

Spinosaurids before Stromer: early finds of spinosaurid dinosaurs and their interpretations

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Abstract: When Stromer described *Spinosaurus aegyptiacus* and erected the family Spinosauridae in 1915 he mentioned that teeth from the Cretaceous of the Djoua region of eastern Sahara, considered by Haug as belonging to a fish, probably belonged to *Spinosaurus*. The teeth from Djoua had been collected by the French Foureaux–Lamy Mission, which had crossed the Sahara from 1898 to 1900. Earlier finds of spinosaurid specimens include the jaw fragments from the Early Cretaceous of Portugal referred by Sauvage to a new species of *Suchosaurus*, *S. girardi*. The genus *Suchosaurus* had been erected by Owen in 1841, with *S. cultridens* as type species, on the basis of ribbed and compressed teeth from the Wealden of England that he considered as belonging to a crocodylian. The *Suchosaurus* material from Portugal actually belongs to *Baryonyx*, as do most of the teeth from the Wealden of England referred to *Suchosaurus*. The teeth described by Owen had been obtained from a quarry in Tilgate Forest (Sussex) by Mantell, who described and illustrated some of them in several of his publications, notably *Illustrations of the Geology of Sussex* in 1827. Several of these specimens can be identified in the collections of the Natural History Museum, London. Mantell's earliest published illustrations of these teeth are predated by Cuvier's illustration of a tooth from Tilgate Forest sent to him by Mantell, published in 1824. It thus appears that baryonychine teeth were among the first dinosaur remains to be described and illustrated (as crocodylian teeth) at the time of the discovery of *Megalosaurus* and *Iguanodon*, and well before the term 'dinosaur' was coined. It was not until the description of *Baryonyx walkeri* in 1986 that the real affinities of *Suchosaurus* could be elucidated. Because of their peculiar morphology, spinosaurid teeth from various parts of the world were frequently mistaken for those of other reptiles.

Between 1910 and 1914 fieldwork in Egypt under the direction of the Bavarian palaeontologist Ernst Stromer von Reichenbach (1870–1952) resulted in the collection of a considerable number of Mesozoic and Cenozoic vertebrate fossils (see Nothdurft & Smith 2002 for a recent account of Stromer's researches). The results of Stromer's work in Egypt were published by the Bavarian Academy of Sciences in a series of monographs, the first of which appeared in 1914 (see Stromer 1936 for a list). In 1915 Stromer described one of the most remarkable discoveries, an incomplete skeleton of an unusual theropod dinosaur, found by his collector Richard Markgraf in the Cenomanian strata of the Baharija oasis, in the western desert of Egypt. He erected the new taxon *Spinosaurus aegyptiacus* for this specimen, which he placed in a new theropod family, the Spinosauridae (Stromer 1915). Stromer subsequently referred to the Spinosauridae additional theropod material from Baharija, which he called '*Spinosaurus B*' (Stromer 1934), and he discussed *Spinosaurus* again in a general review of the Baharija depression and its fossils (Stromer 1936). Although Stromer's original descriptions were detailed and careful, the real significance of

the Spinosauridae as a highly unusual family of theropods was not immediately appreciated, and the destruction of the specimens in a British air raid on Munich in 1944 added to the uncertainty concerning this group of dinosaurs. It was only after the discovery in the Wealden of England of another unusual theropod, described as *Baryonyx walkeri* by Charig & Milner (1986), that a better image of the Spinosauridae began to emerge when it was realized that *Spinosaurus* and *Baryonyx* were closely related dinosaurs (Paul 1988; Buffetaut 1989, 1992), showing a number of unusual specializations, especially in the structure of their jaws and teeth, which to some extent are reminiscent of those of fish-eating crocodylians (Charig & Milner 1997).

In the light of our current knowledge of that group of dinosaurs, re-examination of various fossils reveals that a number of spinosaurid specimens, mostly isolated teeth, had been found and reported, from different localities, before Stromer's original description of *Spinosaurus aegyptiacus*, but had not been interpreted as belonging to dinosaurs, largely because of their fragmentary nature. They are reviewed in the present paper, and their

interpretations are discussed. As will be shown later, it appears that spinosaur remains were among the first dinosaur specimens to be scientifically described and figured, by such eminent palaeontologists as Gideon Mantell, Georges Cuvier and Richard Owen, although their real significance went unrecognized at the time because they were mistaken for crocodylian teeth.

The first *Spinosaurus* teeth from the Sahara: the Foureau-Lamy mission (1898–1900)

In the paper in which he described *Spinosaurus aegyptiacus*, Stromer (1915) mentioned an earlier description of material, probably belonging to a spinosaurid, consisting of two isolated teeth from the eastern part of the Sahara (Fig. 1c). They had been found during the Foureau–Lamy Mission, one of the most remarkable colonial endeavours of late-nineteenth century France (Foureau 1902;

Abadie & Abadie 1989; Buffetaut 2005). This expedition, led by an army officer, François Lamy (1858–1900), and a civilian, the explorer Fernand Foureau (1850–1914; Fig. 1a), started from the French colony of Algeria in October 1898 and crossed the Sahara from north to south, to reach Lake Chad in 1900. Its aim was supposed to be peaceful and scientific, but the explorers were accompanied by a large contingent of several hundred colonial troopers led by French officers and non-commissioned officers, equipped with an impressive assortment of weapons, including field guns. One of the undisclosed aims of the mission was to subdue the Tuareg tribes of the southern Sahara, who in 1881 had murdered a group of French soldiers led by Colonel Flatters, and thus to strengthen French rule in that part of Africa. Furthermore, by pushing further south to Lake Chad, the Foureau–Lamy Mission was to establish a continuous territorial link between the French possessions in North Africa and those of the Congo region in Central Africa, thus thwarting

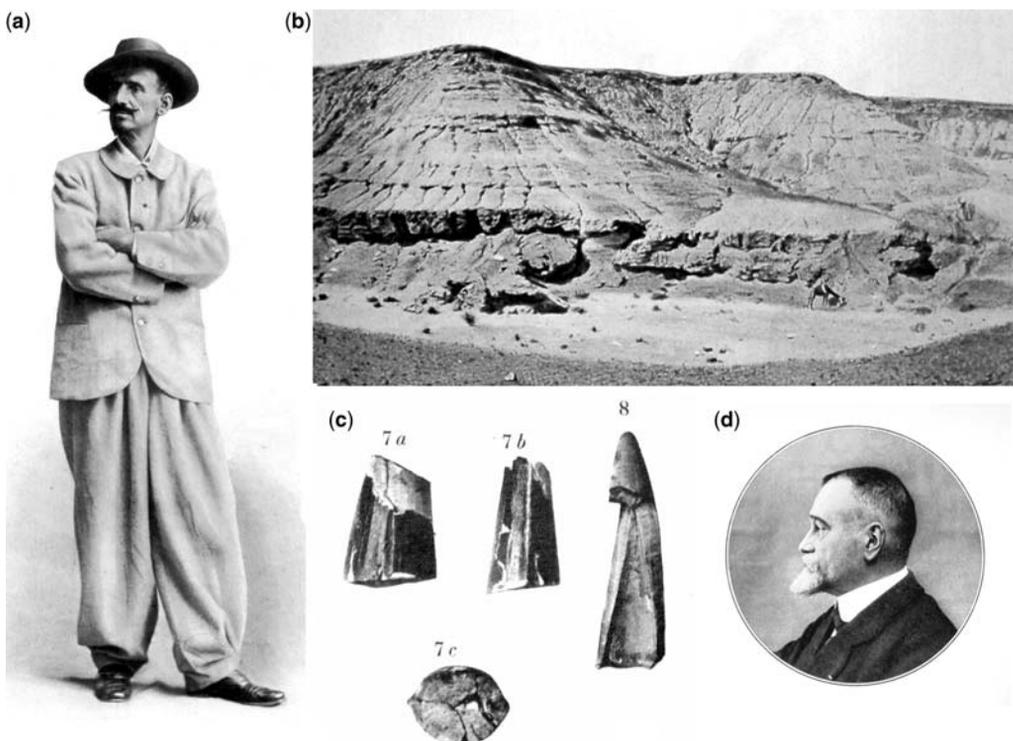


Fig. 1. The first discovery of African spinosaurs. (a) Fernand Foureau (1850–1914) who collected spinosaur teeth in the Djoua region of the Sahara in 1898. (b) The Djoua escarpment in the eastern Sahara (Algeria), showing Cenomanian vertebrate-bearing marls overlain by marine limestones (after Foureau 1905). (c) Teeth collected by Foureau in the Djoua in 1898 (from Haug 1905, plate XVII, figs 7 & 8), identified by Haug (1905) as ? *Saurocephalus*, interpreted as spinosaurid teeth by Stromer (1915). (d) Emile Haug (1861–1927), who described the fossils collected by the Foureau–Lamy Mission.

