A TYRANNOSAUROID DINOSAUR FROM THE UPPER JURASSIC OF PORTUGAL

by OLIVER W. M. RAUHUT

ABSTRACT. Fragmentary theropod remains from the Upper Jurassic (Kimmeridgian) of Guimarota, Portugal, represent a new taxon of theropod dinosaurs, *Aviatyrannis jurassica* gen. et sp. nov. Together with *Stokesosaurus* from the Morrison Formation of North America, *Aviatyrannis* represents the oldest known tyrannosauroid, indicating that tyrannosauroid origins may be found in the Middle–Late Jurassic of Europe/North America. Furthermore, current evidence suggests that early tyrannosaurs were rather small animals, which is in general accordance with their origin amongst the generally rather small coelurosaurs.

KEY WORDS: Upper Jurassic, Iberian peninsula, Theropoda, Tyrannosauroidea, *Aviatyrannis* gen. nov.

TYRANNOSAURIDS were the dominant large terrestrial predators in the Late Cretaceous of the Northern Hemisphere, and ever since the description of *Tyrannosaurus rex* (Osborn, 1905), they have captured the imagination of experts and the general public alike. However, little is still known about their origin and early evolution, although cladistic analysis predicts that the tyrannosauroid lineage reaches back to at least the Late Jurassic (e.g. Sereno 1999; Holtz 2000; Rauhut 2003). Recently, some new material has been described that might shed some light on the early history of this group (Zinke 1998; Manabe 1999; Hutt *et al*. 2001). However, the only Jurassic taxon that has been argued to be a tyrannosauroid is *Stokesosaurus* from the Kimmeridgian–Tithonian of the Morrison Formation of North America (Madsen 1974).

In the present work, a new theropod dinosaur with tyrannosauroid affinities from the Upper Jurassic (Kimmeridgian) of Portugal is described and character evidence for the tyrannosaurid affinities of this taxon and *Stokesosaurus* is presented. The material described here is derived from the Alcobaça Formation of central Portugal. It comes from a lignite coal layer at the locality of Guimarota, which has yielded a wealth of fossils (Martin and Krebs 2000). Other dinosaur remains from this locality, including tyrannosauroid premaxillary teeth, have been described by Thulborn (1973), Zinke and Rauhut (1994), Weigert (1995), Zinke (1998), and Rauhut (2000, 2001).

Institutional abbreviations. AMNH, American Museum of Natural History, New York; BMNH, Natural History Museum, London; BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich; IPFUB, Institut für Geologische Wissenschaften, Fachrichtung Paläontologie, Freie Universität Berlin; MOR, Museum of the Rockies, Bozeman, Montana; OUM, Oxford University Museum; UMNH, Utah Museum of Natural History, Salt Lake City; YPM, Yale Peabody Museum, New Haven.

SYSTEMATIC PALAEONTOLOGY

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1887
THEROPODA Marsh, 1881
COELUROSAURIA von Huene, 1914
TYRANNOSAUROIDEA (Osborn, 1906)

Genus AVIATYRANNIS gen. nov.

Derivation of name. Latin, *avia*, grandmother, and *tyrannis*, genitive form of *tyrannus*, tyrant.

