First tapejarid pterosaur from the Wessex Formation (Wealden Group: Lower Cretaceous, Barremian) of the United Kingdom

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Abstract.

An isolated, partial premaxilla from the Lower Cretaceous (Barremian) Wessex Formation of
Yaverland, Isle of Wight, UK is identified as pterosaurian on account of its overall
morphology and thin bone walls. It is regarded as a tapejarid on account of its unique down-
turned tip with a unique pattern of slit-like foramina on its occlusal surface, while a
combination of sensory foramina and lateral outline identify it as a new genus and species.

The downturn of the occlusal margin lies beyond the anterior margin of the nasoantorbital fenestra suggesting affinities with *Sinopterus* from China rather than South American tapejarids such as *Tapejara*, *Tupandactylus* and *Caiuajara*. This specimen is the first record of Tapejaridae in the Wessex Formation, and is amongst the oldest record of the Tapejaridae outside of China.

Keywords: Pterosauria; Tapejaridae; Wealden Group; Early Cretaceous; Isle of Wight; England

1. Introduction

Tapejarids are remarkable looking members of the Pterosauria that often possess large, highly elaborate soft tissue head crests supported by osseous extensions of the parietals and squamosals posteriorly and an extra osseous spin anteriorly (Frey et al., 2003). They are all the more prominent because of a unique conspicuously downturned anterior rostrum and mandible (Kellner, 2004; Wellnhofer and Kellner, 1991). First described from the Lower cretaceous of South America (Kellner, 2004; Wellnhofer and Kellner, 1991) the Tapejaridae have subsequently been reported from China (Wang and Zhou, 2003; Li et al., 2003; Lü et al., 2005, 2016), Europe (Vullo, et al., 2012), and in Africa from Morocco (Wellnhofer and Buffetaut, 2003; Martill et al., 2020) and an unsubstantiated claim from Niger (Blackburn and Sereno, 2002).

Their remains occur frequently in the Araripe Basin of northeast Brazil in both the Crato Formation Lagerstätte (Sayão and Kellner, 2006; Unwin and Martill, 2008; Pinheiro, 2011; Pegas et al., 2016) and Santana Formation Lagerstätte (Kellner, 2013; Martill and Brito, 2017) where excellent

articulated tapejarid skeletons are reported, often with soft tissue preservation (Frey et al., 2003), in three-dimensions (e.g. Vila Nova et al., 2015) and even examples of multiple specimens in a single concretion (Eck et al., 2011). Elsewhere in Brazil tapejarids have been reported in mass death assemblages forming a pterosaur bone bed in the mid-Late Cretaceous Caiuá Group (Manzig et al., 2014). The Jiufotang Formation of China also yields, with some frequency, complete and fully articulated tapejarid remains (Lü and Yuan, 2005; Lü et al., 2005, 2016; Wang et al., 2008). Elsewhere, however, tapejarid remains are exceedingly rare, with only fragmentary material reported from North Africa (Wellnhofer and Buffetaut, 2003; Martill et al., 2020) and Europe.

The Brazilian tapejarids are generally dated as Aptian (Crato Formation) and possibly Albian (Santana Formation), while the Chinese material is regarded as Aptian (Jiufotang Formation) and Barremian (Yixian Formation) age (Pan et al., 2013). The enigmatic *Bakonydraco* from the Turonian of Hungary, originally described as an azhdarchid (Ősi et al., 2005, 2011) has, in some analyses been found as a tapejarid (Andres et al., 2014; Longrich et al., 2018). Should *Bakonydraco* be a tapejarid, the group has a range spanning almost 40 million years from the Barremian to the Turonian (Barrett et al., 2008). The African tapejarid, *Afrotapejara* Martill, et al., 2020 from the Kem Kem Group of south east Morocco is likely of late Albian age (Ibrahim et al., 2020).

2. Locality and stratigraphy

The specimen (IWCSM. 2020. 401) described here was collected by one of the authors (JW) from a plant debris bed (see Sweetman and Insole, 2010) exposed on the wave cut platform at Yaverland, near Sandown on the Isle of Wight (Fig. 1) (National Grid Reference SZ 61989 85256). At this locality gently dipping ($\sim 10^\circ$) Lower Cretaceous strata of the Wealden Group comprising the upper part of the Wessex Formation and the overlying Vectis Formation form soft, slump-prone cliffs that are daily washed by the high tide. The locality has become well known for an abundance of vertebrate fossils, especially from the plant debris bed horizons of the Wessex Formation (Sweetman and Insole, 2010).

