A new carcharodontosaurian theropod (Dinosauria: Saurischia) from the Lower Cretaceous of Thailand

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Abstract

The isolated fossil remains of an allosauroid theropod from the Lower Cretaceous Khok Kruat Formation of Khorat, Thailand, are described in this study. Detailed observations support the establishment of a new allosauroid, Siamraptor suwati gen. et sp. nov. This new taxon is based on a composite cranial and postcranial skeleton comprising premaxilla, maxilla, jugal, surangular, prearticular, articular, vertebrae, manual ungual, ischium, tibia, and pedal phalanx. It is distinguished from other allosauroids by characters such as a jugal with straight ventral margin and dorsoventrally deep anterior process below the orbit, a surangular with a deep oval concavity at the posterior end of the lateral shelf and four posterior surangular foramina, a long and narrow groove along the suture between the surangular and the prearticular, an articular with a foramen at the notch of the suture with the prearticular, an anterior cervical vertebra with a pneumatic foramen (so-called ‘pleurocoel’) excavating parapophysis, and cervical and posterior dorsal vertebrae penetrated by a pair of small foramina bilaterally at the base of the neural spine. The presence of a huge number of camerae and pneumatopores in cranial and axial elements reveals a remarkable skeletal pneumatic system in this new taxon. Moreover, the phylogenetic analyses revealed that Siamraptor is a basal taxon of Carcharodontosauria, involving a new sight of the paleobiogeographical context of this group. Siamraptor is the best preserved carcharodontosaurian theropod in Southeast Asia, and it sheds new light on the early evolutionary history of Carcharodontosauria.

Introduction

The basal tetanuran clades Allosauroidia and Megalosauroidea appeared by the Middle Jurassic and were soon represented by large-bodied taxa. These two clades are key to understanding Middle Jurassic–early Late Cretaceous dinosaurian ecosystems, in which they comprised almost all large predators over a span of approximately 85 million years. Although large
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theropod records from Early Cretaceous are scarce in Asia [1], some important specimens have been recovered in recent years [2–10]. Allosauroidia, a clade of large-bodied theropod dinosaurs that ranged from the Middle Jurassic until the Late Cretaceous, has been the subject of extensive phylogenetic study (e.g. [11–14]). Among them, Carcharodontosauria is the most inclusive clade, comprising Carcharodontosaurus saharicus and Neovenator salerii, but not Allosaurus fragilis or Sinraptor dongi [14], which was established as a replacement of the original definition of the Carcharodontosauridae named by Stromer [15] defined as C. saharicus, and all the taxa share a more recent common ancestor with it than with A. fragilis or S. dongi [1]. Coincidently, Carcharodontosauridae was redefined as the most inclusive clade comprising C. saharicus but not N. salerii, A. fragilis or S. dongi [1]. However, Asian carcharodontosaurs have been exceptionally poorly known so far in the Early to mid-Cretaceous of Asia [1,9].

In the last decade, Thailand has yielded a huge number of Mesozoic non-marine fossil vertebrates, ranging from the Late Triassic to the late Early Cretaceous [16]. Nevertheless, dinosaur remains from the Lower Cretaceous Khok Krut Formation have hitherto been scarce, and only iguanodontian ornithopods have been described based on isolated remains [17–19]. In this study, a new theropod taxon is described based on extensive cranial and postcranial materials collected in a locality of the Khok Krut Formation of the Japan-Thailand Dinosaur Project (abbreviated as JTDP [19]; Fig 1).

In this study, this new taxon is considered as a member of Allosauroidia in this study based on several features of extensive skull elements, axial material, ischium, tibia, manual ungual, and a pedal phalanx (Fig 2). All the measurements of bones are shown in Table 1. The osteological description of this taxon shows a notorious skeletal pneumaticity in the skull and axial elements, which presents some features that are similar to those observed in derived allosauroids such as Aerosteon [21] and Murusraptor [22], and some particular features, like the presence of pneumatic foramina in the surangular, camerate structures in the cervical vertebrae, or foramina in the base of cervical and dorsal neural spines. The results of the phylogenetic analysis indicate that the new taxon is a new basal member of Carcharodontosauria from the Early Cretaceous of Southeast Asia. Although other carcharodontosaurs have also been reported from Asia such as Fukuiraptor [23], Shaochilong [5], Kelmayisaurus [24] and an indeterminate and fragmentary carcharodontosaurid from Thailand [25], this is the first report of the presence of a more basal carcharodontosaurian theropod in this area. In combination with the presence of carcharodontosaurian materials in the Upper Jurassic of Portugal [26] and Tanzania [12,27], this study also indicates the wide distribution of Carcharodontosauria during the Upper Jurassic and Early Cretaceous, which is consistent with previous paleobiogeographic studies about Mesozoic faunal interchanges [20,28].