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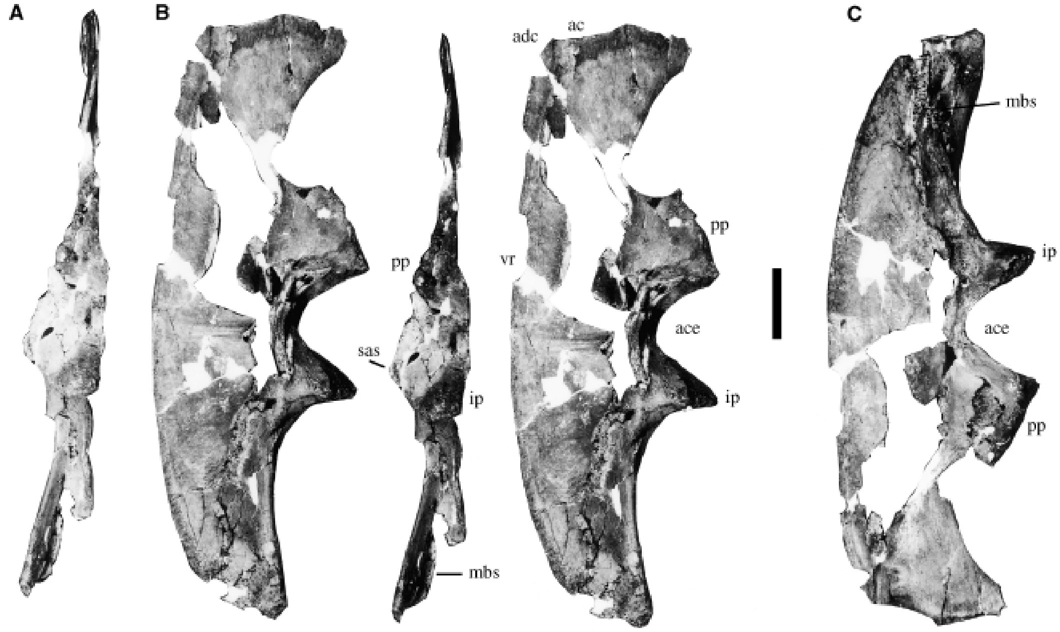


TEXT-FIG. 1. *Aviatyrannis jurassica* gen. et sp. nov., holotype, from the Alcobaça Formation of Guimarota, Portugal, IPFUB Gui Th 1, right ilium. A, ventral view (stereophotographs). B, lateral view (stereophotographs). C, medial view. ac, anterior concavity; ace, acetabulum; adc, antero-dorsal concavity; ip, ischial peduncle; mbs, medial brevis shelf; pp, pubic peduncle; sas, supracetabular shelf; vr, vertical ridge. Scale bar represents 10 mm.

Type and only known species. *Aviatyrannis jurassica* sp. nov.

Diagnosis. As for the only known species, *A. jurassica*.

Aviatyrannis jurassica gen. et sp. nov.

Text-figures 1–3

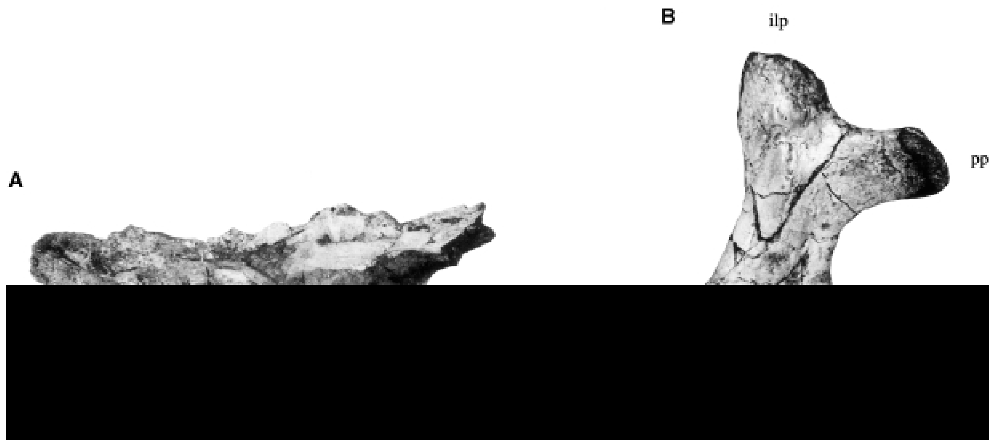
Derivation of name. The specific name refers to the Jurassic age of the taxon; thus, the 'tyrant's grandmother from the Jurassic'.

Holotype. IPFUB Gui Th 1, almost complete right ilium (Text-fig. 1).

Locality and horizon. Guimarota locality, close to Leiria, central Portugal. The material comes from a lignitic coal layer within the Alcobaça Formation, Kimmeridgian (Schudack 2000).

Referred material. A fragmentary ilium IPFUB Gui Th 2 (Text-fig. 2A), partial right ischium IPFUB Gui Th 3 (Text-fig. 2B), several premaxillary teeth (see Zinke 1998; Rauhut 2000), all from the same locality as the type. The ilium is referred to the new taxon by direct comparison with the type ilium. The other material from the type locality is referred to this taxon because it shows clear tyrannosauroid affinities and is of closely matching size.

