UNIVERSITY OF THE WITWATERSRAND, JOHANNESBURG

The 11th of May 2018

Review of the article entitled *Baryonyx* for WikiJournal Preprints

Dear Florian,

Please find bellow my revision of this article on *Baryonyx* for WikiJournal. The authors did a very good job given that the article is well-organized and relatively thorough. Yet, some sections can be improved and expanded, and the text can certainly be better referenced. I would, therefore, like to review the revised version of this article a second time before its publication. Here are the major points that I wish to see addressed by the authors before publication:

- Please first describe the skull of *Baryonyx* then the postcranium. Expand the description of the postcranium to include succinct information on the braincase, tall dorsal neural spine, pelvis, hindlimbs and tail based on the comparison with the closely related taxon *Suchomimus*. Please also mention the preserved bones of the holotype in the descriptive part of the article.

- Please mention the abstract of Munt et al. (2017) on the additional *Baryonyx* material recently unearthed from the Isle of Wight. They have been illustrated in their poster available on their ResearchGate profile.

- Develop the historical section on the discovery of *Suchosaurus*. This story is particularly interesting in regards to discovery of the first theropod remains and the first theropod to be named.

- Provide a brief list of synapomorphies for Spinosaurinae and Baryonychinae.

- Provide additional information on the palaeobiogeography and extinction of Spinosauridae based on the recent work of Candeiro et al. (2017).

- Discuss the hump/sail hypothesis (Bailey, 1997; Gimsa et al. 2015) proposed to explain the hypertrophied dorsal neural spines of Spinosauridae in a small paragraph.

- Cite and briefly mention the recent study of Sales et al. (2016) and Hassler et al. (2018) on Spinosauridae in the palaeogeography and palaeobiology sections.

Kind regards,

Christophe Hendrickx

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Abstract

Figure 1 | Reconstruction of the holotype skeleton, Natural History Museum, London
Ripton Scott, CC-BY-SA-2.0

Baryonyx (/ˌbæriˈɒnɪks/) is a genus of theropod dinosaur which lived in the Barremian stage of the early Cretaceous Period, about 130–125 million years ago. The holotype specimen was discovered in 1983 in Surrey, England, and the animal was named ***B. walkeri*** in 1986. The genus name, *Baryonyx*, means "heavy claw" and alludes to the animal's very large claw on the first finger; the specific name (*walkeri*) refers to its discoverer, amateur fossil hunter William J. Walker. Fragmentary specimens were later discovered in other parts of the United Kingdom and Iberia. The holotype specimen is one of the most complete theropod skeletons from the UK, and its discovery attracted media attention.

The holotype specimen of *Baryonyx*, which may not have pertained to a fully grown individual, ~~*Baryonyx*~~ was estimated to be between 7.5 and 10 m (25 and 33 ft) long and to weight~~ed~~ between 1.2 and 1.7 t (1.3 and 1.9 short tons).~~, but the holotype specimen may not have been fully grown~~. ~~It~~ *Baryonyx* had a long, low and narrow snout ~~and narrow jaws~~, which ~~have~~ has been compared to those of a gharial. The tip of the snout expanded to the sides in the shape of a rosette. Behind this, the upper jaw had a notch which fitted into the lower jaw (which curved upwards in the same area). It had a triangular crest on the top of its nasal bones. *Baryonyx* had many finely serrated, conical teeth, with the largest teeth in front. The neck was less curved than that of other theropods, and the neural spines of its dorsal vertebrae increased in height from front to back. It had robust forelimbs, with the eponymous first-finger claw measuring about 31 cm (12 in) long.

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Now recognised as a member of the family Spinosauridae, *Baryonyx's* affinities were obscure when it was discovered. Apart from the type species (*B. walkeri*), some researchers have suggested that *Suchomimus tenerensis* belongs in the same genus and that *Suchosaurus cultridens* is a senior synonym; subsequent authors have kept them separate. *Baryonyx* was the first theropod dinosaur demonstrated to have been piscivorous (fish-eating), as evidenced by fish scales in the stomach region of the holotype specimen. It may also have been an active predator of larger prey and a scavenger, since it also contained bones of a juvenile *Iguanodon*. The creature would have caught and processed its prey primarily with its forelimbs and large claws. *Baryonyx* may have had aquatic habits, and ~~lived in areas where other~~coexisted with other theropod, ornithopod, and sauropod dinosaurs as well as pterosaurs, crocodiles, turtles and fishes ~~have also been found~~ in a fluvial environment.

Description[edit]

Comment [CH1]: Please provide information on what cranial and postcranial bones are preserved in both the holotype and referred specimens.

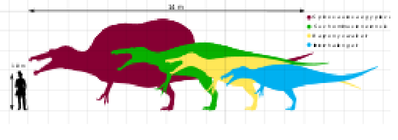

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Figure 2 | Size of spinosaurids (*Baryonyx* in yellow, second from right) compared with a human
PaleoGeekSquared, CC-BY-SA 4.0

In 2010, *Baryonyx* was estimated to have been 7.5 m (25 ft) long and to have weighed 1.2 t (1.3 short tons).[1] It was estimated at 10 m (33 ft) in 1997, and 9.5 m (31 ft) long, 2.5 m (8.2 ft) in hip height, and 1.7 t (1.9 short tons) in weight in 1988. The fact that elements of the skull and vertebral column of the *B. walkeri* holotype specimen (NHM R9951) do not appear to have co-ossified (fused) suggests that the individual was not fully grown, and the mature animal may have been much larger~~ (as attested by the size of the related *Spinosaurus*, which reached 15 m (49 ft) and 10 t (11 short tons)~~. On the other hand, the specimen's fused sternum indicates that it may have been fairly mature.[2][3][4] The second-best-preserved specimen (ML1190) was about the same size as the holotype skeleton.[1][5]

Figure 3 | Three neck vertebrae of the holotype; the third is shown from two angles
Serjoscha Evers et al, CC-BY 4.0

Postcranium[edit]