Geological setting

Cretaceous sediments in Thailand are composed mostly of non-marine deposits. The Khorat Group is the most fossiliferous strata in Southeast Asia, and is distributed on the Khorat Plateau in northeastern Thailand (Fig 1A and 1B; e.g. [29,30]). The Khok Krut Formation is the uppermost unit of the Khorat Group and is widely distributed in the Khorat Basin of northeastern Thailand (Fig 1A, 1B and 1E; [30]). This formation is 430–700m thick and consists mainly of reddish-brown siltstones and sandstones [30,31]. The main locality of the dinosaur fossils of the Khok Krut Formation, where the Japan-Thailand Dinosaur Project (JTDP) has worked, is located in Ban Saphan Hin, the Suranaree Sub-district, northwest of the Muang District, Nakhon Ratചschima Province (Fig 1C and 1D). Yukawa et al. [32] recognized three sedimentary facies of channel and bar, crevasse-splay and floodplain in the Khok Krut
Formation. The bone-bearing beds consist of medium- to coarse-grained sandstones and conglomerates containing clasts of clay rip-up pebble and rounded calcareous nodule granules with planar, cross and large scaled epsilon-type cross laminations. This lithofacies represents the channel and bar deposits. The crevasse-splay facies are characterized by poorly sorted fine-grained massive sandstone and layers of parallel laminated very fine-grained sandstones, while the floodplain facies are composed of massive mudstones with the paleosol [32].

The sedimentary environment of the Khorat Group represents the braided to meandering river systems [30], and the Khok Kruat Formation consists of meandering river deposits in the Khorat Basin. Yukawa et al. [32] interpreted that the deposits at the dinosaur fossil locality

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show point bars, channels and floodplain facies. Meesook [30] reconstructed the Cretaceous paleoclimate based on paleosols in deposits of the Khorat Group because the paleobotanical records are sparse. The paleoclimate represents a semi-arid to humid climate in the Khorat Basin, and, subsequently, again a semi-arid climate in the Sao Khua Formation, and slightly humid in the Phu Phan Formation. The Khok Kruat Formation was deposited under the semi-arid climate. However, Amiot et al. [33] suggest that the Khorat Basin was formed under a subtropical or tropical climate and a semi-humid condition.

The Phu Kradung, Sao Khua and Phra Wihan Formations are assigned to the Early Cretaceous (Berriasian–Barremian). However, the lower part of the Phu Kradung Formation may

Table 1. Measurements of the described materials of *Siamraptor suwati*.

| Element                                      | Specimen Number | Side   | Length (mm) | Width (mm) | Height (mm) |
|----------------------------------------------|-----------------|--------|-------------|------------|-------------|
| Premaxilla                                    | NRRU-F01020001  | Right  | 112         | 40         | 150         |
| Premaxilla                                    | NRRU-F01020002  | Right  | 110         | 31         | 139         |
| Premaxilla                                    | NRRU-F01020003  | Right  | 104         | 33         | 121         |
| Maxilla                                       | NRRU-F01020004  | Right  | 147         | 37         | 76          |
| Maxilla                                       | NRRU-F01020005  | Left   | 115         | 32         | 84          |
| Jugal                                         | NRRU-F01020006  | Left   | 210         | 20         | 135         |
| Posterior part of the mandible (surangular, prearticular, articular) | NRRU-F01020007  | Left   | 250         | 61         | 125         |
| Posterior part of the mandible (surangular, prearticular, articular) | NRRU-F01020008  | Right  | 555         | 126        | 124         |
| Posterior part of the mandible (surangular, prearticular, articular) | NRRU-F01020009  | Left   | 237         | 92         | 133         |
| Posterior part of the mandible (surangular, prearticular) | NRRU-F01020010  | Left   | 148         | 47         | 62          |
| Anterior cervical vertebra                    | NRRU-F01020011  | -      | 112         | 140        | 193         |
| Middle cervical vertebra                      | NRRU-F01020012  | -      | 89          | 91         | 114         |
| Middle cervical vertebra                      | NRRU-F01020013  | -      | 78          | 99         | 107         |
| Posterior dorsal vertebra                     | NRRU-F01020014  | -      | 130         | 116        | 281         |
| Posterior dorsal centrum                      | NRRU-F01020015  | -      | 89          | 85         | 127         |
| Posterior dorsal neural spine                 | NRRU-F01020016  | -      | 246         | 39         | 92          |
| Middle caudal vertebra                        | NRRU-F01020017  | -      | 107         | 35         | 79          |
| Manual ungual                                 | NRRU-F01020018  | ?      | 115         | 19         | 43          |
| Right ischium (distal part)                   | NRRU-F01020019  | Right  | 265         | 45         | 77          |
| Right ischium (proximal part)                 | NRRU-F01020020  | Right  | 250         | 41         | 214         |
| Tibia                                         | NRRU-F01020021  | Right  | 305         | 61         | 180         |
| Pedal phalanx IV-1                            | NRRU-F01020022  | Left   | 93          | 44         | 57          |