British efforts to link Nigeria with the Anglo-Egyptian Sudan (only a couple of months before the start of the Foureau–Lamy Mission, in September 1898, France and Britain had been on the brink of war following the incident at Fashoda, on the Upper Nile, where Kitchener’s Anglo-Egyptian troops had stopped the eastward progression of a French military expedition led by Major Marchand).

After enduring considerable hardships during their crossing of the Sahara and the regions just south of the desert, where the natives, to the astonishment of the French explorers, were not exactly friendly, the Foureau–Lamy Mission finally reached the banks of Lake Chad in January 1900, only to engage in fighting against the troops of the local ruler and slave-holder, Rabah, who eventually was defeated and killed at Kousseri on 22 April 1900, during a battle in the course of which Lamy was fatally wounded. Meanwhile, Fernand Foureau had left the rest of the party and reached the French possessions on the Congo, from which he sailed to France with what was left of the specimens that had been collected by the expedition, reaching Marseilles on 2 September 1900.

These collections formed the basis of a massive two-volume report on the scientific results of the Foureau–Lamy Mission, published in 1905, which included papers, many of them written by Foureau himself, on the geography, meteorology, geology, palaeontology, botany, zoology and ethnography of the regions that had been visited. In the section on geology, Foureau (1905) described the geological succession in the Djoua escarpment of the SE Sahara (now part of Algeria), where he had collected fossils in November 1898. There, Cenomanian marine limestones overlie gypsiferous red clays and sandstones containing vertebrate remains (Fig. 1b). A similar succession is frequently encountered on the outskirts of the Sahara, notably in southern Morocco and western Algeria. The fossils collected by Foureau in the Djoua had originally been entrusted for description to Ernest Munier-Chalmas (1843–1903), but he died before he could complete their study, and they were finally described in the palaeontology section of the report by Emile Haug (1861–1927; Fig. 1c), a geologist and invertebrate palaeontologist who succeeded Munier-Chalmas at the Geology Department of the Sorbonne. On the basis of relatively scanty material, Haug (1905) identified various fish (including a lungfish), chelonians and dinosaurs (on the basis of a single caudal vertebra and large bone fragments). This was the first report of dinosaur bones from the Sahara (Buffetaut 2005). The teeth later interpreted by Stromer (1915) as possibly belonging to *Spinosaurus* were referred by Haug to ? *Saurocephalus*, an ichthyodectid fish. Unfortunately, it has not

been possible to re-examine the original specimens. A search for the fossils collected by Foureau in the palaeontology collection of University Paris 6, where they should be kept, yielded only a single fish vertebra, and the present whereabouts of the *Spinosaurus*-like teeth are unknown. Nevertheless, on the basis of the illustrations published by Haug, there is every reason to believe that Stromer was right in supposing that they possibly belonged to *Spinosaurus aegyptiacus*. His assessment was based on their shape and size, although he admitted that the systematic significance of isolated dinosaur teeth should not be overestimated. Comparison of the teeth from the Djoua escarpment with *Spinosaurus* teeth from the Albian of Tunisia and the Cenomanian of Morocco, and with figures of the type specimen of *Spinosaurus aegyptiacus* from the Cenomanian of Egypt, reveals strong similarities in the conical shape of the crown, smooth enamel and presence of well-defined carinae. Foureau’s finds from the Djoua can thus be considered as the first discovery of spinosaurid remains in Africa.

Spinosaurus teeth are found in abundance in Albian–Cenomanian red beds in various regions on the outskirts of the Sahara, notably in Tunisia (Bouaziz *et al.* 1988), SW Algeria and southern Morocco (Amiot *et al.* 2004). The specimens from the Djoua escarpment were found in a similar geological setting. The vertebrate-bearing beds of that part of SE Algeria have attracted relatively little attention. Lapparent (1960) noted that the Djoua valley is relatively rich in vertebrate remains, including dinosaurs, but did not record *Spinosaurus* specimens from that area (see below for a possible explanation).

An early spinosaurid find from Portugal: Sauvage, *Suchosaurus* and *Baryonyx*

While Stromer could recognize the spinosaurid affinities of the teeth from the Djoua escarpment on the basis of their resemblance with the type of *Spinosaurus aegyptiacus*, identifying isolated teeth or fragmentary jaw remains of less derived taxa of spinosaurid theropods remained extremely difficult until the discovery and description of the holotype of *Baryonyx walkeri*, from the Wealden of Surrey, in the 1980s and 1990s (Charig & Milner 1986, 1990, 1997). *Baryonyx* teeth differ from those of *Spinosaurus* in several respects, being more compressed labiolingually, with serrated carinae, and a ribbed and wrinkled enamel (Buffetaut 2007). Although they are more reminiscent of ‘normal’ theropod teeth than *Spinosaurus* teeth in their compression and serrations, the fairly strong ornamentation of their enamel is reminiscent of crocodylian teeth, which, in the nineteenth century, led to

systematic misinterpretations, *Baryonyx* teeth being routinely ascribed to crocodiles (see below).

A case in point is that of jaw fragments containing broken teeth from the Early Cretaceous (Barremian) of Boca do Chapim, near Cape Espichel on the Portuguese coast south of Lisbon (Fig. 2). The specimens were collected by the Swiss geologist Paul Choffat (1849–1919; Fig. 2a), who worked for many years in Portugal (Fleury 1920), and studied by the French palaeontologist Henri-Emile Sauvage (1842–1917; Fig. 2b). Sauvage was the leading French expert on Mesozoic fish and reptiles in the late nineteenth century, at a time when most French vertebrate palaeontologists were more interested in fossil mammals (Buffetaut *et al.* 1993). In addition to short preliminary papers (Sauvage 1896, 1898), he published a memoir on the Mesozoic fish and reptiles of Portugal (Sauvage 1897–1898), in which he described the above-mentioned jaw fragments as a new species of the genus *Suchosaurus* Owen, *S. girardi*. Sauvage did not doubt that *Suchosaurus* was a crocodilian, and listed it in the section concerning the family Goniopholididae, but he noted that the position of the genus was uncertain. Although no diagnosis was given for the new species *Suchosaurus girardi*, the jaw fragments were described as indicating a species close to *S. cultridens* from the Wealden of the Isle of Wight (the type specimen of *Suchosaurus cultridens* in fact came from Sussex; see below).

The *Suchosaurus* material from Boca do Chapim (Fig. 2c) was redescribed by Buffetaut (2007) as belonging to *Baryonyx* sp., this being the first mention from Portugal of that taxon, originally described from England and otherwise known from various localities in Spain (see reviews in Ruiz-Omeñaca *et al.* 2005; Buffetaut 2007), and possibly in Niger (*Cristatusaurus* and *Suchomimus* probably being junior synonyms of *Baryonyx*; Milner 2003). Sauvage had been the first to describe *Suchosaurus* – and thus (unwittingly) *Baryonyx* – remains from outside England. The reinterpretation of this Portuguese material prompted a re-examination of the original *Suchosaurus* material from the Wealden of England, the results of which are presented below.

Richard Owen and *Suchosaurus*

Teeth now identifiable as belonging to a *Baryonyx*-like theropod were first given a Linnean name by Richard Owen (1804–1892; Fig. 3a), in Part ii of his *Odontography* (Owen 1840–1845), which was published in 1841 (according to Woodward & Sherborn 1890). There (Owen 1840–1845, p. 287) he used the name *Crocodylus cultridens* for teeth from the Wealden of Tilgate Forest, near Cuckfield (Sussex), that had been provided by Gideon Mantell. *Suchosaurus* was used as a subgenus of *Crocodylus* on p. 290 and in the caption of plate

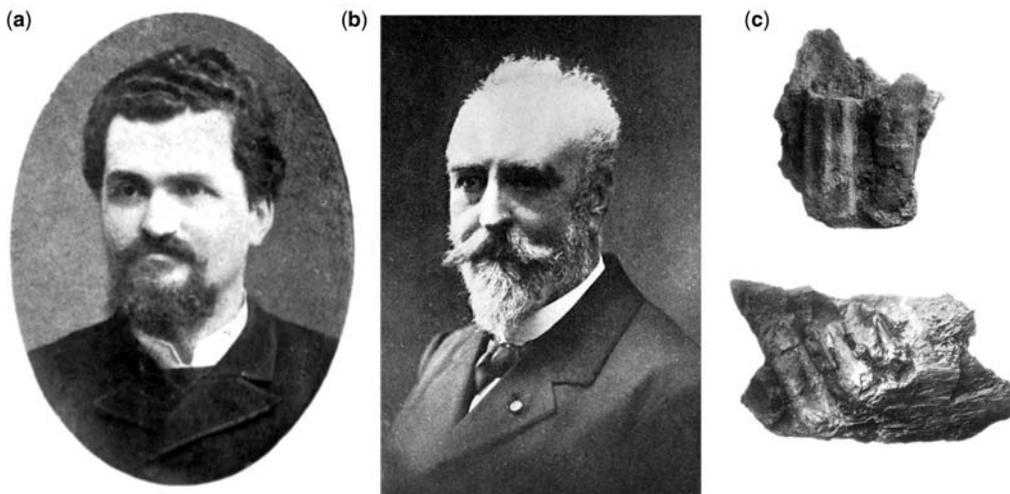


Fig. 2. *Suchosaurus* from Portugal. (a) Paul Choffat (1849–1919), the Swiss geologist who collected Barremian fossil vertebrates at Boca do Chapim. (b) Henri-Emile Sauvage (1842–1917), the French palaeontologist who described the fossils from Boca do Chapim in 1897–1898. (c) Two jaw fragments containing teeth, described by Sauvage (1897–1898) as *Suchosaurus girardi*, reinterpreted by Buffetaut (2007) as *Baryonyx* sp. (from Sauvage 1897–1898, plate IV, figs 4 and 5).