Initially thought to lack the sigmoid curve typical of theropods (reference), t~~T~~he neck appears to formed a straighter *S* shape (a ~~sigmoid curve typical of theropods~~) than that seen in other theropods~~; in fact, the neck was initially thought to lack the *S* curve~~.[6] The ~~shape of the~~ cervical vertebrae ~~indicate that they~~ tapered towards the head and were progressively longer front to back. The neural spines of the cervical vertebrae were low, thin, and were not always sutured to the centra (the bodies of the vertebrae). The axis vertebra were~~,~~ small relative to the size of the skull and~~,~~ had a well-developed hyposphene. The centra of the dorsal vertebrae were similar in size. Like other dinosaurs, *Baryonyx* showed skeletal pneumaticity which enabled to reduce~~d~~ its weight (~~skeletal pneumaticity~~) ~~with~~ through fenestrae (openings) in the neural arches and ~~with~~ pleurocoels (hollow depressions) in the centra (primarily near the transverse processes). From front to back, the neural spines of the dorsal vertebrae changed from short and stout to tall and broad.[2]

The scapulae (shoulder blades) were robust and~~;~~ the bones of the forelimb were short in relation to the animal's size, but broad and sturdy. The humerus was short and stout, with its ends broadly expanded and flattened—the upper side for the deltopectoral crest and muscle attachment and the lower for articulation with the radius and ulna. The radius was short, stout and straight, and the olecranon of the ulna apparently very powerful. The lower part of the ulna had a broad expansion. The hands had three fingers; the first finger bore a large claw (ungual bone) measuring about 31 cm (12 in) along its curve in the holotype specimen. ~~, which~~ This claw would have been lengthened by a keratin sheath in life. Apart from its size, the claw's proportions were fairly typical of a theropod, i.e.,~~;~~ it was bilaterally symmetric, slightly compressed, smoothly rounded, and sharply pointed. A groove for the sheath ran along the length of the claw.
The pubic foot of the pelvis was not expanded.[2][1]

Comment [CH2]: No need to provide the year the length of *Baryonyx* was estimated. Instead, please just provide the length range, or each estimated length citing the reference of the work that provided such estimation. I would advise the authors to favour peer-reviewed articles such as those of Charig and Milner (1997) and Therrien and Henderson (2007),when talking about estimated size. I must admit I'm not a big fan of Paul's book given that his dinosaur phylogeny is highly controversial and does not rely on any cladistic analysis. Up to you!

Comment [CH3]: *Baryonyx* could have been a much smaller individual than *Spinosaurus*, even if they are closely related. Better to remove this.

Comment [CH4]: Please describe the skull first, then the postcranium.

Comment [CH5]: It should be mentioned that the neural spine of the dorsal vertebrae were relatively tall (Charig and Milner, 1990; Ever et al., 2015; n.n., yet not a tall as Spinosaurus' one obviously!), suggesting that *Baryonyx* may have had the incipient development of a sail or hump on its back. This hypothesis should, in fact, be discussed in the Palaeobiology section (see below).

Charig, A. J. and Milner, A. C. 1990. The systematic position of *Baryonyx walkeri*, in the light of Gauthier's reclassification of the Theropoda. *In*: Carpenter, K. and Currie, P. J. (eds.), *Dinosaur Systematics: Approaches and Perspectives*, 127–140. Cambridge University Press, New York, New York.

Evers, S. W., Rauhut, O. W. M., Milner, A. C., McFeeters, B. and Allain, R. 2015. A reappraisal of the morphology and systematic position of the theropod dinosaur *Sigilmassasaurus* from the "middle" Cretaceous of Morocco. *PeerJ*: 3:e1323.

Comment [CH6]: A single sentence describing the rest of the skeleton (i.e., hindlimb, pelvis and tail) is unsatisfactory. Please expand this section based on the preserved material and comparison with the closely related taxon *Suchomimus*.

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Figure 4 | Reconstruction of the holotype skull, Museon, The Hague
Ghedo, CC-BY-SA 3.0

Skull[edit]

The skull of *Baryonyx* is incompletely known, and much of the middle and hind portions are not preserved. The full length of the skull has been estimated to be 950 mm (37.4 in), based on comparison with that of the related genus *Suchomimus* (which is 20% larger; ~~)~~reference). It was elongated, and the front 170 mm (6.6 in) of the premaxillae formed a long, low snout (rostrum) with a rounded upper surface (reference). The nostrils are~~,~~ far back from the tip, ~~passed horizontally from one side of the skull to the other~~. and t~~T~~he front 130 mm (5.1 in) of the snout expanded into a spoon-like ~~spatulate~~ (spatulate~~flared outwards to the sides~~)~~,~~ "terminal rosette", a shape similar to that of the modern gharial rostrum.~~,~~ ~~and~~ T~~t~~he front 70 mm (2.7 in) of the lower margin of the premaxillae was downturned (or hooked) whereas that of the anterior portion of the maxillae was upturned. This morphology resulted in an undulate (sigmoid) margin of the lower upper tooth row, in which the teeth from the front of the maxilla were projecting forward. The snout was ~~very~~ particularly narrow ~~just~~ directly behind the rosette and received the large teeth of the mandible. ~~The *creature's*~~*Baryonyx* maxillae and premaxillae fit together in a complex articulation (reference)~~, resulting in a strongly curved tooth row~~. ~~The gap~~A downturned premaxilla and a sigmoid ventral margin of the upper tooth row ~~in the row is comparable to that~~is also present in distantly related theropods ~~of~~such as *Dilophosaurus* (reference).

The front 140 mm (5.5 in) of the dentary in the mandible curved upwards towards this area, and the gap between the upper and lower jaw is known as the subrostral notch (reference). The dentary was very long and shallow, with a prominent Meckelian groove. The rest of the lower jaw was fragile; the hind third was much thinner than the front, with a blade-like appearance. The front part of the dentary curved outwards to accommodate the large front teeth, and this area formed the mandibular part of the rosette. The dentary had many foramina (openings), which were passages for nerves and blood vessels.[2][1] The snout had extensive pits (which would have been exits for blood vessels and nerves; reference), and the maxilla appears to have housed sinuses.[2][7][1]

Figure 5 | Restoration
Robinson Kunz & Rebecca Slater, CC-BY-SA 3.0

Comment [CH7]: Please list the preserved bones.