In particular, the locality has yielded dinosaurs (Martill and Naish, 2001) and pterosaurs (Steel et al., 2005) that are unique to the locality (*Yaverlandia* and *Caulkicephalus* respectively). The specimen was found in the highest plant debris bed before the Wessex Formation passes up into the Cowleaze Chine Member of the Vectis Formation (bed 38 of Radley, 1994) (Fig. 1). This upper part of the Wessex Formation is considered to be of Barremian age (Batten, 2011).

3. Material and Methods

The new specimen described here (Fig. 2) has been prepared using a fine dental pick, with some concretionary pyrite removed using an air pen. The specimen has been repaired using a cyanoacrylate adhesive with accelerator. Linear measurements were obtained using digital calipers, and CorelDRAW graphics suite software for determining angular measurements. Digital photography and image stacking using CombineZP software was employed for image production. Photomicrographs were taken on a Leica EZ4W light microscope.

The following museum abbreviations are used: **AMNH**, American Museum of Natural History, New York, USA; **CD**, Desiree Collection, Rio de Janeiro, Brazil; **CP.V**, Centro Paleontológico (CENPALEO), Universidade do Contestado, Mafra, Santa Catarina, Brazil; **FSAC**, Faculté de Sciences, Laboratoire de Géosciences, Université Hassan II, Casablanca, Morocco; **GMN**, Geological Museum, Nanjing, China; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; **JPM**, Jinzhou Palaeontological Museum, Jinzhou City, Liaoning Province, China; **MCT**, Paleontological Collections of the Museu de Ciências da Terra (Departamento Nacional da Produção Mineral), Rio de Janeiro, Brazil; **MIWG**, Museum of Isle of Wight Geology (Dinosaur Isle Visitor Centre), Sandown, Isle of Wight, England; **MN**, Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil; **SAO/UOSG**: Collection Urs Oberli, St. Gallen, Switzerland; **SMNK**, Staatliches Museum für Naturkunde, Karlsruhe, Erbprinzenstrasse 13, Karlsruhe, Germany; **XHPM**, Dalian Xinghai Palaeontological Bio Expo Museum; **ZMNH**, Zhejiang Museum of Natural History, Hangzhou, China.

93 **4. Systematic Palaeontology**

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95 Pterosauria Kaup, 1834

96 Monofenestrata Lü et al., 2010

97 Pterodactyloidea Plieninger, 1901

98 Azhdarchoidea Nesov, 1984 *sensu* Unwin, 1992

99 Tapejaramorpha Andres, Clark, Xu, 2014

100 Tapejaridae Kellner, 1989

101 *Wightia* gen. nov

102 *Type and only species* (see below).

103 *Etymology.* *Wightia*, pertaining to the Isle of Wight, southern England from where the type species
104 was discovered

105 *Wightia declivirostris* sp. nov.

106 *Etymology.* *Declivi* (L.) = slanting, and *rostris* (L.) = beak - in combination pertaining to the downward
107 slanting beak tip of this taxon.

108 *Holotype.* IWCMS. 2020. 401 (Figs 2, 3, 4, 5).

109 *Type locality.* Yaverland, Sandown, Isle of Wight, United Kingdom.

110 *Type stratum.* Wessex Formation (Lower Cretaceous, Barremian) (See Radley 1994).

111 *Diagnosis.* Tapejarid with premaxilla in which the occlusal (palatal) surface has only a few small
112 elongate foramina and a single row of widely spaced (~ 1 per 10 mm) foramina on the lateral margin
113 very close to the ventral border. A downturn angle of ~12°.

5. Description and comparisons

5.1 Osteological description

Specimen IWCMS. 2020. 401 comprises fused partial premaxillae of both sides anterior to the nasoantorbital fenestra but lacking the distal tip. The specimen is partially crushed, but is three-dimensional posteriorly and seems laterally compressed in caudal view. The lateral surfaces are somewhat brecciated (Fig. 5A) with spaces between, showing that the specimen has expanded slightly due to minor displacement between fragments. This means that the fossils looks slightly larger than it would have *in vivo* (Fig. 5C). The specimen displays the downturned occlusal margin of the premaxilla that characterises the Tapejaridae, with a down turn angle of $\sim 12^\circ$ (Fig. 5C). The lateral margins are smooth and there are small (less than 1 mm diameter) foramina lying just dorsal of the occlusal margin (ventral border) (Fig. 5B). The occlusal surface is gently sulcate with rounded borders, and displays just a few small, oval foramina (Fig. 4A, B) arranged in irregular clusters of three or four foramina. The dorsal surface is smoothly rounded and defines a slightly concave profile in lateral view (Fig. 2). The bone wall is exceptionally thin, with a maximum thickness of 0.61 mm with no obvious thickening in the corners (Fig. 2E, F). Under the microscope, the bone of the lateral margins is covered with numerous closely-spaced micro-pores (3A, B) some of which are circular or slightly oval, or are more elongate and slightly meandering anteriorly and dorsally, whereas more ventral and posterior surfaces have a ripple-like surface texture (Fig. 3D). Projection of the dorsal and ventral margins until they meet to form a tip suggests this is a long-snouted tapejarid (Fig. 6L). See Table 1 for specimen measurements.