62A, in which figure 10 shows a tooth from Tilgate Forest (kept in the collection of the Natural History Museum, London, under collective number BMNH 36536; Fig. 3b). Owen mainly compared the teeth of *Crocodylus* (*Suchosaurus*) *cultridens* with those of the ‘Argenton crocodile’, described by Cuvier from beds now known to be Eocene in age in central France. The Argenton specimens are now referred to *Pristichampsus*, a ziphodont eusuchian crocodile (Gervais 1853). Owen (1841, p. 287 in Owen 1840–1845) noted that in *Crocodylus cultridens*, ‘the crown of the teeth is thicker than in the Argenton species, and the anterior and posterior edges are unbroken [i.e., not serrated]; a few longitudinal ridges traverse the crown of the tooth in this species, which makes the transition to the ordinary crocodilian teeth’.

In his *Report on British Fossil Reptiles*, in which he erected the ‘distinct tribe or sub-order’ Dinosauria, Owen (1842) discussed *Suchosaurus* at greater length, again as a sub-genus of *Crocodylus*. He again drew attention to similarities with the ‘Argenton crocodile’, but also mentioned resemblance with ‘the teeth of the Megalosaur’. Comparing *Suchosaurus* teeth with that of the gavial, he noted a basic difference that can, indeed, be used to distinguish spinosaur teeth from those of most crocodilians (Owen 1842, p. 68): ‘The crown is laterally compressed, subincurved, with two opposite trenchant edges, one forming the concave, the other the convex outline of the tooth. In the Gavial, the direction of the flattening of the crown and the situation of the trenchant edges are the reverse, the compression being from before backwards, and the edges being lateral’. Owen noted that the teeth in question had been referred by Meyer (1832, p. 115) to the genus *Teleosaurus* (on the basis of figures published by Cuvier 1824 and Mantell 1827 – see below), but commented that ‘no portions of the skeleton of a Teleosaur have hitherto been found in the Wealden’ (Owen 1842, p. 68).

In his *Report* Owen also suggested that large biconcave vertebrae with a compressed, wedge-shaped, body – collected by Mantell from Wealden strata – very probably belonged to *Suchosaurus*, but no special reason was given for associating the vertebrae with the teeth. In later discussions of *Suchosaurus* (Owen 1878, 1884a, b) he, again, mentioned these vertebrae, and provided illustrations of two specimens. Lydekker (1888) considered that the vertebra figured by Owen (1878), BMNH 2138, in fact belonged to an iguanodontid, while another vertebra (BMNH 2123), originally figured by Mantell (1827, plate IX, fig. 11) and discussed by Owen (1842), could be referred to *Hylaosaurus*. However that may be, in view of the lack of similarity with the opisthocoelous

dorsal centra of spinosaurids, it is unlikely that the above-mentioned vertebrae belong to the same taxon as the *Suchosaurus* teeth.

Owen (1878) discussed *Suchosaurus* again in a paper on Wealden and Purbeck crocodilians, in which he reproduced the engraving of the tooth from Tilgate Forest, together with the above-mentioned vertebra. Although he still tentatively associated the vertebrae with the teeth, he admitted that ‘hitherto these teeth have not been found so associated with any part of the skeleton of the same species as to yield unequivocally further characters of the present extinct Crocodilian’ (Owen 1878, p. 14). His description of *Suchosaurus* teeth differed little from that published in 1842. However, he noted that *Suchosaurus cultridens* ‘indicates a nearer affinity or transition to the Dinosaurian order than does any of the mesozoic *Crocodylia*, known by their cranial as well as by their dental, vertebral, and dermal characters’ (Owen 1878, p. 14).

In his *History of British Fossil Reptiles*, a massive review comprising two volumes of text and two volumes of plates that largely consists of reprints of his earlier publications, Owen (1884a, pp. 433–435) reproduced his 1878 description almost *verbatim*, but deleted the final sentence about the ‘nearer affinity or transition to the Dinosaurian order’. The illustration he provided (Owen 1884b, plate 5) differs from that published in 1878 in that it concentrates on specimens referred to *Suchosaurus* (instead of including *Goniopholis* material). In addition to the already illustrated large amphicoelous centrum, it also shows a smaller dorsal vertebra with a partly preserved neural arch. The tooth crown from Tilgate Forest is figured again in side and back views, together with similar views of a *Megalosaurus* tooth crown, presumably for comparison (Fig. 3c). Whether Owen intended to emphasize the similarities or the differences between *Suchosaurus* and *Megalosaurus* teeth is uncertain. The caption of the plate indicates *Suchosaurus laevidens*, instead of *cultridens*, for the tooth crown. This is probably a *lapsus calami*, as Owen did not mention this specific name elsewhere. Lydekker (1888) and Woodward & Sherborn (1890) considered *Suchosaurus laevidens* as a junior synonym of *S. cultridens*.

Despite his remarks about possible affinities with the Dinosauria, Owen consistently placed *Suchosaurus* among the crocodilians in his various publications on this taxon. This interpretation was generally followed by subsequent authors who mentioned this enigmatic form. One of the first to do so was Pictet (1853), who placed *Suchosaurus* (misspelled as *Succhosaurus*) among his ‘crocodiliens douteux’ (‘doubtful crocodilians’) and reproduced Owen’s illustration of the tooth from Tilgate

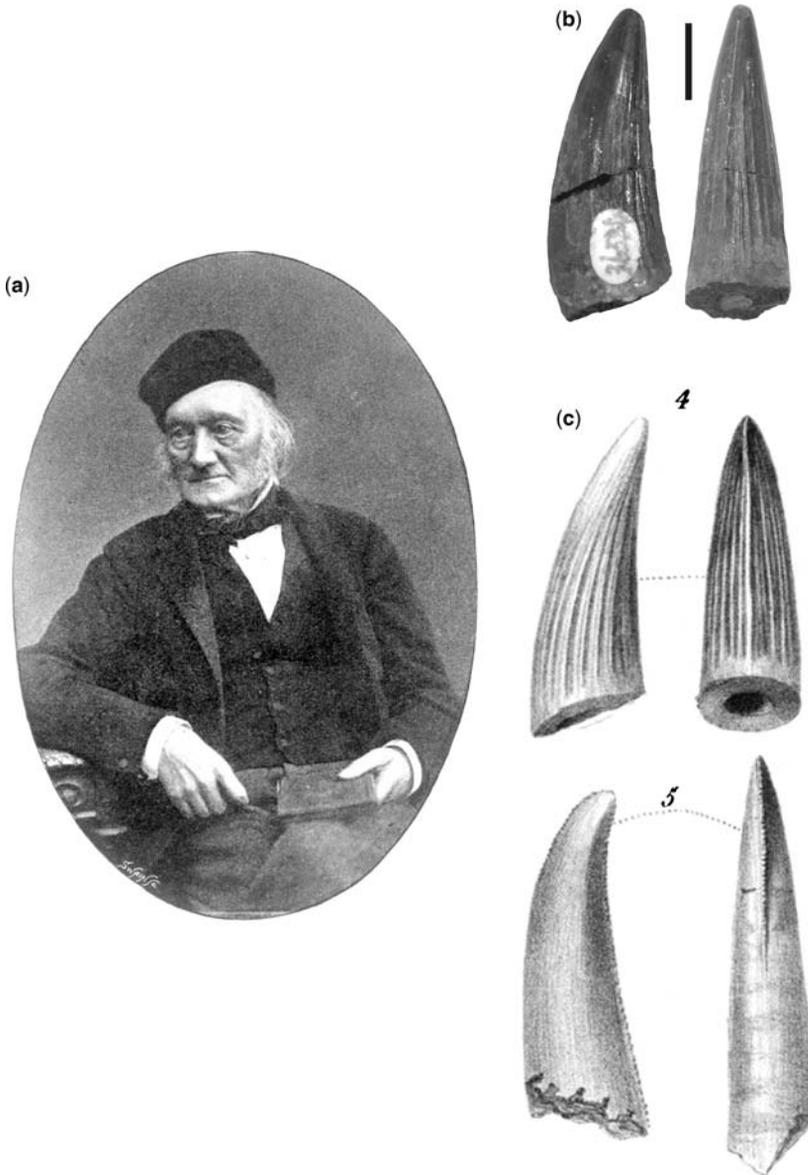


Fig. 3. Richard Owen and *Suchosaurus cultridens* from the Wealden of England. (a) Richard Owen (1804–1892), who erected the taxon *Suchosaurus cultridens* in 1841. (b) The type of *Suchosaurus cultridens*, under collective number BMNH 36536 (Natural History Museum, London), in lingual (?) and posterior views (scale bar, 10 mm). (c) The same tooth (above, 4) figured by Owen (1884b, plate 5), with a *Megalosaurus* tooth (below, 5) for comparison. This engraving of the type of *Suchosaurus cultridens* appeared in Owen's publications of 1840–1845, 1878 and 1884b.