Comment [CH8]: Note that I also provided estimation of the skull length based on the quadrate size (Hendrickx et al., 2016; PLOS ONE). You can cite me if you want!

Comment [CH9]: what do you mean by rounded upper surface?

Comment [CH10]: as it is always the case in theropods, so not sure this should be specified.

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Comment [CH11]: The strongly curved tooth row does not results from this complex articulation.

Comment [CH12]: Which also has a subnarial gap like *Spinosaurus* but unlike *Baryonyx*.

Comment [CH13]: The mandible should be described in this paragraph.

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Baryonyx had a rudimentary secondary palate, similar to crocodiles but unlike most theropod dinosaurs.[8] A rugose (roughly wrinkled) surface of the palate suggests the presence of a horny pad in the roof of the mouth. ~~It had a~~ A sagittal crest was present above the eyes, on the upper mid-line of the nasal bones.~~,~~ ~~which~~ This crest was triangular, narrow, and sharp in ~~front~~its front part. The lacrimal bone in front of the eye appears to have formed a horn core similar to those seen, for example, on *Allosaurus*. ~~The dentary was very long and shallow, with a prominent Meckelian groove. The rest of the lower jaw was fragile; the hind third was much thinner than the front, with a blade-like appearance. The front part of the dentary curved outwards to accommodate the large front teeth, and this area formed the mandibular part of the rosette. The dentary had many foramina (openings), which were passages for nerves and blood vessels.[2][1]~~ It has been suggested that some of *Baryonyx's* cranial bones had been misidentified (resulting in the occiput's too-deep reconstruction), and the skull was probably as low, long and narrow as that of the closely related *Suchomimus*.[9]

Most of the teeth found with the holotype specimen were not ~~attached to the skull~~in articulation; a few remained in the upper jaw, and only small replacement teeth were still bore ~~in~~ by the lower jaw. The teeth had the shape of recurved cones, and slightly flattened ~~somewhat~~ sideways. The larger teeth were less recurved than the smaller ones, but were otherwise uniform. The roots were very long and tapper towards their extremity~~, and the teeth slender~~ (reference). The carinae (sharp edges) of the teeth were finely serrated, with denticles on the front and back and extending all along the crown. There were around ~~seven~~ six to eight ~~narrow, uniform~~ denticles per millimetre (0.039 in), a much larger number than the large-bodied theropods like *Torvosaurus* and *Tyrannosaurus*~~, more than in most theropods~~. Some of the teeth were fluted, with six to eight ridges along the length of their inner sides and fine-grained enamel (reference). The inner side of each tooth row had a bony wall. The number of teeth was large, with six to seven premaxillary teeth ~~in the right premaxilla (other theropods have three to five)~~ and thirty-two in the dentary, where sixteen is typical. The lower jaw would have had sixty-four teeth, and the difference between the number of teeth in the upper and lower jaws is more pronounced than in other theropods (reference). The teeth in the dentary were more densely packed than those in the maxilla, and probably smaller. The terminal rosette in the upper jaw had thirteen dental alveoli (tooth sockets), six on the left and seven on the right side, witnessing tooth count asymmetry in this theropod.~~;~~ ~~T~~The first four upper teeth were large (with the second and third the largest), while the fourth and fifth progressively decreased in size (reference). The diameter of the largest was twice that of the smallest. The first four alveoli of the dentary (corresponding to the tip of the upper jaw) were the largest, with the rest more regular in size. Small subtriangular ~~i~~Interdental plates were present between the alveoli.[2][7]

Comment [CH14]: I'm sure there are some information on the braincase that are worth mentioning, even briefly.

Comment [CH15]: That's incorrect, all teeth share pretty much the same recurvature (pers. obs.).

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Comment [CH16]: You can cite my work on the spinosaurid quadrates from the Kem Kem beds (PLOS ONE), which briefly describe the teeth of *Baryonyx*.

Comment [CH17]: you need to provide references for such statement!!! Sixteen in what theropod clades???

History of discovery[edit]

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Figure 6 | Cast of the holotype hand claw in the Palais de la Découverte, Paris
Thesupermat, CC BY-SA 3.0

On 7 January 1983 the amateur fossil hunter William J. Walker discovered a large claw, a phalanx bone, and part of a rib in Smokejacks Pit, a clay pit near Ockley in Surrey, England (reference). The tip of the claw was missing, but Walker found it a week later. The British palaeontologists Alan J. Charig and Angela C. Milner examined the finds at the Natural History Museum of London and found more bones at the site on 7 February, but the entire skeleton could not be collected until May and June due to conditions at the pit (reference). A team of eight museum staff members and several volunteers excavated two tonnes of matrix. Walker donated the claw to the museum, and the Ockley Brick Company (owners of the pit) donated the rest of the skeleton and provided equipment.[2][10] The area had been explored for 200 years, but no similar remains had been found before.[11]

Most of the bones collected were encased in siltstone nodules surrounded by fine sand and silt, with the rest lying in clay. The bones were disarticulated and scattered over a 5 x 2 m (17 x 8 ft) area, but most were not far from their natural positions. The position of some bones was disturbed by a bulldozer, and some were broken by mechanical equipment before they were collected (reference). Preparing the specimen was difficult, due to the hardness of the siltstone matrix and the presence of siderite; acid preparation was attempted, but most of the matrix was removed mechanically. The skeleton consisted of partial skull bones; teeth; cervical, dorsal and caudal vertebrae; ribs; a sternum; coracoids; arm and hand bones; claws; hip bones, and leg bones.[2][12] ~~The original specimen number was BMNH R9951, but it was later re-catalogued as NHMUK VP R9951~~.[12][13]

Comment [CH18]: this should be moved to the description.