5.2 Affinities

Affinities. Although IWCMS 2020. 401 is merely a partial premaxilla, it nonetheless exhibits several distinctive features that allow it to be recognised as pterosaurian, notably the exceedingly thin walls of the bone. It is regarded as an azhdarchoid on account of its edentuly and the presence of elongate, slit-like or oval foramina on the lateral margins and occlusal surface. It is recognised a premaxilla on account of its remarkable similarity to that bone in members of Tapejaridae Kellner, 1989. Notably, the occlusal margin possesses a conspicuous ventral downturn (Fig. 2A-B, 5), a feature that is unreported for any pterosaur group, except Tapejaridae. In addition to the ventral downturn, it possesses an occlusal (palatal) surface that is moderately sulcate with gently curved margins (Fig. 2E-F).

Of the nine tapejarid genera presently known (Fig. 6, 7, Table 2) with the premaxilla preserved (*Afrotapejara*, *Caiuajara*, *Caupedactylus*, *Huaxiapterus*, *Ingridia*, *?Keresdrakon*, *Tapejara*, *Tupandactylus*, *Sinopterus*), *Huaxiapterus*, *Ingridia*, *Sinopterus* and *Tupandactylus* are preserved laterally crushed, preventing the occlusal surface of the premaxilla from being examined. In all of those specimens that do preserve the premaxilla, the occlusal surface has only been figured infrequently. In a specimen assigned to *Tapejara wellnhoferi*, Eck et al. (2011, Fig. 2C) figured an occlusal surface that seems to possess only one of these slit-like foramina (Fig. 8E) (SMNK PAL 1137). Similarly, another specimen (AMNH 24440) referred to *T. wellnhoferi* is illustrated with a single, centrally located round foramen on the occlusal surface of the premaxilla/palate (Fig. 8D), but only a restoration is provided, rather than a photograph (Wellnhofer and Kellner, 1991, fig. 2A).

5.3 Comparisons

IWCMS. 2020. 401 can be directly compared with only a limited number of other tapejarid specimens in which the premaxillae are preserved in three-dimensions, and thus allow the occlusal surface to be examined. Notably, tapejarids from the Santana Formation of north east Brazil of the genera *Tapejara* and *Caupedactylus* occurring in early diagenetic concretions are preserved in 3-D

(Kellner, 2013; Eck et al., 2011), but genera from the underlying Crato Formation such as *Tupandactylus* and *Aymberedactylus* are usually crushed, although the skull is often complete, or almost so, in some specimens (Campos and Kellner, 1997; Unwin and Martill, 2007). Also in Brazil, specimens of the tapejarid *Caiuajara dobruskii* and the tapejaromorph *Keresdrakon* from the Goio-Erê Formation are uncrushed (Manzig et al., 2014; Kellner et al., 2019). Tapejarids from China (Jehol Group) are always crushed flat, and usually displayed in lateral aspect (Lü et al., 2006), thus the overall shape can be compared, but the palatal surface is never seen. The high degree of compaction also makes identification of small foramina on the lateral surfaces difficult. The sole example of a tapejarid from Spain, *Europejara* from Las Hoyas lacks the premaxillae, which is unfortunate given that this genus is the same age (Upper Barremian) as *Wightia* (Poyato-Ariza and Buscalioni, 2016). Tapejarids from the Kem Kem beds of Morocco are also preserved three-dimensionally, but to date only portions of premaxilla and possible dentary tips have been reported (Wellnhofer and Buffetaut, 1999; Martill et al., 2020). Nonetheless, they do lend themselves to comparison with *Wightia*.