Forest. Laurillard (1867) placed *Suchosaurus* among the crocodylians from the Secondary formations, with vertebrae with weakly concave or sometimes even flat articular faces. He rightly noted that Mantell had referred teeth from the Wealden to a kind of gavial but wrongly considered

him as the author of the name *Crocodylus cultridens*. Owen was correctly identified as the author of the generic name *Suchosaurus*. The description of the teeth followed Owen. Dollo (1883) considered *Suchosaurus* as a crocodylian and noted in what respects it differed from *Goniopholis* and

Bernissartia, but did not elaborate on its systematic position. Woodward (1885) placed *Suchosaurus* among the 'Goniopholidae' and commented that it was very imperfectly known. Following Owen, he emphasized the peculiar position of the carinae on the tooth crown. In a general review of the history of fossil crocodiles, Woodward (1887) discussed *Suchosaurus* again, providing an illustration (fig. 15) of a tooth which is clearly that figured by Owen but differs from Owen's figures in several details and was probably redrawn from the original. He remarked (Woodward 1887, p. 325) that 'at present it is too imperfectly understood to be relegated to any definite family position'. Similarly, Lydekker (1888) considered *Suchosaurus* as a crocodylian of the 'amphicoelian series' of uncertain position at the family level. Nicholson & Lydekker (1889) considered that it 'not improbably' belonged to the Goniopholididae, although its precise affinities were not yet determined. Zittel (1887–1890) listed it as a genus *incertae sedis* among the Macrorhynchidae [= Pholidosauridae]. Van den Broeck (1900) also considered *Suchosaurus* as a longirostrine form belonging to the Macrorhynchidae. Probably following Zittel's opinion, Romer (1956) placed it among the Pholidosauridae, as did Konzhukova (1964), Kuhn (1968) and Steel (1973).

One of the few authors who did not consider *Suchosaurus* as a crocodylian was Plieninger, who in 1846 placed it (misspelled as '*Suchosaurus*') in a group he called the 'Akidodonten', characterized by laterally compressed teeth with cutting edges (Plieninger 1846a). *Suchosaurus* was included in the akidodonts with teeth inserted in sockets (which distinguished them from akidodonts with ankylosed teeth), together with various other forms now considered as phytosaurs, rauisuchians or dinosaurs, including *Thecodontosaurus* and *Megalosaurus*. In a complement to his earlier paper, Plieninger (1846b) discussed his Akidodonten in more detail and placed '*Suchosaurus*' among the 'Thecodonten', themselves a subdivision of the Dactylopoden, one of the two main subgroups of the Akidodonten, the other subgroup being the Pachypoden (a taxon originally erected by Hermann von Meyer (1845) for various taxa now placed among the Dinosauria and including, according to Plieninger, *Megalosaurus* and *Hylaeosaurus*). The concept of akidodonts never gained widespread acceptance, and Plieninger's interpretation of *Suchosaurus* as something other than a crocodile was soon forgotten. One of the few authors to have partly followed Plieninger, albeit only temporarily, was Bronn, who, in his *Index Palaeontologicus* (1849, p. 693) placed *Suchosaurus* among the 'Saurii incertae sedis' and the '? Dactylopoden', together with various other taxa Plieninger had

referred to the Akidodonten. However, soon thereafter Bronn (1851–1852) returned to Owen's original interpretation and classified *Suchosaurus* among the amphicoelous crocodiles.

Another researcher who doubted the crocodylian nature of *Suchosaurus* was Hulke, who in 1879 briefly mentioned it in a paper on the ornithopod *Vectisaurus*. In it he compared the vertebrae of *Vectisaurus* with those referred by Owen to *Suchosaurus*. In a footnote (Hulke 1879, p. 423), he noted 'From evidence in my possession I rather incline to regard *Suchosaurus* as not improbably a Dinosaur'. He did not mention what this evidence was nor whether it was based on the teeth or on the vertebrae at that time referred to *Suchosaurus*.

Although an inspection of the Natural History Museum collection in London shows that isolated teeth collected from the Wealden of Sussex and the Isle of Wight were routinely labelled as *Suchosaurus*, that taxon was seldom mentioned in print after the end of the nineteenth century, presumably because it was based on insufficient material and therefore rather enigmatic (for an exception see Allen (1949), who listed *Suchosaurus* among vertebrates found in Wealden bone beds). Interestingly, one of the few reports of *Suchosaurus* finds in the twentieth century is from Spain, where Royo y Gómez (1927) mentioned the presence of that genus in the Wealden of Morella, in Castellón Province. No description of this material seems to have been published, although Bataller (1960) mentioned it again, noting that *Suchosaurus* was a longirostrine crocodylian. Baryonychine teeth from the Aptian of that area were reported by Canudo *et al.* (2004), and it thus seems likely that the *Suchosaurus* material mentioned by Royo y Gómez did belong to spinosaurids. It will be difficult to confirm this, however, as most of the fossil material mentioned by Royo y Gómez appears to have been lost during the Spanish Civil War (Sanz *et al.* 1982).

After the description of *Baryonyx walkeri* by Charig & Milner (1986, 1990) had revealed the peculiar characters of its teeth, isolated teeth from the Wealden of England showing these characters were identified as *Baryonyx* (Martill & Hutt 1996) rather than as *Suchosaurus*. Milner (2003) was the first to note that teeth in the Natural History Museum collections previously identified as *Suchosaurus* in fact belong to *Baryonyx* (see also Buffetaut 2007; Fowler 2007). The similarities between *Suchosaurus cultridens* teeth (including the type specimen, under collective number BMNH 36536; Fig. 3b) and *Baryonyx* teeth have been discussed by Buffetaut (2007). They include a similar labiolingual compression, carinae in the same position, more or less extensive ribbing of the crown and a fine wrinkling of the enamel. The fine serrations on the carinae that are visible on

the teeth of the holotype of *Baryonyx walkeri* are not always clearly visible on *Suchosaurus* teeth (this lack of serrations was noted by Owen, see earlier), but this seems to be the result of wear. There seems to be no doubt that the teeth referred by Owen to *Suchosaurus cultridens* belong to a spinosaurid theropod, very probably *Baryonyx*, not to a crocodylian. However, as noted by Buffetaut (2007), it does not seem advisable to use the taxon name *Suchosaurus cultridens* instead of *Baryonyx walkeri* because it cannot really be demonstrated that the isolated tooth described and illustrated by Owen and the partial skeleton on the basis of which *Baryonyx walkeri* was erected by Charig & Milner (1986) belong to the same species. There is a fairly large amount of variation, notably in enamel ornamentation, among the ‘baryonychine’ teeth from the Wealden of England, and it cannot be excluded that more than one species is present (Buffetaut 2007; Naish & Martill 2007).

The original discoverer: Gideon Mantell and the gavial from Tilgate Forest

As noted above, Owen’s *Suchosaurus cultridens* was based on teeth found by Gideon Mantell (1790–1852; Fig. 4a) at the famous quarry in Tilgate Forest (Fig. 4b), near Cuckfield, Sussex,

that also yielded the original material of *Iguanodon*. Mantell first described teeth from Tilgate Forest referable to crocodylians in his *Fossils of the South Downs* (1822). He distinguished three distinct types on the basis of crown morphology. Attribution to crocodiles or monitors was suggested by William Clift, the curator of the Hunterian Museum of the Royal College of Surgeons, who at that time was Mantell’s mentor in comparative anatomy. Mantell’s variety b corresponded to ‘a slender, delicate tooth, rather compressed, curvature gradual, apex slightly acuminate’ (Mantell 1822, p. 50). Compression of the crown suggests that this may have been a *Baryonyx* tooth, but in the absence of an illustration no firm conclusion can be drawn.