Comment [CH19]: Is this really important in a Wikipedia page??? Please delete.

Figure 7 | Snout of the holotype specimen, from the left and below
Andrew Cuff et al, CC BY 3.0

In 1986 Charig and Milner made the skeleton the holotype specimen of a new genus and species: *Baryonyx walkeri*. The genus name derives from ancient Greek; βαρύς (*barys*) means "heavy" or "strong", and ὄνυξ (*onyx*) means "claw" or "talon". The specific name honours Walker, for discovering the specimen. At that time, the authors did not know if the large claw belonged to

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the hand or the foot (as in dromaeosaurs, which it was then assumed to be; reference). Due to ongoing work on the bones (70 percent had been prepared at the time), they called their article preliminary (a "Letter to *Nature*") and promised a more detailed description at a later date. *Baryonyx* was the first large Early Cretaceous theropod found anywhere in the world by that time.[12][14] Before the discovery of *Baryonyx*, the last significant theropod find in the United Kingdom was *Eustreptospondylus* in 1871, and in a 1986 interview Charig called *Baryonyx* "the best find of the century" in Europe.[2][10] It was widely featured in international media, and its discovery was the subject of a 1987 BBC documentary. *Baryonyx* was nicknamed "Claws" by journalists punning on the title of the film *Jaws*. The skeleton is mounted at the Natural History Museum in London, and in 1997 Charig and Milner published a monograph describing the holotype skeleton in detail.[2][11]

Fossils from other parts of the UK and Iberia, mostly isolated teeth, have subsequently been attributed to *Baryonyx* or similar animals.[2] Isolated teeth and bones from the Isle of Wight, including hand bones and a vertebra, have been attributed to this genus.[15] A maxilla fragment from La Rioja, Spain, was attributed in 1995 (though it is also possible it belonged to *Suchomimus*).[16][17] In 1999 a postorbital bone, a squamosal bone, a tooth, vertebra remains, metacarpals, and a phalanx from the Sala de los Infantes deposit in Burgos Province, Spain, were attributed to an immature *Baryonyx* (though some of these elements are unknown in the holotype),[18][19] and dinosaur tracks near Burgos have been identified as those of *Baryonyx* or a similar theropod.[20] In 2011 a specimen (ML 1190) from the Papo Seco Formation in Boca do Chapim, Portugal, with a fragmentary dentary, teeth, vertebrae, ribs, hip bones, a scapula, and a phalanx bone, was attributed to *Baryonyx*, the most complete Iberian remains of the animal. The skeletal elements of this specimen are also represented in the more complete holotype NHM R9951, except for the mid-neck vertebrae.[5]

Comment [CH20]: What is the case before? Only a fully reconstructed cast of the specimen can be seen in the dinosaur gallery of the NHM, certainly not a mounted skeleton with the original bones.

Comment [CH21]: Additional material from the Isle of Wight were described by Munt et al. (2017) in an abstract/poster presented at the SVPCA of last year. Worth mentioning and referring according to me.

https://www.researchgate.net/publication/319879409_New_spinosaurid_dinosaur_finds_from_the_Wessex_Formation_Wealden_Group_Early_Cretaceous_of_the_Isle_of_Wight.

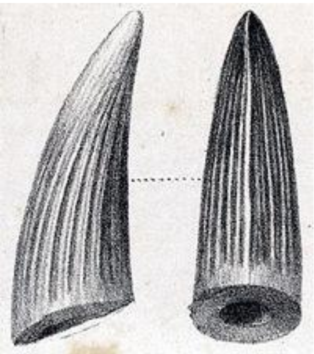

Figure 8 | 1878 lithograph showing the holotype tooth of *Suchosaurus cultridens*, which may represent the same animal as *B. walkeri*
James Erxleben, public domain

Possible synonyms[edit]

In 1997, Charig and Milner noted that two fragmentary spinosaurid snouts from the Elrhaz Formation of Niger were similar enough to *Baryonyx* that they considered them to belong to an indeterminate species of *Baryonyx*, despite their much younger geological age.[2] In 1998, these fossils became the basis of the genus *Cristatusaurus*. The authors of a 2002 article about the spinosaur *Irritator* proposed that *Suchomimus tenerensis* was similar enough to *B. walkeri* to be considered a species within the same genus (as *B. tenerensis*), and suggested that *Suchomimus* was identical to *Cristatusaurus*; both are from the Elrhaz Formation.[21] At about

Comment [CH22]: You should detail the discovery and description of *Suchomimus* here before stating that *Suchomimus* was proposed to be a junior synonym of *Baryonyx* by Sues et al. (2002).

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9.5 m (30 ft) and 2.5 tonnes (5,511 lb), *Suchomimus* was larger than *Baryonyx*.[1] In a 2004 conference abstract, the British palaeontologists Steve Hutt and Penny Newbery supported the synonymy based on a large theropod vertebra from the Isle of Wight which they attributed to an animal closely related to *Baryonyx* and *Suchomimus*, and used to reconfigure the spinal column of *Baryonyx*.[22] Later studies have kept the genera separate.[5][23][24] A 2017 review paper stated that this debate was more in the realm of semantics than science, as it is generally agreed these dinosaurs are distinct, related species.[25]