Diagnosis. Small tyrannosauroid theropod. Ilium low and elongate, with a well-developed, vertical, hollow ridge above the acetabulum. Dorsal half of anterior margin of preacetabular blade shallowly concave; this part is set off from the dorsal rim by an even smaller, anterodorsally facing concavity. Differs from the vast majority of theropods in the presence of a strongly developed ridge above the acetabulum



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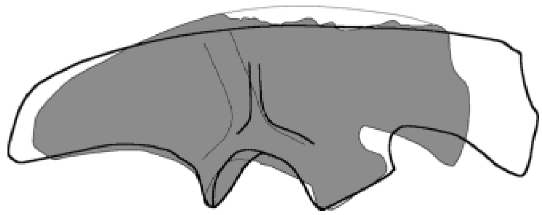
TEXT-FIG. 2. *Aviatyrannis jurassica* gen. et sp. nov., referred material from the Alcobaça Formation of Guimarota, Portugal. A, ilium IPFUB Gui Th 2 in lateral view. B, ischium IPFUB Gui Th 3 in lateral view. ace, acetabulum; df, distal flange; ilp, iliac peduncle; ip, ischial peduncle; op, obturator process; pp, pubic peduncle. Scale bars represent 10 mm.

and a dorsally concave part of the anterior rim; from *Piatnitzkysaurus* and one specimen referred to *Megalosaurus* (OUM J 13560) in the more elongate shape of the ilium, the relatively longer preacetabular blade, the relatively narrower pubic peduncle, and the vertical ridge being more clearly defined; from *Iliosuchus* (BMNH R 83) in the lack of a bulge of the dorsal rim above the acetabular part, the ridge not being inclined posteriorly, and the posteriorly expanding, relatively broader brevis fossa; from *Stokesosaurus* in the more elongate shape, the ridge not being inclined posteriorly, and the overall shape; from *Siamotyrannus* in the more elongate shape of the ilium, the relatively longer preacetabular blade, the relatively narrower pubic peduncle, the presence of only one vertical ridge, and the presence of the dorsal concavity in the anterior rim; from later tyrannosaurids in being relatively lower and more elongate and lacking the very strongly ventrally expanded anterior hook.

Description. Only the postcranial remains are described here; for a description and figures of the teeth, see Zinke (1998) and Rauhut (2000). None of the ilia from Portugal is complete. The type, IPFUB Gui Th 1, is the most complete element, in which only parts of the iliac blade are missing and the anterior rim of the pubic peduncle is damaged (Text-fig. 1). IPFUB Gui Th 2 is only represented by a well-preserved acetabular rim of an ilium, including both peduncles, of a slightly larger individual (Text-fig. 2A). The ischium IPFUB Gui Th 3 is of an individual of slightly larger size as Gui Th 2. It is missing the distal end and most of the obturator process, but is otherwise rather well preserved (Text-fig. 2B).

The type ilium is *c*. 90 mm long. The iliac blade is relatively low, its height above the acetabulum being only 21 mm. The dorsal margin of the acetabular blade is gently curved throughout its entire length. The preacetabular process is slightly longer than the postacetabular one (measured from the ventral acetabular rim of the respective peduncle). As in most non-avian tetanuran theropods, the anterior end of the preacetabular process is ventrally expanded. The anterior margin of the bone is concave in its dorsal half. The pubic peduncle is short and very long antero-posteriorly. Gui Th 2 shows that the anterior margin of the peduncle is concave, with the ventral part ending in an anteriorly directed tip. The anterior iliac blade arises from a point at the mid-length of the dorsal part of the peduncle. The ischial peduncle is much less broad than the pubic peduncle and tapers ventrally. As in most theropods, the dorsal margin of the acetabulum is laterally expanded into a supraacetabular crest. Above the crest, a well-developed, sharply defined vertical ridge is present. This ridge is hollow, as is evident from its broken ventral part. The dorsal margin of the postacetabular blade curves downward posteriorly and meets the posterior end in a wide angle. The medial brevis shelf extends from the posterior brevis fossa to the posterior end of the dorsal margin; thus, the brevis fossa is very deep, but narrow. Anterodorsally of the pubic peduncle, the beginning of a medial ridge or shelf is visible; the structure itself is not preserved in any of the specimens.