Here we compare two features, the value of the deflection angle (downturn of the premaxilla tip from the 'horizontal maxilla-jugal bar: Table 3) and the length of the premaxilla from the point of downturn. While the former can be measured with some degree of accuracy, the latter relies on restoration of the distal tip by projection of the dorsal and occlusal margins for some specimens, and is somewhat qualitative. The lowest value for the downturn of the premaxilla is 7° for *Afrotapejara* from the Kem Kem beds of Morocco, whereas the largest value 42° for an example of *Caiuajara* from the Late Cretaceous Goio-Erê Fm. of Brazil. Where multiple examples are known, as in *Caiuajara*, a sample of 11 specimens displays a range of deflection angles from as low as 30° to a high of 42° with a mean of 38°. The sample represents a growth series from individuals that can be considered juveniles to probably mature adults collected from a single event horizon (Manzig et al., 2014). Notably, there is no increase of the angle with age suggesting that this feature does not change with

ontogeny. In three examples of *Tapejara wellnhoferi* (Kellner, 1989; Wellnhofer and Kellner, 1991; Eck et al., 2011) the downturn is between 20° and 25° while in *Tupandactylus imperator* the downturn is 27° and in *Ingridia navigans* 21° and 22° for SMNK 243 and 2344 respectively (Frey et al., 2003). Only in one Brazilian taxon, the tapejaromorph *Caupedactylus ybaka*, is the downturn a low angle at 19° (Kellner, 2013). Chinese tapejarids, on the other hand, seem to be characterised by low angles of deflection of the rostrum. In *Huaxiapterus corollatus* it is 18°, and in *H. atavismus* and *H. jii* it is 16° (Table 3). It is not possible to detect the downturn in the holotype of the only tapejarid from the Yixian Formation, *Eopteranodon lüi* Lü and Zhang, 2005 due to poor illustration. Originally considered to be a dsungaripterid by Lü and Zhang (2005), Lü and Ji (2006) later regarded it as a tapejarid. Better material and a re-study of the holotype of *Eopteranodon* would seem desirable.

In *Wightia*, the premaxilla is deflected ventrally by only 12°, and thus more comparable with the lower values found in the Chinese tapejarids *Sinopterus* and *Huaxiapterus*, although it is somewhat shallower. Only in the Moroccan *Afrotapejara* (7°) (Martill et al., 2020) is a deflection angle found that is smaller than that of *Wightia*.

The second feature of *Wightia* that is comparable, albeit qualitatively, with other tapejarids is the shape of the rostrum anterior to the nasoantorbital fenestra (naof). Although the margin of the naof is not preserved, the point of downturn is preserved, and clearly lies anterior to the naof margin. This is also the case for many tapejarids, but there are some exceptions where the down turn is coincident with the margin of naof, as in *Tupandactylus imperator* (Fig. 4 I), *Caupedactylus ybaka* (Fig. 4 D) and *Caiuajara dobruskii* (Fig. 4 K). In examples of *Tapejara* the downturn and the margin of naof lies anterior of the naof margin in SMNK PAL 1137 figured by Eck et al. (2011), coincident with the margin in CD-R-080/MCT 1500R and slightly caudal of the margin in SAO/UOSG 12891 (Fig. 4, C, A, B respectively). The overall shape of the anterior premaxilla is also distinctive, tapering to a slender point in the Chinese tapejarids *Huaxiapterus* and *Sinopterus*, but having a wider lateral angle in *Tapejara* and *Tupandactylus* (Fig. 4). In *Wightia* the tip of the premaxilla is missing, but projection

of the dorsal and ventral margins to a point, suggests it has a slender rostral tip, comparable with *Huaxiapterus atavismus* (Fig. 4 H) and *Sinopterus lingyuanensis* (Fig. 4 J).

6. Discussion

The partial premaxilla of *Wightia declivirostris* displays a number of features that allow it to be compared with a range of other tapejarid genera from a wide range of localities (Fig. 7, Table 2), representing a time span of potentially ~40 million years (Barremian to Turonian). Its sparse distribution of small foramina on the occlusal surface, its overall slender shape and its low angle of deflection of the anterior premaxilla distinguish it as a distinct taxon. Despite the number of near complete skeletons of tapejarids from China and three dimensionally preserved examples of Tapejaridae from Brazil, elsewhere in the World, many tapejarids are highly fragmentary, and there remains much to learn about the group, especially from the tantalising remains representing taxa from Spain, Morocco and now the Isle of Wight.