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include the Upper Jurassic, based on dinosaur fossils [29,34]. Although the geological age of the Khok Kruat Formation is not definitively decided due to the lack of age-diagnostic fossils, the Aptian age is widely accepted based on the palynological data, the occurrences of the fresh water hybodont shark *Thaoidus ruchae*, and the basal ceratopsian *Psittacosaurus sattayaraki*. The overlying Maha Sarakham Formation is inferred to belong to the Albian–Cenomanian age [10,29,35,36]. In this study, we adopt the Aptian age for the Khok Kruat Formation.

Nomenclatural acts
The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is: urn:lsid:zoobank.org:pub:8702-A94C-F2BS-4A4D-9454-52220F2D1C85. The electronic edition of this work was published in a journal with an ISSN and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS.

Materials and methods
The specimens described here (NRRU-F01020001–NRRU-F01020022) are housed at public and permanent repository in the collection of the Northeastern Research Institute of Petrified Wood and Mineral Resources, Nakhon Ratchasima Rajabhat University, Thailand, and are accessible to all researchers. No permits were required for the described study, which complies with all the relevant regulations. The excavation and collection of fossil remains were agreed with the landowner and were officially reported to the Department of the Mineral Resources, Thailand.

Institutional abbreviations; BMNH, Natural History Museum, London, England, UK; BYU, Brigham Young University, Provo, UT, USA; DINO, Dinosaur National Monument, Vernal, UT, USA; IVPP, Institute of Paleontology and Paleoanthropology, Beijing, China; FPDM, Fukui Prefectural Dinosaur Museum, 51–11 Muroko, Terao, Katsuyama, Fukui, 911–8601, Japan; MCF, Museo Munucipal "Carmen Funes", Plaza Huincul, Argentina; MIWG, Dinosaur Isle Museum of Isle of Wight, Sandown, UK; MCCM, Museo de Ciencias de Castilla-La Mancha, Cuenca, Spain, now MUPA, Museo de Paleontología de Castilla-La Mancha; MPEF, Museo Paleontológico "Egidio Feruglio", Trelew, Argentina; MUCPv-CH, Museo de la Universidad del Comahue, Colección Chocón, Villa El Chocón, Argentina; NCSM, North Carolina Museum of Natural Science, Raleigh, NC, USA; OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, OK, USA; UMNH, Natural History Museum of Utah/University of Utah, Salt Lake City, UT, USA.

Systematic paleontology

Dinosauria Owen, 1842 [37]
Theropoda Marsh, 1881 [38]
Tetanurae Gauthier, 1986 [39]
Allosauroidea Marsh, 1878 [40]
Carcharodontosauria Benson, Carrano and Brusatte, 2010 [14]

**Siamraptor** gen. nov.

urn:lsid:zoobank.org:act:70FBCCF0-1547-420F-AC6E-FA0BE799CAE5

**Siamraptor suwati** sp. nov.

urn:lsid:zoobank.org:act:46E1572B-54CE-4276-A6C0-8FF783D75954

**Etymology.**  *Siam* (Latin): in reference to Thailand; *raptor* (Latin): meaning a robber; *suwati*: in honour of Mr. Suwat Liptapanlop, who supports and promotes the work of the Northeastern Research Institute of Petrified Wood and Mineral Resources.