TEXT-FIG. 3. Comparison of the shapes of the type ilia of *Aviatyrannis* gen. nov. (IPFUB Gui Th 1; thick line) and *Stokesosaurus* (UMNH VP 7434; shaded). Both ilia drawn to same acetabular length.

The proximal end of the ischium is transversely flattened and bifurcates into the iliac peduncle dorsally and the pubic peduncle anteriorly. The iliac peduncle is anteroposteriorly long and has a low triangular flange posteriorly, on which a very faint semilunate muscle attachment area is found. The facet for the reception of the ischial peduncle of the ilium is developed as an oval concavity. The pubic peduncle is more slender than the iliac peduncle and has a sharp ventral margin. The acetabular rim of the pubic peduncle is wider than that of the iliac peduncle and widens towards the connection with the pubis. The latter is poorly preserved, but was most probably developed as a simple butt-joint. The gradually tapering shaft of the ischium indicates that no distal expansion was present. In contrast to the plate-like proximal section, the shaft becomes more massive distally and is broader transversely than anteroposteriorly at the break. The obturator process was clearly separated from the pubic peduncle by a broad obturator notch, and it seems to have been confluent with the ischial shaft distally, where it continues almost up to the break as a distally narrowing flange on the anterior side of the shaft. The shaft of the ischium shows a conspicuous bend just below the obturator process, so that the distal end is set at an angle to the proximal part and points more posteriorly.

Discussion. The type ilium of *Aviatyrannis jurassica* gen. et sp. nov. was tentatively referred to *Stokesosaurus* by Rauhut (2000), based on the shared characters of a well-defined ridge above the acetabulum and a dorsally concave anterior rim of the acetabular blade. However, both characters are not restricted to this genus (see character analysis below), and the ilia of *Stokesosaurus* and *Aviatyrannis* differ greatly in their general shape and the orientation of the ridge above the acetabulum, making a referral to the same taxon seem very unlikely (Text-fig. 3).

Foster and Chure (2000) referred a small ilium from the Kimmeridgian of the Morrison Formation of South Dakota to *Stokesosaurus*, despite differences in the orientation of the ridge and the shape of the postacetabular blade, mainly basing this referral on the presence of a vertical ridge, the rounded posterodorsal rim of the postacetabular blade and a squared off posterior end of the brevis fossa. However, all of these characters are found in other theropods, including *Aviatyrannis*. Indeed, the postacetabular blade of the ilium from South Dakota is very similar in shape and relative length to the postacetabular blade of the type of *Aviatyrannis*, indicating that this specimen might be referable to the latter taxon. Unfortunately, the specimen from South Dakota was lost, so the matter cannot be resolved.

Bakker (2000) figured an isolated premaxillary tooth from the Morrison Formation. Although the tooth was identified as dromaeosaurid by this author, its characteristics, especially the D-shaped cross-section, is more consistent with tyrannosauroid affinities. This tooth is very similar to the tyrannosauroid teeth referred to *Aviatyrannis* and differs from other tyrannosauroid teeth from the Morrison Formation reported by Ford and Chure (2001; Chure, pers. comm. 2002). Thus, this might be further evidence for the presence of at least two taxa of tyrannosauroid in the Morrison Formation.

CHARACTER ANALYSIS

The dolichoiliacic morphology of the specimens from Guimarota clearly demonstrates that they represent theropod ilia. Within theropods, they exhibit several tetanuran synapomorphies, such as the dorsoventrally expanded anterior end of the iliac blade, the anteroposteriorly elongated pubic peduncle, and the ventrally tapering ischial peduncle with a reduced articular facet. The detailed relationships of *Aviatyrannis* and *Stokesosaurus* within Tetanurae are discussed below.

