostrum. Scale bar equals 1 cm.

teeth. The mesial tooth is separated by similar gaps from the odontoid process and the second tooth. The second and third teeth are separated by a slightly larger gap. The gaps between the third – eighth teeth are very small. The gaps considerably increase in size posteriorly between the ninth to eleventh teeth.

## 6. Comparison

SGM 1810-01 is referred to the Istiodactylidae by the combination of the following characters: terminal rostrum rounded, isodont dentition consisting of labiolingually compressed lancet-shaped



**Fig. 3.** μCT reconstruction of the rostrum of *Istiodactylus latidens*, SGM 1810-01, in anterior (A), right lateral (B), ventral (C), left lateral (D), and dorsal (E) views. Possible Vectis Formation (Barremian-Aptian), England. Abbreviations: pmc, premaxillary crest; pr, palatal ridge. Figures denote tooth positions. Scale bar equals 1 cm.

teeth with truncated triangular roots (Hooley, 1913; Andres and Ji, 2006; Martill, 2014).

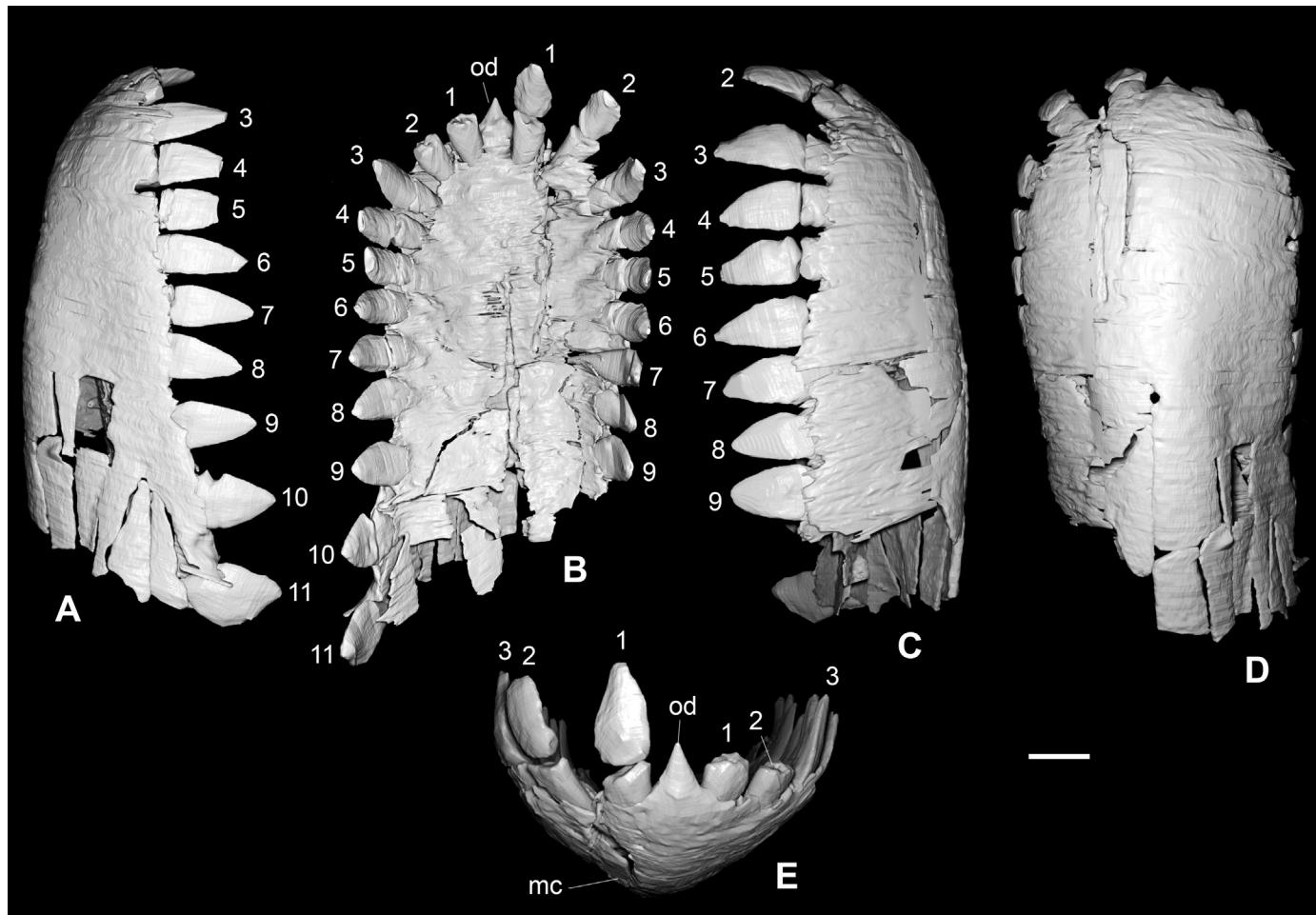
Martill (2014) considered the presence of an odontoid process at the mandibular symphysis as a possible autapomorphy for the Istiodactylidae, but this character has a wider distribution (Rigal et al., 2017; Kellner et al., 2019; Pégas et al., 2019; Zhou et al., 2019; Averianov, 2020). The triangular odontoid process with wide base of SGM 1810-01 matches closely the shape of this process in *Istiodactylus latidens* NHMUK R3877 (Martill, 2014: fig. 6). In the istiodactylid *Longchengpterus zhaoi* Wang, Duan and Cheng (2006) from the Barremian Yixian Formation of Liaoning Province, China, the odontoid process has a distinctly narrower base (Wang et al., 2006; Martill, 2014: fig. 7).