**Diagnosis.**  Allosauroid theropod with the following autapomorphies among allosauroids: Jugal with straight ventral margin, and dorsoventrally deep anterior process below the orbit; surangular with a deep oval concavity at the posterior end of the lateral shelf and four posterior surangular foramina; long and narrow groove along the suture between surangular and prearticular; articular with a foramen at the notch of the suture with prearticular; anterior cervical vertebra with an additional pneumatic foramen excavating parapophysis; cervical and posterior dorsal vertebra penetrated by a pair of small foramina bilaterally at the base of neural spine.

**Holotype.**  An articulated posterior half of the right mandible comprising the surangular, prearticular, and articular (NRRU-F01020008).

**Referred materials.**  Disarticulated cranial and postcranial elements from at least three individuals; three right premaxillae (NRRU-F01020001–F01020003), a right (NRRU-F01020004) and a left (NRRU-F01020005) maxillae, a left jugal (NRRU-F01020006), two posterior parts of the left mandible comprising the surangular, prearticular, and articular (NRRU-F01020007, F01020009), a posterior part of the left mandible comprising the surangular and prearticular (NRRU-F01020010), three anterior cervical vertebrae (NRRU-F01020011–F01020013), three posterior dorsal vertebrae (NRRU-F01020014–F01020016), a middle caudal vertebra (NRRU-F01020017), a manual ungual (NRRU-F01020018), a right ischium (NRRU-F01020019 and F01020020), a distal part of the right tibia (NRRU-F01020021), and a left pedal phalanx IV-1 (NRRU-F01020022). All of these are materials comparable to Allosauroidea that were found in a small area (125 m x 160 m) of a single layer of a single locality, and the overlapping materials exhibit the same diagnostic features.

**Locality and horizon.**  In Ban (meaning “village”) Saphan Hin, Suranaree Subdistrict, Muaeng Nakhon Ratchasima District, Nakhon Ratchasima Province, Thailand. Lower Cretaceous (Aptian) Khok Kruat Formation.

**Description**

**Premaxilla.**  The premaxillary body is preserved on each of the three right premaxillae (NRRU-F01020001–F01020003; Fig 3). The proportion of the main premaxillary body is approximately as anteroposteriorly long as dorsoventrally deep. The anterior margin of the premaxillary body is almost vertical unlike carcharodontosaurs, which have a posterodorsally inclined margin [11]. The narial fossa is well developed and situated just ventral to the external naris, unlike *Concavenator* and *Acrocanthosaurus* [41,42], in which the fossa is situated anterior to the external naris. Only the basalmost part of the supranarial and subnarial processes are preserved in NRRU-F01020001. As preserved, the supranarial process is dorsally directed and the subnarial one is posterodorsally directed.

The posterior surface for the contact with the maxilla is preserved but somewhat eroded in each specimen. In lateral view, the contact is almost perpendicular to the ventral margin of the
bone, and is almost straight, as in *Allosaurus* [43], rather than convex, as in *Sinraptor* [44] and *Acrocanthosaurus* [41]. There is a marked subnarial foramen in the contact surface for the maxilla, which makes a small notch in lateral view. This foramen is deeply excavated and wide in posterior view, although is not an expanded channel as those observed in spinosaurids [12]. Ventral to this subnarial foramen, there are smaller foramina in a row on the posterior surface of the premaxilla. The lateral surface is almost smooth, lacking extensive external sculpturing, unlike derived carcharodontosaurids [11]. However, several foramina and ventrally-directed grooves puncture the lateral surface of the premaxillary body, these foramina and grooves being as abundant and developed as in other allosauroids, such as *Allosaurus* (e.g. UMNH-VP 9248, 9250, 6502) and *Neovenator* (MIWG 6348).