Mantell described the fossils from Tilgate Forest in much greater detail, and figured many of them for the first time in his *Illustrations of the Geology of Sussex* (1827). Having by then become familiar with the work of Cuvier (see below), he distinguished two main types of crocodile teeth (Mantell 1827, p. 65). One consisted of teeth with an obtuse crown (they are now referred to *Goniopholis*). The others were more slender and curved, resembling the crocodile from Caen described by Cuvier (now called *Teleosaurus*) or the ‘crocodile of the Ganges’ or gavial. The teeth later described by Owen as *Suchosaurus cultridens* were part of that second group. Owen (1842) indicated that the

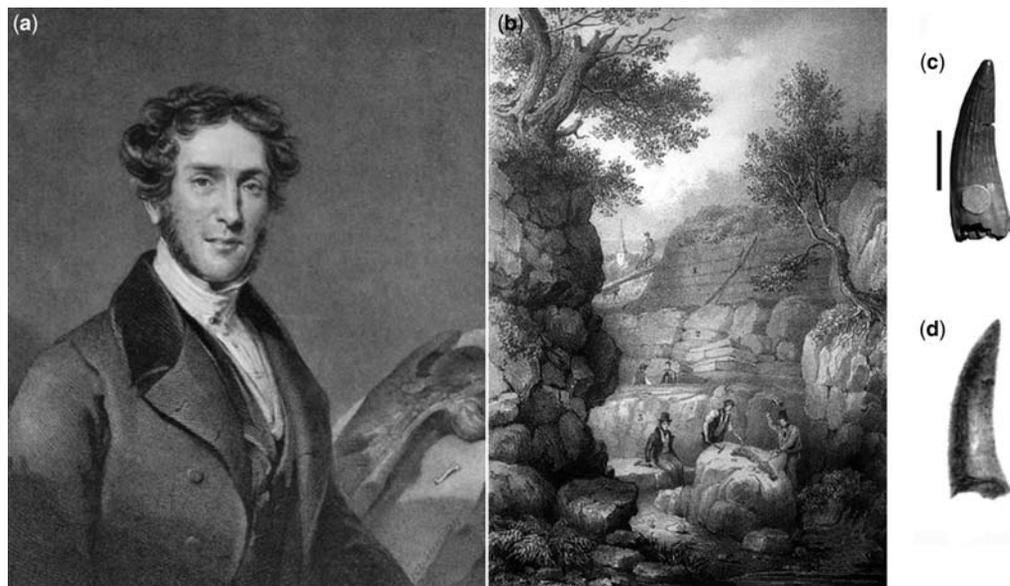


Fig. 4. Gideon Mantell and the original discovery of *Suchosaurus/Baryonyx* at Tilgate Forest. (a) Gideon Mantell (1790–1852), who collected spinosaurid teeth from quarries in Tilgate Forest, near Cuckfield, Sussex, around 1820. (b) Tilgate Forest quarry, as illustrated by Mantell (1833). (c) A *Baryonyx* tooth from Tilgate Forest (scale bar, 10 mm), Natural History Museum, London, collective number BMNH 36536, illustrated (d) as plate V, figure 6 of Mantell’s *Illustrations of the Geology of Sussex* (1827).

teeth figured by Mantell (1827) on his plate V under numbers 5, 6 and 8 belonged to *Suchosaurus cultridens*. Although Mantell's figures are not of the highest quality, it has proved possible to locate at least some of these teeth in the collections of the Natural History Museum. In particular, one of the teeth (Fig. 4c) under collective number 36536 is certainly the specimen figured by Mantell (1827) on plate V, figure 6 (Fig. 4d). Not only are the shape and dimensions the same, but the specimen shows a break at the level of the upper third of the crown that is clearly shown on Mantell's figure. The 30 mm-long tooth is compressed labiolingually, bears an anterior convex carina and a posterior concave carina, and both the labial and lingual faces show ridges (seven on both sides). The enamel is covered with a fine wrinkling of the type seen in *Baryonyx* and 'Suchosaurus' teeth (Charig & Milner 1997; Buffetaut 2007). Although the carinae are fairly worn, faint serrations can be seen at the base of the posterior carina. There is no doubt that this tooth (as well as several others in the Mantell collection at the Natural History Museum) belongs to a *Baryonyx*-like spinosaurid theropod. This also applies, as mentioned earlier, to the tooth figured by Owen (1841 (of 1841–1845), 1878 and 1884b) as *Suchosaurus cultridens*, which can be considered as the type of that species, and is also part of the Mantell collection at the Natural History Museum under collective number 36536 (Fig. 3b, c).

In his 'Tabular arrangement of the organic remains of the county of Sussex' (1829a – also published separately as *A Scientific Catalogue of the Organic Remains of Sussex*, Mantell 1829b) and reprinted as an appendix to *The Geology of the South-East of England* (Mantell 1833), Mantell listed crocodylians among the fossil vertebrates from the 'Tilgate Beds', with reference to the illustrations of his 1827 book. Together with various other crocodylian remains (mainly teeth), figures 5, 6 and 8 of 'plate 7' (by which Mantell certainly meant his plate V, since plate VII shows only turtle remains) are listed as belonging to *Leptorhynchus*, with a footnote indicating that this is 'the fossil species of Caen' (Mantell 1829a, b, p. 214, 1833, p. 394). The name *Leptorhynchus* had, in fact, first been used by Clift (1829) for portions of elongate crocodylian lower jaws collected on the banks of the Irrawaddy, in Burma, by John Crawford's embassy to the Burmese court in Ava in 1826–1827 (for more details on Crawford's collecting activity see Buffetaut 1987). Clift (1829, p. 375) had rightly concluded that this crocodile, now known to be from Pleistocene deposits, was 'allied to, if not identical with, the great gavial'. Why Mantell chose to use this name for the 'species of Caen' is unclear, but the teleosaurids from the

Bathonian of Caen were at that time commonly referred to as 'gavials', including by such leading authorities as Cuvier and Geoffroy Saint-Hilaire (Buffetaut 2008). Moreover, as mentioned above, Clift had helped Mantell with the identification of several of his vertebrate fossils, including *Iguanodon* remains (Buffetaut 1999), and the use of a name he had coined may reflect his influence. Be that as it may, that designation confirms that Mantell considered the teeth later described as *Suchosaurus* as belonging to a long-snouted, gavial-like crocodylian. Interestingly, even after these teeth had been redescribed and named by Owen, some authors still depicted *Suchosaurus* as a long-snouted, gavial-like crocodylian. Ansted (1844, pp. 437–438) thus noted that 'judging from the structure of the teeth (which somewhat resemble those of the Megalosaurus), the *Suchosaurus* was probably a long-snouted crocodile, not unlike the Gavial or piscivorous crocodile of the Ganges'. Similarly, Gray & Adams (1863, p. 225) mentioned that 'the *Suchosaurus* was a long-snouted crocodile resembling the gavial of the Ganges. The crowns of its teeth were slender, compressed, and acute'.

In later works, Mantell (1833, 1839) added little on the crocodile remains from Tilgate Forest, and they were less fully illustrated than in his 1827 book. His main interests now were *Iguanodon* and other giant 'saurians', and the crocodiles took second place. In his *Wonders of Geology* (1839, p. 386), he apparently got confused about the identification of the teeth from Tilgate Forest, remarking that 'they appear to referable to two kinds – the one belonging to that division of crocodiles, with a long slender muzzle, named *gavial*; the other to a species of crocodile, properly so-called, and resembling a fossil species found at Caen'. After he sold his fossil collection to the British Museum and it was transferred there in 1838, access to the crocodile teeth he had collected became much more difficult, as he noted with some bitterness in *Petrifactions and their Teachings* (Mantell 1851, p. 172): 'There were a considerable number of teeth of crocodylian reptiles from the Wealden in my collection, but I do not know in what part of the Museum they are placed'. After Owen erected the taxon *Suchosaurus* in 1841, Mantell used that name in some of his books. In *The Medals of Creation* (Mantell 1844, pp. 720–721), in particular, he noted that:

In the strata of Tilgate Forest, associated with innumerable remains of reptiles of various kinds, teeth of the Crocodylian type, belonging to two genera, are not uncommon. The first kind (*Suchosaurus cultridens* of Prof. Owen) is a tooth about an inch in length, of a slender acuminate form, compressed laterally, and gently recurved, with a sharp edge in front and behind; resembling, in its general figure, the tooth of

a Megalosaurus, with the serrations on the edges worn off (Pl. VI, fig. 7). The sides of the crown are marked with a few longitudinal grooves. Some biconcave vertebrae found in the same quarries, and characterised by the compressed wedge-shaped form of the centre (*Foss. Til. For.* pl. ix, fig. 11), are supposed by Professor Owen to belong to the same reptile as the teeth above described; but it is hazardous to pronounce on the identity of these detached teeth and bones, without more corroborative proof than has hitherto been obtained.