The Tapejaridae was erected by Kellner (1989) to accommodate *Tapejara wellnhoferi*, a (at the time) highly unusual anteriorly crested, edentulous pterosaur, and *Tupuxuara longicristatus*, also edentulous but bearing a posterior crest, both from the Santana Formation of Brazil (Kellner and Campos 2007). Since then many other pterosaurs from around the World have been assigned to this family such that, in a cladistic analysis by Longrich et al. (2018), two distinct sub clades occur within a Tapejaridae with a rather different content from Kellner's (1989) original concept. *Tupuxuara* falls out of Tapejaridae and lies instead within a clade comprising Azhdarchoidea and Dsungaripteroidea. The Tapejaridae comprises two 'subfamilies' in the Longrich et al. (2018) analysis, although neither of these is named. It should be noted however that several cladistic analyses including tapejarids have been published in recent years, all presenting very different models of their relationships (e.g. Andres and Myers, 2013; Andres et al., 2014; Vidovic and Martill, 2017).

Kellner and Campos (2007), without producing a cladistic analysis, defined a clade, Tapejarinae (incorrectly credited to Kellner, 1989: Kellner and Campos, 2007, p. 2) that comprised *Tapejara wellnhoferi*, *Tupandactylus imperator*, “*Tapejara*” *navigans*, *Sinopterus dongi*, *Sinopterus jii* and “*Huaxiapterus*” *corollatus*, but this grouping of taxa does not match any of the more recent cladistic analyses. Rather, we consider the analysis by Longrich et al. (2018), to better reflect the relationships of tapejarids (see Fig. 9). Accordingly, we retain the name Tapejarinae of Kellner and Campos (2007), but restrict its content to *Tapejara wellnhoferi*, *Caiuajara dobruskii*, *Tupandactylus* spp., *Europejara olcadesorum* and perhaps *Vectidraco daisymorrisae*. Its sister clade we name Sinopterinae nom. nov., and consider its content to be *Eopteranodon*, *Huaxiapterus* and *Sinopterus*. Tapejarinae are dominantly, but not exclusively from South America, while Sinopterinae are largely from China. Anomalous, the North America *Bennettazhia oregonensis* (Gilmore, 1928; Nesov, 1991) (Fig. 7) falls within this clade but we note that this taxon is known only from a humerus and may well not be a tapejarid. It is likely that *Wightia declivirostris* lies within Sinopterinae on account of its long tapering premaxilla, and its low (12°) downturn angle.

A pterosaurian pelvis from the Isle of Wight discovered in the Aptian (Early Aptian, *Deshayesites forbesi* Zone, *Deshayesites fittoni* Subzone) Atherfield Clay Formation of Atherfield Point was reported by Naish et al., (2013). The specimen, named *Vectidraco daisymorrisae* was assigned to Azhdarchoidea, without referral to a family. However, in their cladistic analysis (Naish et al., 2013, fig. 11a) the specimen nests with *Tapejara*, suggesting that it too is a Tapejarid. Unfortunately, *Vectidraco* and *Wightia* are not comparable, and are separated by perhaps as much as three million years.

7. Conclusions

Wightia declivirostris gen. et sp. nov. is clearly a member of Tapejaridae on account of the features discussed above and is the first record of Tapejaridae in the United Kingdom, though not the first

from Europe. Although the holotype is highly fragmentary, it is nonetheless distinctive, and adds to the growing diversity of pterosaurs from the Wessex Formation, that now includes Ornithocheiridae, Istiodactylidae and perhaps Ctenochasmatidae among toothed forms (Howse et al., 2001; Witton et al., 2009; Sweetman and Martill 2010), and the edentulous Tapejaridae. In addition, *Wightia* increases the geographic range of Tapejaridae into north-western Europe. The more anteriorly located jaw down turn implying affinities with *Sinopterus* and *Huaxiapterus* may suggest the presence of an Asian clade of tapejarids forming a distinct biogeographical province (Fig. 7). Sweetman and Martill (2010) noted “The apparent absence of toothless forms [pterosaurs] in the Wessex Formation [of the Isle of Wight] may be an artefact of preservation and/or collecting bias”. Clearly it was the latter, and this has now been rectified.

The new specimen demonstrates the need for continued palaeontological fieldwork. This is the first occurrence of an edentulous pterosaur in the Wealden Group of the UK and is a result of more than two hundred years of collecting Wealden Group vertebrates by many hundreds of people, both amateur and professional.