Coelurosaurian characters

1. Preacetabular blade of the ilium as long as or longer than postacetabular blade. Although the enlargement of the preacetabular blade of the ilium (dolichoiliacic condition) is a general feature of all neotheropods, the preacetabular blade is significantly shorter than the postacetabular blade in all non-tetanuran theropods and in basal tetanurans such as *Allosaurus* (Madsen 1976) and *Sinraptor* (Currie and Zhao 1993). In *Aviatyrannis* and *Stokesosaurus* (UMNH VP 7434), the preacetabular process is approximately as long as the postacetabular process, which is the situation found in many basal coelurosaurs (e.g. *Compsognathus*: BSP A.S. I 563; tyrannosaurids: Osborn 1916; ornithomimosaurs: Osmólska *et al*. 1972). In more advanced coelurosaurs, the preacetabular blade is even relatively longer (e.g. Norell and Makovicky 1997; see also Hutchinson 2001).
2. Pubic peduncle of ilium transversely narrow and more than three times longer anteroposteriorly than wide at its middle. In non-tetanuran theropods, the pubic peduncle is approximately as long anteroposteriorly as the ischial peduncle, and the latter has a well-defined facet for the contact with the ischium. In tetanurans, the pubic peduncle is considerably longer than the ischial peduncle, and the latter tapers ventrally. However, in coelurosaurs the pubic peduncle is narrow with subparallel margins and at least three times longer anteroposteriorly than wide transversely, whereas it is transversely broad in basal tetanurans such as *Allosaurus* (Madsen 1976). In connection with this even-further-increased anteroposterior length of the pubic peduncle in coelurosaurs, the preacetabular blade arises from the mid-length of the peduncle, instead of its anterior margin. This is also the situation found in *Aviatyrannis* and in *Stokesosaurus*.
3. Anterior margin of the pubic peduncle concave, with an anteriorly expanded 'lip' at its ventral end. Whereas the anterior margin of the pubic peduncle is straight or even slightly convex in non-tetanuran theropods and basal tetanurans (e.g. Madsen 1976; Currie and Zhao 1993), it is concave and shows an expansion ventrally in basal coelurosaurs (Martill *et al*. 2000), ornithomimosaurs (*Archaeornithomimus*: AMNH 21790), dromaeosaurids (*Saurornitholestes*: MOR 660), tyrannosaurids (Osborn 1916), *Stokesosaurus*, and *Aviatyrannis*.
4. Obturator process of ischium clearly offset from the pubic peduncle and confluent with ischial shaft distally. In the vast majority of basal theropods and basal tetanurans, the obturator flange or obturator process is separated from the ischial shaft distally by a small notch (e.g. Madsen 1976). Only in the most basal theropods, *Eoraptor* and herrerasaurids, and in *Elaphrosaurus* and *Torvosaurus*, is this notch absent; however, in these taxa the obturator process is not offset from the pubic peduncle of the ischium. In all coelurosaurs, the obturator process is offset from the pubic peduncle of the ischium by a broad obturator notch, and is confluent with the shaft of the ischium distally. This also seems to be the situation in IPFUB Gui Th 3.
5. Ischial shaft with a pronounced bend underneath the obturator process. In non-tetanuran theropods and basal tetanurans, the ischial shaft is straight throughout its entire length beneath the origin of the iliac peduncle. In *Compsognathus* (BSP AS I 563), oviraptorosaurs (e.g. Barsbold *et al*. 1990), dromaeosaurids (*Deinonychus*: YPM 5235), tyrannosaurids (e.g. Carpenter 1990), and IPFUB Gui Th 3, the section of the shaft below the obturator process is flexed posteriorly, resulting in an offset of this part from the proximal shaft at a wide angle. It is difficult to determine if this character is present in ornithomimosaurs and therizinosaurids, owing to the very proximally placed obturator process in the former and the very distally placed process in the latter.

Tyrannosauroid characters

6. Strongly developed and well-defined vertical ridge above the acetabulum on the ilium. In the majority of theropods, the iliac blade above the acetabulum is smooth, but in a few theropods, such as *Piatnitzkysaurus floresi* (Bonaparte 1986), or an ilium referred to *Megalosaurus* (OUM J 13560), it is subdivided by a ridge into an anterior and a posterior part. However, within coelurosaurs, a vertical ridge above the acetabulum is only found in tyrannosaurids (e.g. Osborn 1916; Lambe 1917), the therizinosaur *Segnosaurus* (Barsbold and Maryanska 1990) and some birds (e.g. *Apteryx*; McGowan 1979). The ilia of therizinosauroids and birds are strongly modified, so that a close relationship between *Aviatyrannis* and

these taxa can be excluded, especially since basal members of these clades do not show this character. Furthermore, in most non-coelurosaurian taxa that show a vertical ridge, it is faint and developed as a lateral bulge rather than a ridge, or is very broad at its base and tapers dorsally. A narrow, sharply defined, rounded vertical ridge that extends over almost the complete height of the ilium is only found in tyrannosaurids, *Stokesosaurus*, and *Aviatyrannis*. As discussed by Rauhut (2003), this ridge might have served as a boundary between attachment sites for the M. iliotrochantericus and the M. iliofemoralis, although some caution is needed in this reconstruction (Hutchinson 2001).