In a 2003 article, Milner noted that the teeth of *Baryonyx* were very similar to those of the genus *Suchosaurus* and suggested that their remains represented the same animal.[26] The type species of the genus, *S. cultridens*, was named by sir Richard Owen in 1841 (three years before he famously coined the word Dinosauria) based on teeth from Tilgate Forest in Sussex; a second species, *S. girardi*, was named by French geologist Sauvage in 1897 based on jaw fragments and a tooth from Boca do Chapim. In 2007 Buffetaut considered the teeth of *S. girardi* very similar to those of *Baryonyx* (and *S. cultridens*) except for the stronger development of the crown ribs, suggesting that the remains belonged to the same genus. Buffetaut agreed with Milner that the teeth of *S. cultridens* were almost identical to those of *B. walkeri*, but with a ribbier surface. The former taxon might be a senior synonym of the latter (since it was published first), depending on whether the differences were within a taxon or between different ones. According to Buffetaut, since the holotype specimen of *S. cultridens* is one worn tooth and that of *B. walkeri* is a skeleton it would be more practical to retain the newer name.[27] In 2011 Portuguese palaeontologist Octávio Mateus and colleagues agreed that *Suchosaurus* was closely related to *Baryonyx*, but considered both species in the former genus *nomina dubia* (dubious names) since their holotype specimens were not considered diagnostic (lacking distinguishing features) and could not be definitely equated with other taxa.[5]

Classification[edit]

In their original description, Charig and Milner (reference) found *Baryonyx* unique enough to warrant a new family of theropod dinosaurs: Baryonychidae. They found *Baryonyx* to be unlike any other theropod group (and considered the possibility that it was a thecodont, due to apparently primitive features; reference), but noted that the articulation of the maxilla and premaxilla was similar to that in *Dilophosaurus*. They also noted that the two snouts from Niger (which later became the basis of *Cristatusaurus*), assigned to the family Spinosauridae by the French palaeontologist Philippe Taquet in 1984, appeared almost identical to those of *Baryonyx* and they referred them to Baryonychidae instead.[12] In 1988, the American palaeontologist Gregory S. Paul agreed with Taquet that *Spinosaurus*, described in 1915 based on fragmentary remains from Egypt which were destroyed in World War II, and *Baryonyx* were similar and (due to their kinked snouts) possibly late-surviving dilophosaurs.[3] The French palaeontologist Eric Buffetaut also supported this relationship in 1989.[28] In 1990 Charig and Milner dismissed the spinosaurid affinities of *Baryonyx*, since they did not find their remains similar enough.[29] In 1997, they agreed that Baryonychidae and Spinosauridae were related, but disagreed that the former name should become a synonym of the latter, because the completeness of *Baryonyx* compared to *Spinosaurus* made it a better type genus for a family, and because they did not find the similarities between the two ~~great~~ significant enough.[2]

Comment [CH23]: Please cite the recent work of Sales and Shultz, 2017, which consider *Baryonyx*, *Cristatusaurus* and *Suchomimus* as separate taxa based on a cladistic analysis. My work (i.e., Hendrickx et al., 2016 PLOS ONE; Appendix) also discuss the morphological differences and synonymy of *Cristatusaurus* and *Suchomimus*, so if you want to cite it, go ahead!

Sales, M. A. F. and Schultz, C. L. 2017. Spinosaur taxonomy and evolution of craniodental features: Evidence from Brazil. *PLOS ONE* 12 (11): e0187070.

Comment [CH24]: This historical section should be slightly expanded to include the fact that the teeth were found by Gideon Mantell. This story is particularly interesting given that *Suchosaurus*, which is most likely the same taxon as *Baryonyx*, corresponds to the very first theropod to be named if I'm not mistaken. It was discovered by Gideon Mantell, like the first *Iguanodon* material, and was named and studied by Richard Owen who coined and first defined the group Dinosauria. *Suchosaurus* was, however, considered to belong to a crocodile. I've written something about that on my website in French a long time ago. Some illustrations are in English so this may help you to develop this section:

https://spinosauridae.fr.gd/Historique-des-decouvertes.htm

Comment [CH25]: which are called flutes in my terminology (Hendrickx et al., 2015 dental terminology of theropod teeth JVP).

Comment [CH26]: It's actually a pretty well-preserved tooth, but it's only a single tooth so yes, better retain the Baryonyx name and holotypic material described by Charig and Milner.

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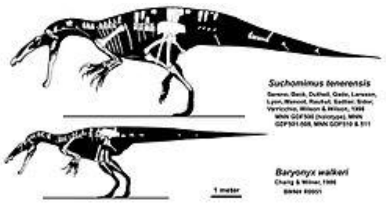
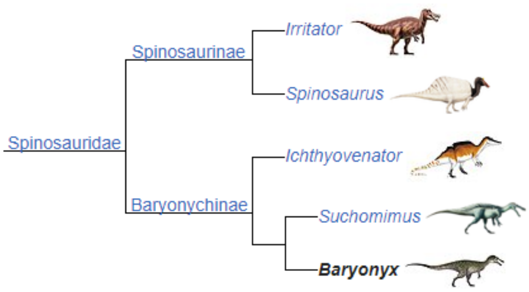


Figure 9 | Skeletal diagram of the holotype specimen (below) compared with the closely related genus *Suchomimus*
Jaime Headden, CC BY 3.0

Discoveries in the 1990s shed more light on the relationships of *Baryonyx* and its relatives. In 1996, a snout from Morocco was referred to *Spinosaurus*, and *Irritator* and *Angaturama* from Brazil (the two are possible synonyms) were named.[30][21] In 1998, *Cristatusaurus* and *Suchomimus* were named based on fossils from Niger. In their description of *Suchomimus*, Sereno and colleagues placed it and *Baryonyx* in the new subfamily Baryonychinae within Spinosauridae; other members of the group were placed in the subfamily Spinosaurinae.[9][31] They also united the spinosaurids and their closest relatives in the superfamily Spinosauroidea, but in 2010 Roger Benson considered this a junior synonym of Megalosauroidea (an older name).[32] The *Baryonyx walkeri* holotype specimen remains the most completely known spinosaurid skeleton.[33] The following cladogram shows the position of *Baryonyx* within Spinosauridae, after Ronan Allain and colleagues, 2012:[23]

Comment [CH27]: You can briefly provide a list of few derived features (synapomorphies) diagnosing each sub-family level clade such as the absence of denticulated carinae in Spinosaurinae and the anterior position of the nares in Baryonychinae.