Among the first Wealden Group vertebrate fossils to be reported were those described by Gideon Mantell in the early 19th century. Pterosaur bones were present in Mantell’s collection, but were figured by him as bones from a heron-like bird (Mantell, 1837). The first pterosaur to be named from the Wealden Group was *Palaeornis cliftii* Mantell, 1844, but the generic name was preoccupied by a recent parrot, and Witton et al., 2009, in a reevaluation regarded it as an indeterminate lonchodectid. The first valid pterosaurs to be described from the Wealden Group are *Coloborhynchus clavirostris* and *Lonchodectes sagittirostris*, both from Sussex described by Richard Owen (1874). The first pterosaur to be reported from the Wealden Group of the Isle of Wight was *Pterodactylus nobilis*, a fragmentary wing bone now regarded as a nomen dubium (Howse et al., 2001). The first valid Isle of Wight pterosaur is *Istiodactylus latidens* described by Seeley (1901) as

285 *Ornithodesmus latidens*. It can be assumed many more exciting discoveries will be made in the next
286 200 years.

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450 **Figure Captions**

451

452 Fig. 1. Isle of Wight map and stratigraphy of the Wealden Group at Yaverland.

453

454 Fig. 2 *Wightia declivirostris* gen. et sp. nov. (IWCMS 2020. 401) from the Wessex Formation of
 455 Yaverland, Isle of Wight. Seen in A, right lateral; B, left lateral; C, dorsal; D, ventral; E, posterior, and
 456 F, anterior views. Scale bars = 10 mm.

457

458 Fig. 3. *Wightia declivirostris* gen. et sp. nov. (IWCMS 2020. 401) from the Wessex Formation of
 459 Yaverland, Isle of Wight. A, surface texture of fine 'groove-like' micro pores; B, patterned micro
 460 pores changing from elongate to pit-like; C, ripple-like texture on bone surface; D, quadrangular
 461 depressions where outer wall has been compacted into voids defined by internal , parallel partitions;
 462 E, detail of elongate foramina of occlusal surface.

463

464 Fig. 4. *Wightia declivirostris* gen. et sp. nov. (IWCMS 2020. 401). Occlusal surface of premaxilla and B,

465 interpretive drawing showing distribution of foramina. Abbreviations: Ant. anterior; nf, neural

466 foramina; ra, relic alveolus.

467

468 Fig. 5. Restoration of outline of *Wightia declivirostris* gen. et sp. nov.; A, right lateral view
 469 emphasising the degree of fracturing and expansion between fractures; B, right lateral view with
 470 fractures deleted, highlighting the limited distribution of lateral foramina; C, anterior and posterior
 471 portions restored so that dorsal and ventral margins are confluent.

Fig. 6. Tapejarid jaw tip outlines. **A**, *Tapejara wellnhoferi* MCT 1500-R/CD-R-080 (Kellner, 1989, fig. 1); **B**, *T. wellnhoferi* SAO/UOSG 12891 (Wellnhofer and Kellner, 1991, Pl. 1, fig 2B); **C**, *T. wellnhoferi* SMNK PAL 1137 (Eck, et al., 2011, fig. 2, pl. 1A); **D**, *Caupedactylus ybaka* MN 4726-V (Kellner, 2013, fig. 1); **E**, *Tupandactylus navigans* SMNK 2344 PAL (Frey, et al., 2003, fig. 1B); **F**, *Keresdrakon wilsoni* CP.V 2069 (Kellner, et al., 2019, fig. 3); **G**, *Huaxiapterus corollatus* ZMNH M8131 (Lü, et al., 2006, fig. 2); **H**, *Huaxiapterus atavismus* XHPM. 1009 (Lü, et al., 2016, fig. 5A); **I**, *Tupandactylus imperator* non-access (Unwin and Martill, 2007, fig. 17.9A); **J**, *Sinopterius lingyuanensis* JPM-2014-005 (Lü, et al., 2016, fig. 3); **K**, *Caiuajara dobruskii* Holotype CP.V 1449 (Manzig, et al., 2014, fig. 3); **L**, *Wightia*

481 *declivirostris* gen. et sp. nov. IWCMS 2020. 401 (this paper). Illustrations not to scale. All are drawn
 482 such that, with the jugal process of the maxilla orientated horizontally, the distance between the
 483 rostrum tip and the anterior border of the nasoantorbital fenestra is constant. Black arrow indicates
 484 point at which the occlusal margin is deflected downwards. Grey shading: light grey = bone; medium
 485 grey = bone of crest support; dark grey = restoration. Light grey vertical bands align the anterior
 486 border of the nasoantorbital fenestra.