7. Dorsal part of the anterior margin of the preacetabular blade concave. In theropods generally, the entire anterior margin of the preacetabular blade of the ilium forms an anteriorly convex arch or a straight line. In tyrannosaurids only, the dorsal part of this margin is conspiciously concave (e.g. Molnar *et al*. 1990). This character is also found in *Aviatyrannis* and *Stokesosaurus*.

8. Distal flange on the ischium that extends from the obturator process to at least halfway along the shaft of the ischium. In theropods ancestrally, the obturator process or flange on the ischium is restricted to the proximal third of this bone, and this is the situation retained in the vast majority of tetanurans, with the exception of maniraptorans, in which the process as a whole is placed distally. In tyrannosaurs (e.g. Lambe 1917), a thin flange of bone extends from the proximally placed obturator process distally and extends to at least half the length of the shaft. Such a flange was obviously also present in IPFUB Gui Th 3.

DISCUSSION

Based on the character analysis presented above, both *Aviatyrannis* and *Stokesosaurus* can be shown to represent the only known Jurassic representatives of the tyrannosauroid lineage. However, given the poor fossil record of Middle Jurassic theropods, the origin of tyrannosauroids might even be pushed back further by new finds. Indeed, the small Middle Jurassic theropod *Iliosuchus* might be an even earlier representative of this lineage, since it also has a well-developed vertical ridge above the acetabulum (von Huene 1932). An ilium referred to *Iliosuchus* (OUM 29871) furthermore also shows an elongate pubic peduncle, indicating coelurosaurian affinities (Chure, pers. comm. 2002). Unfortunately, however, not enough of *Iliosuchus* is known to establish tyrannosaur affinities with more certainty.

The presence of basal tyrannosauroids in both the Kimmeridgian of Portugal and the Morrison Formation of North America (Madsen 1974; Foster and Chure 2000; Ford and Chure 2001) strengthens the close biogeographic relationships between these two areas in the Late Jurassic, which are also indicated by a variety of other vertebrates (e.g. Evans and Chure 1998; Martin 1999; Pérez-Moreno *et al*. 1999). In the Lower Cretaceous, tyrannosauroids are known from Europe (Hutt *et al*. 2001) and Asia (Manabe 1999). The referral of *Siamotyrannus* from the Lower Cretaceous of Thailand to the Tyrannosauroidea (Buffetaut *et al*. 1996) is questionable, since this taxon lacks any unambiguous coelurosaurian synapomorphies.

In the Late Cretaceous, tyrannosauroids are known from both Asia and North America. The probable oldest Late Cretaceous record of this group is isolated teeth from the Cenomanian of Utah (Kirkland and Parrish 1995), whereas the genus *Alectrosaurus* from the Iren Dabasu Formation of central Asia probably represents the oldest skeletal record (Mader and Bradley 1989; Currie and Eberth 1993). Towards the end of the Late Cretaceous, tyrannosaurids were widely distributed in both Asia and North America (Carpenter 1992). Thus, the available evidence indicates a Euro-North American origin of tyrannosauroids and a probable subsequent Asian diversification of this group, but more material, especially of small Middle and Late Jurassic theropods from Asia, is needed to test this hypothesis.

Furthermore, the material described here, and the teeth described by Zinke (1998) and Manabe (1999), indicate that early tyrannosauroids were rather small animals, and that this group attained giant size mainly in the Late Cretaceous, as already suspected by Manabe (1999). This is in general accordance with tyrannosaurid origins among the mostly rather small coelurosaurs (Holtz 1994). However, the recovery of *Eotyrannus* from Barremian deposits in England (Hutt *et al*. 2001) also shows that some early tyrannosaurs had already attained a large size.

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