Evolution[edit]

Figure 10 | Model of the snout-tip, NHM
Emőke Dénes, CC BY-SA 3.0

Spinosaurids appear to have been widespread from the Barremian to the Cenomanian ages of the Cretaceous, about 130 to 95 million years ago. They shared features such as long, narrow,

Comment [CH28]: where? Note that putative spinosaurid teeth from the Middle Jurassic of Niger (Serrano-Martínez et al., 2016), the Tithonian of the Tendaguru Beds of Tanzania (Buffetaut, 2012) and the Coniacian-Santonian of China (Hone et al. 2010) have been reported. This should be mentioned if you want to talk about the stratigraphic and palaeogeographic distribution of Spinosauridae.

Serrano-Martínez, A., Vidal, D., Sciscio, L., Ortega, F. and Knoll, F. 2016. Isolated theropod teeth from the Middle Jurassic of Niger and the early dental evolution of Spinosauridae. *Acta Palaeontologica Polonica* 61 (2): 403–415.

Buffetaut, E. 2011. An early spinosaurid dinosaur from the Late Jurassic of Tendaguru (Tanzania) and the evolution of the spinosaurid dentition. *Oryctos* 10: 1–8.

Hone, D. W. E., Xu, X. and Wang, D. Y. 2010. A probable baryonychine (Theropoda: Spinosauridae) tooth from the Upper Cretaceous of Henan Province, China. *Vertebrata PalAsiatica* 48 (1): 19–26.

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crocodile-like skulls; sub-circular teeth, with fine to no serrations; the ~~snout~~ terminal rosette of the snout, and a secondary palate which made them more resistant to torsion. In contrast, the primitive and typical condition for theropods was a tall, narrow snout with blade-like (ziphodont) teeth with serrated ~~front and back~~carinae (references). The skull adaptations of spinosaurids converged with those of crocodilians; early members of the latter group had skulls similar to typical theropods, later developing elongated snouts, conical teeth, and secondary palates (references). These adaptations may have been the result of a dietary change from terrestrial prey to fish. Unlike crocodiles, the post-cranial skeletons of ~~most spinosaurids~~ baryonychine spinosaurids ~~(except *Spinosaurus*)~~ do not appear to have aquatic adaptations.[4][34] Sereno and colleagues proposed that the large thumb-claw and robust forelimbs of spinosaurids evolved in the Middle Jurassic, before the elongation of the skull and other adaptations related to fish-eating, since the former features are shared with their megalosaurid relatives. They also suggested that the spinosaurines and baryonychines diverged before the Barremian age of the Early Cretaceous.[9]

Several theories have been proposed about the biogeography of the spinosaurids. Since *Suchomimus* was more closely related to *Baryonyx* (from Europe) than to *Spinosaurus*—although that genus also lived in Africa—the distribution of spinosaurids cannot be explained as vicariance resulting from continental rifting (reference). Sereno et al. (reference) proposed that spinosaurids were initially distributed across the supercontinent Pangea, but split with the opening of the Tethys Sea. Spinosaurines would then have evolved in the south (Africa and South America: in Gondwana~~land~~) and baryonychines in the north (Europe: in Laurasia), with *Suchomimus* the result of a single north-to-south dispersal event.[9] It has also been suggested that baryonychines could be the ancestors of spinosaurines, which appear to have replaced the former in Africa.[35] In 2006, it was demonstrated that Iberia was near northern Africa during the Early Cretaceous; some researchers have argued that the Iberian region was a stepping stone between Europe and Africa, which is supported by the presence of baryonychines in Iberia. The direction of the dispersal between Europe and Africa is still unknown,[27] and subsequent discoveries of spinosaurid remains in Asia and Australia indicate that it may have been complex.[5]

Comment [CH29]: Additional information on the biogeography and extinction, especially, of spinosaurids should be provided based on the recent paper by Candeiro et al. (2017), which is already cited in the text.

Palaeobiology[edit]

Figure 11 | Animatronics display depicting *Baryonyx* hunting fish, NHM
Ballista, CC BY-SA 3.0

Diet and feeding[edit]

In 1986 Charig and Milner (reference) ~~first~~ suggested that its elongated snout with many finely serrated teeth indicated that *Baryonyx* was piscivorous(a fish-eater), speculating that it crouched on a riverbank and used its claw to gaff fish out of the water (similar to the modern grizzly bear). ~~In 1984~~Two years early, Taquet (reference) pointed out that the spinosaurid snouts from Niger were similar to those of the modern gharial and suggested a behaviour similar to herons or storks. In 1997 Charig and Milner rejected their initial proposal that the articulation between the premaxilla and maxilla was mobile.[2][12] In 1987 Andrew Kitchener disputed the piscivorous behaviour of *Baryonyx* and suggested that it would have been a scavenger, using its long neck to feed on the ground, its claws to break into a carcass, and its long snout (with nostrils far back for breathing) for investigating the body cavity (reference). Kitchener argued that *Baryonyx's* jaws and teeth were too weak to kill other dinosaurs and too heavy to catch fish, with too many adaptations for piscivory.[36] According to Robin~~.~~ ~~E. H.~~ Reid, a scavenged carcass would have been broken up by its predator and large animals capable of doing so—such as grizzly bears—are also capable of catching fish (at least in shallow water).[37]

Figure 12 | The skull of the modern gharialhas been compared with that of *Baryonyx*]
Vince Smith, CC BY-SA 3.0

In 1997, Charig and Milner demonstrated direct dietary evidence in the stomach region of the *B. walkeri* holotype. It contained the first evidence of piscivory in a theropod dinosaur, acid-etched scales and teeth of the common fish *Scheenstia mantelli* (then classified in the genus *Lepidotes*), and abraded bones of a young *Iguanodon*. An apparent gastrolith (gizzard stone) was also found. They also presented circumstantial evidence for piscivory, such as crocodile-like adaptations for catching and swallowing prey: long, narrow jaws with their "terminal rosette", similar to those of a gharial, and the downturned tip and notch of the snout. In their view, these adaptations suggested that *Baryonyx* would have caught small to medium-sized fish in the manner of a crocodilian: gripping them with the notch of the snout (giving the teeth a "stabbing function"), tilting the head backwards, and swallowing them headfirst (reference). Larger fish would be broken up with the claws. That the teeth in the lower jaw were smaller, more crowded and numerous than those in the upper jaw may have helped the animal grip food. Charig and Milner maintained that *Baryonyx* would primarily have eaten fish (although it would also have been an active predator and opportunistic scavenger), but it was not equipped to be a macro-predator like *Allosaurus*. They suggested that *Baryonyx* mainly used its forelimbs and large claws to catch, kill and tear apart larger prey.[2][38]

Comment [CH30]: You can also mention the association of *Baryonyx* material with isolated *Iguanodon* teeth from Portugal (Hendrickx et al., 2016 PLOS ONE, p. 34).