487

488 Fig. 7. World map with tapejarid localities highlighted. Based on 130 mya map by Colorado Plateau
 489 Geosystems, Inc. 2016. [http://deeptimemaps.com/global-paleogeography-and-tectonics-in-deep-](http://deeptimemaps.com/global-paleogeography-and-tectonics-in-deep-time-series/)
 490 [time-series/](http://deeptimemaps.com/global-paleogeography-and-tectonics-in-deep-time-series/)

Fig. 8. Premaxillae of tapejarids compared. A, unnamed tapejarid from Kem Kem beds, Morocco; B, *Caiuajara dobruskii*; C, *Tapejara wellnhoferi*; D, *Tapejara wellnhoferi*; E, *Tapejara wellnhoferi*; F, *Caupedactylus ybaka*; G, *Wightia declivirostris* gen. et sp. nov. IWCMS 2020. 401; G1, *Wightia declivirostris* gen. et sp. nov. IWCMS 2020. 401 with restored tip. Not drawn to scale. A, after Wellnhofer and Buffetaut, 1999; B, after Manzig et al., 2014; C, after Kellner, 1989; D, after Wellnhofer and Kellner, 1991; E, after Eck et al., 2011; F, after Kellner, 2013.

Fig. 9. Time calibrated cladogram of the Tapejaridae extracted from a larger analysis by Longrich et al., 2018. The black star suggests the position of *Wightia declivirostris* on the basis only that it has a shallow downturn of the premaxilla and a long slender tip. The extended ranges of *Bennettazhia* and *Caiuajara* are a consequence of the insecure dating of the host formation.

Table 1. Selected measurements for the holotype premaxilla of *Wightia declivirostris* sp. nov. from the Wessex Formation of Yaverland, Isle of Wight, UK.

Parameter	Measurement
Average lateral angle	19°
Average dorsal angle	6°
Average angle of rostral deflection	~12°
Average apical angle of cross section anteriorly	83°
Average apical angle of cross section posteriorly	85°
Max length	38 mm
Anterior width (occlusal)	5 mm
Posterior width (occlusal)	7 mm
Anterior height	8 mm
Posterior height	19 mm

509 Table 2. Distribution of tapejarid pterosaurs in space and time.

Formation	Environment	Age	Location	Name	References
Caiua' Grp., Goio-Erê Fm./Rio Paraná Fm.	Desert with inter-dunal wetland	Disputed mid to Upper Cretaceous	Cruzeiro do Oeste, Paraná, Brazil	<i>Caiuajara dobruskii</i> <i>Keresdrakon wilsoni</i> ^a	Manzig et al. (2014) Kellner et al. (2019)
Csehbánya Fm.	Fluvial	Santonian	Northern Bakony Mountains, western Hungary	<i>Bakonydraco galaczi</i> ^b	Ősi et al. (2005)
Kem Kem Group	Fluvial-shallow marine	Albian?- Cenom.	Tafilalt, South- east Morocco	<i>Afrotapejarazouhrii</i>	Wellnhofer & Buffetaut (1999) Martill et al., 2020
Santana Fm./Romualdo Mbr.	Shallow marine	Aptian- Albian	Araripe Basin, northeastern Brazil	<i>Caupedactylus ybaka</i> <i>Tapejara wellnhoferi</i>	Eck et al. (2011) Kellner (2013)
Crato Fm./Nova Olinda Mbr.	Coastal lagoon	Late Aptian- early Albian	Araripe Basin, Brazil	<i>Aymberedactylus</i> <i>cearensis</i> <i>Tupundactylus</i> <i>imperator</i> <i>T. navigans</i>	Frey et al. (2003) Kellner & Campos (2007) Pêgas et al. (2016)
Elrhaz Fm.	Fluvial	Late Aptian	Département d'Agadez, Niger	? Tapejaridae indet.	Blackburn & Serenó (2002)
Jiufotang Fm.	Lacustrine	Aptian	Liaoning Province, China	<i>Sinopterus dongi</i> (<i>Huaxiapterus jii</i> <i>H. atavismu</i> <i>H. benxiensis</i> <i>H. corollatus</i> <i>Nemicolopterus</i> <i>crypticus</i> ^c)	Wang & Zhou (2003) Lü & Yuan (2005) Lü et al., 2006a, Lü et al., 2007, Lü et al., 2016 Wang et al.

Formation	Environment	Age	Location	Name	References
					(2008) Pan et al. (2013)
Atherfield Clay Fm. Chale Clay Mbr.	Marine	Early Aptian	Atherfield Point, Isle of Wight, UK	<i>Vectidraco daisymorrisae</i> ^b	Naish et al. (2013)
Yixian Fm.	Lacustrine	Late Barremian-early Aptian	Liaoning Province, China	Tapejaridae indet.	Barrett et al. (2008)
La Huérguina Fm.	Continental subtropical, wet and forested	Late Barremian	Las Hoyas, Cuenca, Spain	<i>Europejara olcadesorum</i>	Vullo et al. (2012)
Wessex Fm.	Fluvial	Barremian	Yaverland, Isle of Wight, United Kingdom	<i>Wightia declivirostris</i> gen. et sp. nov.	This paper

510 a

511 Tapejaromorpha.

512 b

513 possible tapejarid.