Mantell's caution concerning Owen's attribution of the biconcave vertebrae to *Suchosaurus* was clearly justified. His remark about the serrations on the edges of the teeth being worn off is worth noting, too, as wear very probably explains the more or less complete lack of serrations on many *Suchosaurus/Baryonyx* teeth from the Wealden.

In retrospect, Gideon Mantell should thus be considered as the first palaeontologist to have (unwittingly) discovered spinosaurid teeth – in the Wealden of Tilgate Forest, probably around 1820. In the entry in his journal for 26 September 1820, for instance (Curwen 1940), Mantell noted that he had obtained a crocodile tooth from a quarry at Cuckfield (see Dean 1999 for further details about Mantell's researches at Tilgate Forest). However, he was not the first to figure such fossils.

Georges Cuvier: the first illustration of a spinosaurid tooth

The story of how Georges Cuvier (1769–1832; Fig. 5a) contributed to Mantell's work on the *Iguanodon* remains from Sussex has often been told (Buffetaut 1999; Dean 1999). What has often been overlooked is that among the fossils brought to Paris by Charles Lyell in June 1823, to be examined by Cuvier, were not only *Iguanodon* specimens, but also remains of other vertebrates collected by Mantell in the Wealden of Tilgate Forest, including crocodile and turtle material. In the second edition of his *Recherches sur les ossements fossiles* (Cuvier 1824, pp. 161–163), Cuvier included a whole section entitled 'Des os de crocodiles des sables ferrugineux du dessous de la craie, trouvés dans le Comté de Sussex, par M. Mantell' ['On the crocodile bones from the iron-sand below the Chalk, found in the county of Sussex, by Mr Mantell']. In it he referred to Mantell's mention of the Tilgate Forest fossils, including crocodiles, in his *Fossils of the South Downs* (Mantell 1822), and added that Mantell had sent him some teeth and vertebrae that he had identified as, indeed, belonging to crocodiles. Mantell's identification was thus confirmed by the leading authority of the time on fossil vertebrates. Cuvier noted that the biconcave vertebrae (probably from

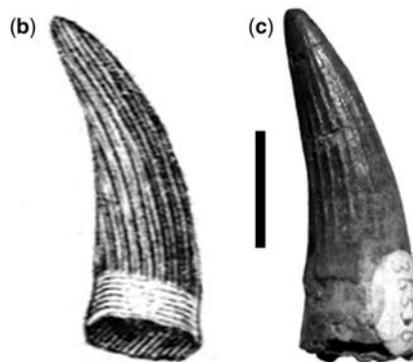


Fig. 5. Georges Cuvier and the first illustration of a spinosaurid tooth. (a) Georges Cuvier (1769–1832), who figured a spinosaurid tooth sent to him by Mantell in the second edition of his *Recherches sur les ossements fossiles* (1824). (b) Spinosaurid tooth from Tilgate Forest figured by Cuvier (1824, plate X, fig. 30). (c) The original specimen (scale bar, 10 mm), Natural History Museum, London, collective number BMNH 36536 – also illustrated by Mantell (1827), see Figure 4.

goniopholidids) resembled those of the crocodiles from Caen & Honfleur (now referred to thalattosuchians: Buffetaut 2008). Concerning the teeth, he simply noted that most of them were more obtuse than in the common crocodiles, and thus resembled some large, obtuse teeth from the Swiss Jura that had been sent to him by Mr Hugi from Solothurn (retrospectively, it appears that the teeth from the

Jura belonged to the teleosaurid *Machimosaurus* (see Krebs 1967), whereas the obtuse teeth from Tilgate Forest belonged to goniopholidids. Cuvier did not comment on the other, slender teeth sent to him by Mantell. However, he illustrated four of the teeth from Tilgate Forest on his plate X, as figures 25, 26, 27 and 30. Figures 25, 26 and 27 show teeth with a blunt apex that in all likelihood belong to goniopholidids. The 30 mm-long tooth shown in figure 30, however, is more slender, more recurved, with a pointed apex (Fig. 5b). Although the drawing lacks details, except for the ribbing of the enamel and the boundary between the crown and root, because of remarkable correspondence in size and shape there is every reason to believe that it depicts the tooth figured by Mantell (1827) on plate V, figure 6 (Fig. 4d). This tooth, as mentioned above, is kept in the collection of the Natural History Museum under collective number 36536, and belongs to a *Baryonyx*-like spinosaurid theropod (Fig. 5c). The first illustration of a spinosaurid fossil was thus published in 1824 by Cuvier, who, as was his wont, had no qualms about publishing or illustrating the discoveries of his correspondents before they had done so themselves (see Buffetaut 2000 about Cuvier's publication of *Iguanodon* teeth). Mantell obviously had no ill feelings about that and was proud to note in his *Illustrations of the Geology of Sussex* (1827, p. 64) that 'M. Cuvier, in his immortal work, confirms our conjectures'. The last, posthumous, edition of Cuvier's *Recherches sur les ossements fossiles* (Cuvier 1836) simply reproduces the second edition and does not mention Mantell's intervening publications.

Other misinterpretations of spinosaurid teeth

Because of their morphological convergence with those of crocodylians and other fish-eating reptiles, isolated spinosaurid teeth have frequently been misinterpreted. The longest-lasting case is that of the '*Suchosaurus*' teeth from the Wealden of England, which were mistaken for crocodile teeth for nearly two centuries, as discussed earlier. In Africa, it seems that in many cases spinosaurid teeth were misidentified as those of non-dinosaurian reptiles by various collectors. For instance, in his review of the dinosaurs of the Sahara, Lapparent (1960, p. 49) noted that *Spinosaurus aegyptiacus* was lacking from the central Sahara. However, spinosaurid teeth are abundant at several of the sites he explored, notably in the Albian of Tunisia (Bouaziz *et al.* 1988; Buffetaut & Ouaja 2002) and it seems very unlikely that he did not find any; the most likely explanation is that he mistook them

for crocodylian teeth (which are mentioned in his lists of fossils). Similarly, Lavocat (1954) did not mention *Spinosaurus* among the vertebrates he collected from the Cenomanian Kem Kem beds of southern Morocco, although spinosaurid teeth are very abundant there (Amiot *et al.* 2004). A clear example of misidentification of spinosaurid material from North Africa is provided by the paper by Schlüter & Schwarzhan (1978) on an Early Cretaceous bone bed in southern Tunisia, in which teeth that clearly belong to *Spinosaurus* were referred to *Plesiosaurus* sp. Similar misidentifications also occurred in Asia. Kobayashi *et al.* (1964) identified as ichthyosaurian a tooth from the Early Cretaceous of Thailand that apparently belongs to the spinosaurid *Siamosaurus suteethorni* (Buffetaut *et al.* 2008). It has recently been shown (Buffetaut *et al.* 2008) that teeth from the Early Cretaceous of Guangxi, South China, referred by Hou *et al.* (1975) to a pliosaur (*Sinopliosaurus fusuiensis*), in fact belong to a *Siamosaurus*-like spinosaurid.

Conclusions

Although Stromer's original description of *Spinosaurus aegyptiacus* was published in 1915, it is only since the 1980s that a more complete and detailed picture of spinosaurid anatomy, evolution and biogeography has begun to emerge. It is all the more unexpected to realize that spinosaurid teeth were, in fact, among the first dinosaur fossils to be found, described and illustrated, albeit unwittingly, more or less at the same time as *Megalosaurus* and *Iguanodon*, in the first decades of the nineteenth century. It appears that *Baryonyx*-like teeth were collected by Gideon Mantell in Sussex around 1820. Georges Cuvier was the first to publish an illustration of such a tooth in 1824, followed by Mantell in 1827. These teeth, however, were generally considered as belonging to crocodylians, and when Richard Owen erected the taxon *Suchosaurus cultridens* to designate them he placed it among the crocodiles. Although Owen realized that they were peculiar in many respects and hinted at possible affinities with dinosaurs, he persistently classified *Suchosaurus* as a crocodylian, an interpretation that was accepted by most subsequent authors, including Henri-Emile Sauvage when he described material from Portugal that closely resembled the specimens from the English Wealden.

When Stromer described *Spinosaurus aegyptiacus* in 1915 he emphasized the peculiar character of the teeth of this unusual theropod, and this led him to regard the teeth from the Djoua, collected by Foureau and described by Haug, as belonging to *Spinosaurus*. However, the smooth, almost

uncompressed, teeth of *Spinosaurus aegyptiacus* were sufficiently different from the ribbed, labiolingually compressed teeth of *Suchosaurus cultridens* to prevent recognition of the fairly close relationships between these two forms. It was not until Charig & Milner (1986, 1990, 1997) described *Baryonyx walkeri* on the basis of a partial skeleton that its close affinities with *Spinosaurus* were recognized (Paul 1988; Buffetaut 1989, 1992). Only then did the morphological diversity of spinosaurid teeth become apparent. This in turn led to a reappraisal of *Suchosaurus* teeth as those of a *Baryonyx*-like spinosaurid (Milner 2003; Buffetaut 2007; Fowler 2007).