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Figure 13 | Video showing a CT scan 3D model of the holotype snout in rotation
Andrew Cuff et al, CC BY 3.0

In 2004, a pterosaur neck vertebra from Brazil with a spinosaurid tooth embedded in it confirmed that the latter were not exclusively piscivorous.[39] A 2007 finite element analysis of CT scanned snouts indicated that the biomechanics of *Baryonyx* were most similar to those of the gharial and unlike those of the American alligator and more-conventional theropods, supporting a piscivorous diet for spinosaurids.[8] Their secondary palate helped them resist bending and torsion of their tubular snouts.[8] A 2013 beam-theory study compared the biomechanics of CT-scanned spinosaurid snouts with those of extant crocodilians, and found the snouts of *Baryonyx* and *Spinosaurus* similar in their resistance to bending and torsion. *Baryonyx* was found to have relatively high resistance in the snout to dorsoventral bending compared with *Spinosaurus* and the gharial. The authors concluded (in contrast to the 2007 study) that *Baryonyx* performed differently than the gharial; spinosaurids were not exclusive piscivores, and their diet was determined by their individual size.[13]

Comment [CH31]: The work of Therrien et al. (2005) on theropod and baryonychine mandible based on beam-theory as well, should also be mentioned in this section:

Therrien, F., Henderson, D. M. and Ruff, C. B. 2005. Bite me: biomechanical models of theropod mandibles and implications for feeding behavior. *In*: Carpenter, K. (ed.), *The Carnivorous Dinosaurs*, 179–237. Indiana University Press, Bloomington, Indiana.

A 2016 study found that adult spinosaurs could displace their mandibular rami (halves of the lower jaw) sideways when the jaw was depressed, which allowed the pharynx (opening that leads from the throat to the stomach) to be widened. This jaw-articulation is similar to that seen in pterosaurs and living pelicans, and would likewise have allowed spinosaurids to swallow large prey such as fish and other animals.[7] Another 2016 study found that the jaws of spinosaurids were convergent with those of pike conger eels; these fish also have sideways compressed jaws (whereas the jaws of crocodilians are compressed from top to bottom), an elongated snout with a "terminal rosette" that bears enlarged teeth, and a notch behind the rosette with smaller teeth. This type of jaws were likely evolved for grabbing prey in aquatic environments with low light, and may have helped in prey detection.[40]

Motion and aquatic habits[edit]

Figure 14 | Restoration of *Baryonyx* with a fish
Nobu Tamura, CC-BY-SA 3.0

In their original description, Charig and Milner did not consider *Baryonyx* to be aquatic (due to its nostrils being on the sides of its snout—far from the tip—and the form of the post-cranial skeleton), but thought it was capable of swimming, like most land vertebrates (reference). They speculated that the elongated skull, long neck, and strong humerus of *Baryonyx* indicated that the animal was a facultative quadruped, unique among theropods.[12] In their 1997 article they found no skeletal support for this, but maintained that the forelimbs would have been strong enough for a quadrupedal posture and it would probably have caught aquatic prey while crouching—or on all fours—near (or in) water.[2] A 2014 re-description of *Spinosaurus* based on new remains suggested that it was a quadruped, based on its anterior centre of body mass. The authors found quadrupedality unlikely for *Baryonyx*, since the better-known legs of the closely related *Suchomimus* did not support this posture.[4]

Comment [CH32]: Given that Baryonyx had relatively elongated dorsal? neural spine (Charig and Milner, 1990), please add a paragraph on the hump theory explored by Bailey (1997) and Gimsa et al. (2015). I know that they focus their work on the hypertrophied neural spine of Spinosaurus but given that you are sometimes talking about the palaeobiology of spinosaurids, it is worth mentioning this interesting topic.

Bailey, J. B. 1997. Neural spine elongation in dinosaurs: Sailbacks or buffalo-backs? *Journal of Paleontology*: 1124–1146.

Gimsa, J., Sleigh, R. and Gimsa, U. 2016. The riddle of *Spinosaurus aegyptiacus*' dorsal sail. *Geological Magazine* 153 (03): 544–547.

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Figure 15 | Restoration of a sunbathingBaryonyx being groomed by small pterosaurs and birds
Josep Asensi, CC BY 3.0

In 2017, David E. Hone and Thomas R. Holtz pointed out that (like other theropods) there was no reason to believe that the forelimbs of *Baryonyx* were able to pronate, and thereby make it able to rest or walk on its palms. Resting on or using the forelimbs for locomotion may have been possible (as indicated by tracks of a resting theropod), but if this was the norm, the forelimbs would probably have showed adaptations for this. Hone and Holtz furthermore suggested that the forelimbs of spinosaurids do not seem optimal for trapping prey, but instead appear similar to the forelimbs of digging animals. They suggested that the ability to dig would have been useful when excavating nests, digging for water, or to reach some kinds of prey. Hone and Holtz also believed that spinosaurids would have waded and dipped in water rather than submerging themselves, due to their sparsity of aquatic adaptations.[33]