514 c

515 junior synonyms.

516

517 Table 3. Premaxillae deflection angles for Tapejaridae.

Taxon	Deflection angle	Horizon	Age (stage)	Reference
<i>Afrotapejara zoughrii</i> FSAC-KK 5004	7°	Kem Kem Group	?Albian-Cen.	Martill et al., 2020
<i>Caiuajara dobruskii</i> CP.V-1001	41°	Goio-Erê Fm.	Tur.-Camp.	Manzig et al. (2014)

Taxon	Deflection angle	Horizon	Age (stage)	Reference
<i>C. dobruskii</i> CP.V 1447	40°	Goio-Erê Fm.	Tur.- Camp.	Manzig et al. (2014)
<i>C. dobruskii</i> CP.V 1005	32°	Goio-Erê Fm.	Tur.- Camp.	Manzig et al. (2014)
<i>C. dobruskii</i> CP.V 1449	31°	Goio-Erê Fm.	Tur.- Camp.	Manzig et al. (2014)
<i>C. dobruskii</i> CP.V 1001	38°	Goio-Erê Fm.	Tur.- Camp.	Manzig et al. (2014)
<i>C. dobruskii</i> UEPG/DEGEO/MP- 4151 2nd	37°	Goio-Erê Fm.	Tur.- Camp.	Manzig et al. (2014)
<i>C. dobruskii</i> CP.V 1023	42°	Goio-Erê Fm.	Tur.- Camp.	Manzig et al. (2014)
<i>C. dobruskii</i> UEPG/DEGEO/MP- 4151 1st	32°	Goio-Erê Fm.	Tur.- Camp.	Manzig et al. (2014)
<i>C. dobruskii</i> CP.V 866	30°	Goio-Erê Fm.	Tur.- Camp.	Manzig et al. (2014)
<i>C. dobruskii</i> CP.V 1003	39°	Goio-Erê Fm.	Tur.- Camp.	Manzig et al. (2014)
<i>C. dobruskii</i> CP.V 1050-2	34°	Goio-Erê Fm.	Tur.- Camp.	Manzig et al. (2014)
<i>C. dobruskii</i> CP.V 1050-1	37°	Goio-Erê Fm.	Tur.- Camp.	Manzig et al. (2014)
<i>Caupedactylus ybaka</i> MN 4726-V	19°	Santana Fm.	?Albian	Kellner (2013)
<i>Nemicolopterus</i> IVPP V-14377	18°	Jiufotang Fm.	Aptian	Wang et al., 2008
<i>Huaxiapterus atavismus</i> XHPM 1009	16°	Jiufotang Fm.	Aptian	Lü et al. (2016)
<i>Huaxiapterus corallatus</i> ZMNH M8131	18°	Jiufotang Fm.	Aptian	Lü et al. (2006)

Taxon	Deflection angle	Horizon	Age (stage)	Reference
<i>Huaxiapterus jii</i> GMN-03-11-001	16°	Jiufotang Fm.	Aptian	Lü & Yuan, 2005
<i>Sinopteris dongi</i> IVPP V 13363	10°	Jiufotang Fm.	Aptian	Wang & Zhou (2003)
<i>S. lingyuanensis</i> JPM-2014-005	15°	Jiufotang Fm.	Aptian	Lü et al. (2016)
<i>Tapejara wellnhoferi</i> holotype CD-R-080	24°	Santana Fm.	?Albian	Kellner (1989)
<i>Tap. wellnhoferi</i> AMNH 24440	20°	Santana Fm.	?Albian	Wellnhofer & Kellner (1991)
<i>Tap. wellnhoferi</i> juvenile SMNK PAL 1137	25°	Santana Fm.	?Albian	Eck et al. (2011)
<i>Tupandactylus navigans</i> SMNK 2344 PAL	22°	Crato Fm.	Aptian	Frey et al. (2003)
<i>Tup. navigans</i> SMNK 2343 PAL (<i>Ingridia</i>)	21°	Crato Fm.	Aptian	Frey et al. (2003)
<i>Tup. imperator</i> private coll. specimen	27°	Crato Fm.	Aptian	This paper
<i>Wightia declivirostris</i> IWCMS. 2020. 401	12°	Wessex Fm.	Barremian	This paper