Two characters listed in the diagnosis of *Istiodactylus* provided by Andres and Ji (2006) are present in SGM 1810-01: rostrum dorsoventrally depressed but not laterally expanded and distances between successive teeth less than the width of the teeth.

Four characters of the anterior snout were included in the revised diagnosis of *I. latidens* by Witton (2012): teeth confined to pre-nasoantorbital portion of the rostrum; no more than 48 teeth; upper toothrow occupying less than 25 percent of jaw length; sagittal ridge on rostrum. The anterior margin of the nasoantorbital fenestra is not preserved on the rostrum fragment SGM 1810-01. The total number of preserved teeth in SGM 1810-01 is 41 (21 upper and 20 lower) and it is unknown how many teeth were present in the missing parts of the jaws. The sagittal ridge on the rostrum (the premaxillary crest) is the only character from this diagnosis that can be observed on SGM 1810-01.

The anterior rostrum and mandibular symphysis of *I. latidens* were known previously from specimens NHMUK R3877 (Hooley, 1913: pl. 36, fig. 1; pl. 37, fig. 1; Witton, 2012: figs. 3–4; Martill, 2014: figs. 3–6) and CAMMZ T706. The latter specimen has not been described or illustrated, so the comparison is based on the first specimen. SGM 1810-01 is about 5% smaller than NHMUK R3877. SGM 1810-01 differs from NHMUK R3877 by a dorsal profile of the rostrum, which has a distinct point of curvature change above the third tooth from more steep profile anteriorly to gently concave profile posteriorly in the Moscow specimen, but more round, convex anteriorly and concave posteriorly in the London specimen. In the shape of the rostrum dorsal profile, SGM 1810-01 is more similar to NGMC 99-07-001, the holotype of *Istiodactylus sinensis* Andres and Ji (2006) (Andres and Ji, 2006: fig. 2) than to NHMUK R3877.

In the Moscow specimen, the rostrum is somewhat constricted mediolaterally at the beginning of the premaxillary crest (at the seventh tooth). According to Hooley (1913: p. 374), in NHMUK R3877 the rostrum is also constricted mediolaterally after the seventh tooth, although this constriction is less evident than in the Moscow specimen. The alveolar border of the upper jaw is more convex in lateral view in NHMUK R3877 compared with SGM 1810-01. The mandibular symphysis in SGM 1810-01 has a low mandibular crest that is absent in the London specimen. In NHMUK R3877 the posterior end of the mandibular symphysis is at the tenth tooth. In SGM 1810-01 the mandibular symphysis extends posteriorly at least to the eleventh tooth.



**Fig. 4.** μCT reconstruction of the mandibular symphysis of *Istiodactylus latidens*, SGM 1810-01, in left lateral (A), dorsal (B), right lateral (C), ventral (D), and anterior (E) views. Possible Vectis Formation (Barremian-Aptian), England. Abbreviations: mc, mandibular crest; od, odontoid process. Figures denote tooth positions. Scale bar equals 1 cm.