Besides its historical interest, the story of the various spinosaurid elements that have been misinterpreted as belonging to other groups of reptiles (or fish) since the days of Mantell, Cuvier and Owen is also an incitement to look for such fossils in old collections. Spinosaurid teeth misidentified as those of crocodiles or other reptiles may await rediscovery in unexpected places.

Dr I. Rouget helped me in my (unfortunately unsuccessful) search for Fourreau's material from the Djoua in the palaeontological collection of University Paris 6. Professor M. Ramalho kindly made the *Suchosaurus* material from Portugal at my disposal at the Museu Geológico in Lisbon. Special thanks to Dr A. Milner for her constant support of my research on spinosaurid material in the collections of the Natural History Museum (London) and for her review of this paper. Dr J. I. Ruiz-Omeñaca is thanked for his useful comments. Dr A.-M. Lezine (CNRS) kindly scanned the photograph of Fernand Fourreau for me.

References

- ABADIE, J. C. & ABADIE, F. 1989. *Sahara-Tchad (1898–1900). Carnets de route de Prosper Haller, médecin de la Mission Fourreau-Lamy*. L'Harmattan, Paris.
- ALLEN, P. 1949. Notes on Wealden bone-beds. *Proceedings of the Geologists' Association*, **60**, 275–283.
- AMIOT, R., BUFFETAUT, E., TONG, H., BOUDAD, L. & KABIRI, L. 2004. Isolated theropod teeth from the Cenomanian of Morocco and their palaeobiogeographical significance. *Revue de Paléobiologie*, Volume Spécial, **9**, 143–149.
- ANSTED, D. T. 1844. *Geology, Introductory, Descriptive and Practical*. John Van Voorst, London.
- BATALLER, J. R. 1960. Los vertebrados del Crétácico español. *Notas y Comunicaciones del Instituto Geológico y Minero de España*, **60**, 141–164.
- BOUAZIZ, S., BUFFETAUT, E., GHANMI, M., JAEGER, J. J., MARTIN, M., MAZIN, J. M. & TONG, H. 1988. Nouvelles découvertes de vertébrés fossiles dans l'Albien du Sud tunisien. *Bulletin de la Société géologique de France*, **4**, 335–339.
- BRONN, H. G. 1849. *Index Palaeontologicus*, 2. *Abtheilung*. Schweizerbart, Stuttgart.
- BRONN, H. G. 1851–1852. *Lethaea Geognostica*. 3. *Auflage*, Volume 2. Schweizerbart, Stuttgart.
- BUFFETAUT, E. 1987. *A Short History of Vertebrate Palaeontology*. Croom Helm, London.
- BUFFETAUT, E. 1989. New remains of the enigmatic dinosaur *Spinosaurus* from the Cretaceous of Morocco and the affinities between *Spinosaurus* and *Baryonyx*. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1989**, 79–87.
- BUFFETAUT, E. 1992. Remarks on the Cretaceous theropod dinosaurs *Spinosaurus* and *Baryonyx*. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1992**, 88–96.
- BUFFETAUT, E. 1999. Mantell, Cuvier, Buckland and the identification of *Iguanodon*: a contribution based on unpublished annotations by Mantell. *Oryctos*, **2**, 101–109.
- BUFFETAUT, E. 2000. Mantell, Cuvier, Buckland and the identification of *Iguanodon*: a correction. *Oryctos*, **3**, 95–97.
- BUFFETAUT, E. 2005. Les premiers dinosaures sahariens. *Pour la Science*, **331**, 8–11.
- BUFFETAUT, E. 2007. The spinosaurid dinosaur *Baryonyx* (Saurischia, Theropoda) in the Early Cretaceous of Portugal. *Geological Magazine*, **144**, 1021–1025.
- BUFFETAUT, E. 2008. A l'aube de la paléontologie des vertébrés: Cuvier, Geoffroy Saint-Hilaire et les «gavials» de Honfleur, du Havre et de Caen. *Bulletin de la Société géologique de Normandie*, **95**, 153–162.
- BUFFETAUT, E. & OUAJA, M. 2002. A new specimen of *Spinosaurus* (Dinosauria, Theropoda) from the Lower Cretaceous of Tunisia, with remarks on the evolutionary history of the Spinosauridae. *Bulletin de la Société géologique de France*, **173**, 415–421.
- BUFFETAUT, E., CUNY, G. & LE LOEFF, J. 1993. The discovery of French dinosaurs. *Modern Geology*, **18**, 161–182.
- BUFFETAUT, E., SUTEETHORN, V., TONG, H. & AMIOT, R. 2008. An Early Cretaceous spinosaurid theropod from southern China. *Geological Magazine*, **145**, 745–748.
- CANUDO, J. I., GASULLA, J. M., ORTEGA, F. & RUIZ-OMEÑACA, J. I. 2004. Presencia de Baryonychinae (Theropoda) en el Aptiense inferior (Cretácico Inferior) de Laurasia: Cantera Mas de la Parreta, Formación Arcillas de Morella (Morella, Castellón). *III Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno*, abstract. Colectivo Arqueológico–Paleontológico, *Salas de Los Infantes* (Abstract).
- CHARIG, A. J. & MILNER, A. C. 1986. *Baryonyx*, a remarkable new theropod dinosaur. *Nature*, **324**, 359–361.
- CHARIG, A. J. & MILNER, A. C. 1990. The systematic position of *Baryonyx walkeri*, in the light of Gauthier's reclassification of the Theropoda. In: CARPENTER, K. & CURRIE, P. J. (eds) *Dinosaur Systematics: Approaches and Perspectives*. Cambridge University Press, Cambridge, 127–140.
- CHARIG, A. J. & MILNER, A. C. 1997. *Baryonyx walkeri*, a fish eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum, Geology Series*, **53**, 11–70.
- CLIFT, W. 1829. On the fossil remains of two new species of *Mastodon*, of other vertebrate animals found on the left bank of the Irawadi. *Transactions of the Geological Society, London*, **2**, 369–375.
- CURWEN, E. C. 1940. *The Journal of Gideon Mantell*. Oxford University Press, Oxford.