A 2010 study proposed that spinosaurids were semiaquatic, based on the oxygen isotope composition of spinosaurid teeth from around the world compared with that of other theropods and extant animals. Spinosaurids probably spent much of the day in water, like crocodiles and hippopotamuses, and had a diet similar to the former; both were opportunistic predators. Since most spinosaurids do not appear to have anatomical adaptations for an aquatic lifestyle, the authors proposed that submersion in water was a means of thermoregulation similar to that of crocodiles and hippopotamuses. Spinosaurids may also have turned to aquatic habitats and piscivory to avoid competition with large, more-terrestrial theropods.[41]

A 2017 histological study of growth lines found that the Portuguese *Baryonyx* specimen had died between the age of 23 and 25 years old, and was close to its maximum size and skeletal maturity. This contradicted a younger age indicated by the neurocentral sutures not being fused, and the presence of both mature and sub-adult traits may be due to paedomorphosis (where juvenile traits are retained into adulthood). Paedomorphic traits may be related to swimming locomotion, as they have been suggested in other extinct animals thought to have been aquatic (such as plesiosaurs and temnospondyls). The study also found that the animal had reached sexual maturity at the age of 13 to 15 years, due to a decrease in growth rate at this point.[42]

Comment [CH33]: Definitely not your fault because it has just been published but you should mentioned Hassler et al.'s (2018) paper from Proceeding on that topic.

Hassler, A., Martin, J. E., Amiot, R., Tacail, T., Godet, F. A., Allain, R. and Balter, V. 2018. Calcium isotopes offer clues on resource partitioning among Cretaceous predatory dinosaurs. *Proc. R. Soc. B* 285 (1876): 20180197.

~~Palaeoecology~~Palaeoenvironment[edit]

Figure 16 | Reconstructed head and arm, NHM
Ballista, CC BY-SA 3.0

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The Weald Clay formation consists of sediments of Hauterivian (Lower Weald Clay) to Barremian (Upper Weald Clay) in age, about 130–125 million years old. The *B. walkeri* holotype was found in the latter, in clay representing non-marine still water, which has been interpreted as a fluvial or mudflat environment with shallow water, lagoons, and marsh (reference). During the Early Cretaceous, the Weald area of Surrey, Sussex, and Kent was partly covered by the large, fresh-to-brackish water Wealden Lake. Two large rivers drained the northern area (where London now stands), flowing into the lake through a river delta; the Anglo-Paris Basin was in the south. Its climate was sub-tropical, similar to the present Mediterranean region. Since the Smokejacks Pit consists of different stratigraphic levels, fossil taxa found there are not necessarily contemporaneous.[2] Dinosaurs from the locality include the ornithopods *Mantellisaurus*, *Iguanodon*, and small sauropods (references). Other vertebrates include sharks (such as *Hybodus*), bony fishes (including *Scheenstia*), crocodiles, and pterosaurs (references). Members of ten orders of insects have been identified, including *Valditermes*, *Archisphex*, and *Pterinoblattina* (reference). Other invertebrates include ostracods, isopods, conchostracans, and bivalves (reference). The plants *Weichselia* and the aquatic, herbaceous *Bevhalstia* were common. Other plants found include ferns, horsetails, club mosses, and conifers.[43]

Other dinosaurs from the Wessex Formation of the Isle of Wight include the theropods *Neovenator*, *Aristosuchus*, *Thecocoelurus*, *Calamospondylus*, and *Ornithodesmus*; the ornithopods *Iguanodon*, *Hypsilophodon*, and *Valdosaurus*; the sauropods *Pelorosaurus* and *Chondrosteosaurus*, and the ankylosaur *Polacanthus*.[44] The Papo Seco Formation of Portugal where *Baryonyx* has been identified is composed of marl, representing a lagoon environment. Other dinosaur remains from the area include fragments tentatively assigned to *Mantellisaurus*, a macronarian sauropod, and *Megalosaurus*.[5][27]

Figure 17 | Model carcass based on the position of the holotype bones, NHM
Ballista, CC BY-SA 3.0

Taphonomy[edit]

Charig and Milner presented a possible scenario explaining the taphonomy (changes during fossilisation) of the *B. walkeri* holotype specimen (reference). The fine-grained sediments around the skeleton, and the fact that the bones were found close together (skull and forelimb elements at one end of the excavation area and the pelvis and hind-limb elements at the other), indicates that the environment was quiet at the time of fossilisation and water currents did not carry the carcass far—possibly because the water was shallow. The area where the specimen died seems to have been suitable for a piscivorous animal. It may have caught fish and scavenged on the mud plain, becoming mired before it died and was buried. Since the bones are well-preserved and had no gnaw marks, the carcass appears to have been undisturbed by scavengers (suggesting that it was quickly covered by sediment). The disarticulation of the bones may have been the result of soft-tissue decomposition. Parts of the skeleton seem to have weathered to different degrees, perhaps because water levels changed or the sediments shifted (exposing parts of the skeleton). The girdle and limb bones, the dentary, and a rib were broken before fossilisation, perhaps from trampling by large animals while buried. The orientation of the bones

Comment [CH34]: I'm afraid you cannot rely on one reference only when talking about a whole ecosystem like this one. Just provide the most important works for at least the dinosaurs, crocodiles, turtles, insects, invertebrates and plants. No need to cite every single work on each taxa of courses, but at least several major works on the Weald Clay formation ecosystem.

Comment [CH35]: Please briefly mention the work of Sales et al. (2016) on the palaeoenvironment of spinosaurids.

Sales, M. A. F., Lacerda, M. B., Horn, B. L. D., Oliveira, I. A. P. de and Schultz, C. L. 2016. The "χ" of the matter: Testing the relationship between paleoenvironments and three theropod clades. *PLOS ONE* 11 (2): e0147031.

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indicates that the carcass lay on its back, which may explain why all the lower teeth had fallen out of their sockets and some upper teeth were still in place.[2]

Most of the bones of Portuguese specimen ML1190 were damaged, and some scratches may be marks from small scavengers. The specimen's disarticulation indicates it was transported from a more-terrestrial environment (since many bones are missing), but those found were close together.[5][27]

Acknowledgements[edit]

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