## 7. Discussion

SGM 1810-01 lacks the dorsal deflection of the alveolar border on the rostrum, when the alveoli are partially visible from the lateral view. This feature, seen in the middle of the upper tooth row of *I. sinensis* (Andres and Ji, 2006: fig. 3A), was considered by these authors as a synapomorphy uniting *Istiodactylus* with the clade containing *Lonchodectes* and “*Anhangueridae*” (Ornithocheiridae in our usage). For the lower jaw, this feature should be termed the “ventral deflection.” This ventral deflection is very weak in the middle of the lower tooth row in *I. sinensis* (Andres and Ji, 2006: fig. 3B). The ventral deflection is not present on the dentary of SGM 1810-01 and none of these depressions can be seen in NHMUK R3877. *I. latidens* clearly lacks this feature and its presence in *I. sinensis* is likely a preservation artifact. Similarly, this character can be seen in the dentary of IVPP V13288, the holotype of *Nurhachius ignaciobrtoi* Wang et al. (2005) (Wang et al., 2008: fig. 15), and it was cited as diagnostic for that species (Wang et al., 2005). However, this character is absent in a better preserved specimen of *Nurhachius luei* Zhou et al. (2019) (Zhou et al., 2019: fig. 1). Most likely, this character in *N. ignaciobrtoi* is an artifact of the flattened preservation.

*Istiodactylus* is quite dissimilar within Ornithocheiridae in having homodont dentition with lanceolate interlocking teeth, wide rostrum and mandibular symphysis, lack or weak development of terminal cranial crests, and asymmetric articulation facets for

coracoid on the sternum. *Istiodactylus latidens* is similar with the Ornithocheiridae by having a warped deltopectoral crest in the humerus, seen in the holotype NHMUK R176 (Hoole, 1913: pl. 39, fig. 1). In *I. sinensis* the deltopectoral crest was described as “warped” (Andres and Ji, 2006: p. 75), which contradicts the published illustration (Andres and Ji, 2006: fig. 4G), where the deltopectoral crest has subparallel proximal and distal margins that are slightly curving ventrally at a similar extent.

SGM 1810-01 documents for the first time the presence of the palatal ridge in *Istiodactylus*. Among istiodactylids, the palatal ridge was known previously for *Nurhachius luei* and *Mimodactylus libanensis* Kellner et al. (2019) (Kellner et al., 2019; Zhou et al., 2019). The palatal ridge in *I. latidens* has a more posterior origin compared with *M. libanensis* (Kellner et al., 2019: fig. 3). Zhou et al. (2019) described for *N. luei* a mandibular groove (sulcus), which is absent in other istiodactylids. More likely, this “groove” is an artifact of preservation caused by compression of the mandibular symphysis.

A peculiar character of SGM 1810-01 and other specimens of *Istiodactylus* is the lack of replacement teeth. Zhou et al. (2019: p. 11) reported “an interesting pattern” of tooth replacement for the istiodactylid *Nurhachius luei*. According to their interpretation, the replacement tooth erupts anterolabially to the functional tooth, instead of posterolingually as typical for other pterosaurs and archosaurs. However, in this specimen the replacing tooth is anterolabial to the tenth functional dentary tooth, but the tenth and

ninth dentary teeth are separated by a space about twice as large as the space between the other dentary teeth (Zhou et al., 2019: fig. 1). Moreover, there is a diastema between these teeth and the replacing tooth is distal to this diastema. It seems likely that the functional tooth between the tenth and ninth preserved teeth was shed and its replacing tooth is in the normal distal position. The suppressed dental replacement in *Istiodactylus* is likely related to their specialized interlocking dentition, when tooth replacement would disrupt the interlocking.

## Conclusions

Associated rostrum and mandibular symphysis of a toothed pterodactyloid pterosaur, found in the Moscow Vernadsky State Geological Museum, has no provenance data. This specimen shows diagnostic characters of the Istiodactylidae, such as rounded terminal rostrum and isodont dentition consisting of labiolingually compressed lancet-shaped teeth with truncated triangular roots. Such characters as rostrum dorsoventrally depressed but not laterally expanded, distances between successive teeth less than the width of the teeth, and the premaxillary crest on the rostrum suggest attribution of this specimen to *Istiodactylus latidens*, known only from the Lower Cretaceous (Barremian-Aptian) Vectis Formation of the Isle of Wight, southern England. Pollen analysis of the matrix associated with the fossil suggests its provenance from the Lower Cretaceous of Western Europe, likely from the Vectis Formation. Most likely, this specimen was bought in England in late 19 century and it might be the missing part of the holotype of *I. latidens*. CT scanning of the Moscow specimen reveals its anatomical details, including the palatal ridge, reported here for the first time for *Istiodactylus*.

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