- CUVIER, G. 1824. *Recherches sur les ossements fossiles, deuxième édition*, Volume 5, 2e partie. Dufour & d'Ocagne, Paris.
- CUVIER, G. 1836. *Recherches sur les ossements fossiles, quatrième édition*, Volume 9. Edmond d'Ocagne, Paris.
- DEAN, D. R. 1999. *Gideon Mantell and the Discovery of Dinosaurs*. Cambridge University Press, Cambridge.
- DOLLO, L. 1883. Première note sur les crocodiliens de Bernissart. *Bulletin du Musée royal d'Histoire naturelle de Belgique*, **2**, 309–340.
- FLEURY, E. 1920. Une phase brillante de la géologie portugaise. Paul Choffat. 14 Mars 1849–6 Juin 1919. *Mémoires de la Société Portugaise des Sciences Naturelles, Série Géologique*, **9**, 1–54.
- FOUREAU, F. 1902. *D'Alger au Congo par le Tchad*. Masson, Paris.
- FOUREAU, F. 1905. Géologie. Description géologique de l'itinéraire. In: FOUREAU, F. (ed.) *Documents scientifiques de la Mission saharienne*, Volume 2. Masson, Paris, 555–696.
- FOWLER, D. 2007. Recently rediscovered baryonychine teeth (Dinosauria: Theropoda): new morphologic data, range extension and similarity to ceratosaur. *Journal of Vertebrate Paleontology*, **27**, Suppl. 3, 76A.
- GERVAIS, P. 1853. Observations relatives aux reptiles fossiles de France. *Comptes Rendus de l'Académie des Sciences de Paris*, **36**, 374–377.
- GRAY, A. & ADAMS, C. B. 1863. *Elements of Geology*. Harper & Brothers, New York.
- HAUG, E. 1905. Paléontologie. In: FOUREAU, F. (ed.) *Documents scientifiques de la Mission saharienne*, Volume 2. Masson, Paris, 751–832.
- HOU, L., YEH, H. & ZHAO, X. 1975. Fossil reptiles from Fusui, Kwangshí. *Vertebrata Palasiatica*, **13**, 23–33.
- HULKE, J. W. 1879. *Vectisaurus*, a new Wealden dinosaur. *Quarterly Journal of the Geological Society, London*, **35**, 421–424.
- KOBAYASHI, T., TAKAI, F. & HAYAMI, I. 1964. On some Mesozoic fossils from the Khorat Series of East Thailand and a note on the Khorat Series. *Japanese Journal of Geology and Geography*, **34**, 181–192.
- KONZHUKOVA, E. D. 1964. Crocodilia. In: ORLOV, YU. A. (ed.) *Osnovy Paleontologii*, Volume 12. Nauka, Moscow, 506–523 (in Russian).
- KREBS, B. 1967. Der Jura-Krokodilier *Machimosaurus* H. v. Meyer. *Paläontologische Zeitschrift*, **41**, 46–59.
- KUHN, O. 1968. *Die vorzeitlichen Krokodile*. Oeben, Krailing bei München.
- LAPPARENT, A. F. DE 1960. Les dinosauriens du «Continental Intercalaire» du Sahara central. *Mémoires de la Société géologique de France*, **88A**, 1–57.
- LAURILLARD, C. 1867. Crocodiliens fossiles. In: ORBIGNY, C. D' (ed.) *Dictionnaire universel d'Histoire naturelle*, Volume 4, Houssiaux, Paris, 476–481.
- LAVOCAT, R. 1954. Sur les Dinosauriens du Continental Intercalaire des Kem-Kem de la Daoura. *Comptes Rendus du 19e Congrès Géologique International (Alger, 1952)*, **15**, 65–68.
- LYDEKKER, R. 1888. *Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History). Part I*. British Museum (Natural History), London.
- MANTELL, G. A. 1822. *The Fossils of the South Downs or Illustrations of the Geology of Sussex*. Lupton Relfe, London.
- MANTELL, G. A. 1827. *Illustrations of the Geology of Sussex*. Lupton Relfe, London.
- MANTELL, G. A. 1829a. A tabular arrangement of the organic remains of the county of Sussex. *Transactions of the Geological Society of London, Series 2*, **3**, 201–216.
- MANTELL, G. A. 1829b. *A Scientific Catalogue of the Organic Remains of Sussex*. Richard Taylor, London.
- MANTELL, G. A. 1833. *The Geology of the South-East of England*. Longman, Rees, Orme, Brown, Green & Longman, London.
- MANTELL, G. A. 1839. *The Wonders of Geology*, 3rd edn. Relfe & Fletcher, London.
- MANTELL, G. A. 1844. *The Medals of Creation*. Bohn, London.
- MANTELL, G. A. 1851. *Petrifactions and their Teachings*. Bohn, London.
- MARTILL, D. M. & HUTT, S. 1996. Possible baryonychid dinosaur teeth from the Wessex Formation (Lower Cretaceous, Barremian) of the Isle of Wight, England. *Proceedings of the Geologists' Association*, **107**, 81–84.
- MEYER, H. VON 1832. *Palaeologica zur Geschichte der Erde und ihrer Geschöpfe*. Sigmund Schmerber, Frankfurt am Main.
- MEYER, H. VON 1845. System der fossilen Saurier. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde*, **1845**, 278–285.
- MILNER, A. C. 2003. Fish-eating theropods: a short review of the systematics, biology and palaeobiogeography of spinosaurs. In: HUERTA HURTADO, P. & TORCIDA FERNÁNDEZ-BALDOR, F. (eds) *Actas de las II Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno (2001)*, *Colectivo Arqueológico-Paleontológico, Salas de Los Infantes*, 129–138.
- NAISH, D. & MARTILL, D. M. 2007. Dinosaurs of Great Britain and the role of the Geological Society of London in their discovery: basal Dinosauria and Saurischia. *Journal of the Geological Society, London*, **164**, 493–510.
- NICHOLSON, H. A. & LYDEKKER, R. 1889. *A manual of palaeontology for the use of students with a general introduction on the principles of palaeontology*, Volume II. William Blackwood, Edinburgh.
- NOTHDURFT, W. & SMITH, J. 2002. *The Lost Dinosaurs of Egypt*. Random House, New York.
- OWEN, R. 1840–1845. *Odontography*. Hippolyte Baille, London.
- OWEN, R. 1842. Report on British fossil reptiles. Part II. *Reports of the meetings of the British Association for the Advancement of Science*, **11**, 61–204.
- OWEN, R. 1878. Monograph on the fossil Reptilia of the Wealden and Purbeck Formations. Supplement n-VIII. Crocodilia (*Goniopholis*, *Petrosuchus* and *Suchosaurus*). *Palaeontographical Society Monographs*, **1878**, 1–15.
- OWEN, R. 1884a. *A History of British Fossil Reptiles*, Volume I. Cassell, London.
- OWEN, R. 1884b. *A History of British Fossil Reptiles*, Volume II. Cassell, London.
- PAUL, G. 1988. *Predatory Dinosaurs of the World: A Complete Illustrated Guide*. Simon and Schuster, New York.
- PICTET, F. J. 1853. *Traité de paléontologie ou histoire naturelle des animaux fossiles considérés dans leurs*

- rapports zoologiques et géologiques. Tome premier.* Baillière, Paris.
- PLIENINGER, T. 1846a. Über ein neues Sauriergenus und die Einreihung der Saurier mitflachen, schneidenden Zähnen in eine Familie. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg*, **2**, 148–154.
- PLIENINGER, T. 1846b. Nachträgliche Bemerkungen zu dem Vortrage (S. 148 dieses Heftes) über ein neues Sauriergenus und die Einreihung der Saurier mit flachen, schneidenden Zähnen in eine Familie. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg*, **2**, 247–254.
- ROMER, A. S. 1956. *Osteology of the Reptiles*. University of Chicago Press, Chicago, IL.
- ROYO Y GÓMEZ, J. 1927. Sur les faciès wealdien d'Espagne. *Comptes Rendus de la Société géologique de France*, **10**, 125–128.
- RUIZ-OMEÑACA, J. I., CANUDO, J. I., CRUZADO-CABALLERO, INFANTE, P. & MORENO-AZANZA, M. 2005. Baryonychine teeth (Theropoda: Spinosauridae) from the Lower Cretaceous of La Cantalera (Josa, NE Spain). *Kaupia*, **14**, 59–63.
- SANZ, J. L., CASANOVAS, M. L. & SANTAFÉ, J. V. 1982. Paleontología. In: *Geología y Paleontología (Dinosaurios) de las Capas rojas de Morella (Castellón, España)*, Diputación Provincial de Castellón y Diputación de Barcelona, Castellón and Barcelona, 69–169.
- SAUVAGE, H. E. 1896. Les crocodiliens et les dinosauriens des terrains mésozoïques du Portugal. *Bulletin de la Société géologique de France*, **24**, 46–48.
- SAUVAGE, H. E. 1897–1898. *Vertébrés fossiles du Portugal. Contribution à l'étude des poissons et des reptiles du Jurassique et du Crétacé*. Direction des Travaux Géologiques du Portugal, Lisbon.
- SAUVAGE, H. E. 1898. Les reptiles et les poissons des terrains mésozoïques du Portugal. *Bulletin de la Société géologique de France*, **26**, 442–446.
- SCHLÜTER, T. & SCHWARZHANS, W. 1978. Eine Bonebed-Lagerstätte aus dem Wealden Süd-Tunesiens (Umgebung Ksar Krerachfa). *Berliner geowissenschaftliche Abhandlungen, A*, **8**, 53–65.
- STEEL, R. 1973. Crocodylia. *Handbuch der Paläoherpetologie*, **16**, 1–116.
- STROMER, E. 1915. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 3. Das Original des Theropoden *Spinosaurus aegyptiacus*. *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Mathematisch-physikalische Klasse*, **28**, 1–32.
- STROMER, E. 1934. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 13. Dinosauria. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, Neue Folge*, **22**, 1–79.
- STROMER, E. 1936. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. VII. Baharije-Kessel und -Stufe mit deren Fauna und Flora. Eine ergänzende Zusammenfassung. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, Neue Folge*, **33**, 1–102.
- VAN DEN BROECK, E. 1900. Les dépôts à Iguanodon de Bernissart et leur transfert dans l'étage purbeckien ou aquilonien du Jurassique supérieur. Exposé comprenant une revue de la faune des vertébrés du Purbeckien et du Wealdien dans le Sud-Est de l'Angleterre. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie*, **14**, 39–112.
- WOODWARD, A. S. 1885. On the literature and nomenclature of British fossil Crocodylia. *Geological Magazine*, **2**, 496–510.
- WOODWARD, A. S. 1887. The history of fossil crocodiles. *Proceedings of the Geologists' Association*, **9**, 288–344.
- WOODWARD, A. S. & SHERBORN, C. D. 1890. *A Catalogue of British Fossil Vertebrata*. Dulau, London.
- ZITTEL, K. A. 1887–1890. *Handbuch der Paläontologie. I. Abtheilung. Paläozoologie. III Band. Vertebrata (Pisces, Amphibia, Reptilia, Aves)*. Oldenbourg, München.