In NRRU-F01020003, just ventral to the external naris, there are two foramina on the medial surface. These foramina are not observed in the other two specimens because of the breakage in the corresponding region. Although only one large foramen is present in *Sinraptor* [44] and *Neovenator* (MIWG 6248), the number of foramina varies among the specimens of *Allosaurus* from one to three, so that two foramina are also seen in some specimens (UMNH-VP 6504, 9238, 9252). The presence of these foramina is common in most large theropods [45]. The maxillary processes are well developed on the medial surface of NRRU-F01020002 and NRRU-F01020003 as a posterodorsally-oriented flange beneath the base of the subnarial

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Fig 3. Right premaxillae, NRRU-F01020003 (A–G), F01020002 (H–K) and F01020001 (L, M) in anterior (A), dorsal (B), medial (C, D, H, L), posterior (E), lateral (F, G, K, M) and alveolar (I) views. The rectangle in H indicates the area magnified in J to show premaxillary teeth. Abbreviations: ac, alveolar channel; en, external naris; fo, foramen; mp, maxillary process; nfo, nasal fossa; pa, possible pathology; snf, subnarial fossa; t, tooth. Scale bar equals 50 mm.

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process, but its posteromedial end is broken in each specimen and missing in NRRU-F01020001. The location of this process is relatively higher than in *Sinraptor* [44], as in *Allosaurus* (e.g. UMNH-VP 9238, 9248, 6502, 9252) and *Neovenator* (MIWG 6348). Dorsally, the medial surface between the external naris and the maxillary process is excavated to form a broad posteriorly-oriented groove for the contact with the anteromedial process of the maxilla, as in *Allosaurus* [43] and *Neovenator* [45]. More ventrally, the medial surface has four alveolar channels as openings in a row at the mid-height of the maxillary body with visible unerupted teeth.

Four alveoli are present in the premaxilla. NRRU-F01020003 has three incomplete teeth, NRRU-F01020002 has two complete erupted teeth, and NRRU-F01020001 has three incomplete erupted teeth and two unerupted teeth. The shape of each alveolus is oval, and the size is similar to each other. Each of these alveoli has the alveolar channel on the medial surface of the premaxilla.

In premaxillary teeth in all the premaxillae, both the anterior and posterior carinae are in the lingual side as in Averostra [46] but unlike the symmetrical carinae in Carcharodontosauridae [47]. Both carinae have serration and have two to three denticles per millimeter in the middle region. In NRRU-F01020002, the first and third teeth show mesial and distal carinae situated at the mesial and distal margins of the lingual surface to adopt a D-shaped cross section at its mid-crown. In NRRU-F01020003, the mid-crown cross section of the posteriormost teeth is elliptical and transversally compressed. The teeth seem to not present marked enamel wrinkles. The interdental plates are completely ossified. In ventral view, the premaxilla is almost straight, indicating an acute morphology of the symphysis, although the specimen lacks the left premaxilla in articulation.

In NRRU-F01020002, there is an unusual oval opening below the posteroventral margin of the narial fossa in lateral view. Anterior to this fossa, there is an oval, slightly swelling area composed of an apparently different, abnormal bone tissue. These opening and swelling are absent in the other two specimens; therefore, they possibly indicate pathologies.

**Maxilla.** Partial posteroventral ramus of the right (NRRU-F01020004) and left (NRRU-F01020005) maxillae are preserved (Fig 4). Based on the small size and the absence of any following alveoli, the preserved posteriormost alveolus of the left maxilla should be that of the maxilla itself. The jugal contact is not preserved in both materials. Both taper posteriorly, as in most theropods. Both lateral and medial surfaces are almost smooth.

The lateral surface exhibits the posteroventral part of the antorbital fossa as a depression near the dorsal margin. The ventral rim of the fossa is demarcated by a well-developed ridge, which becomes sharper and step-like posteriorly. The dorsal extent of the antorbital fossa is unknown because of the breakage of a thin, plate-like bone above its ventral rim. Along the ventral margin of the maxilla, the lateral surface is pierced by many small foramina, namely the superior labial foramina for branches of the superior alveolar nerve and maxillary artery.

In medial view, the interdental plates are fused to form a continuous lamina as in most allosauroids, except for *Sinraptor* [14,44,45,48]. However, in NRRU-F01020004, the suture between plates is slightly marked. Most interdental plates are dorsoventrally deeper than anteroposteriorly wide. Above the fused interdental plate, the dorsal half of the medial wall forms a raised area, which is demarcated dorsally by a sharp ridge, and ventrally by the paradental groove, also known as 'groove for the dental lamina' (e.g. [49–51]) and 'nutrient groove' [52], which separate it from the interdental plates [49]. In NRRU-F01020005, the area is well developed as a striated surface, and the groove composing its ventral margin forms a step-like ridge. A broad, shallow, longitudinal groove is also present in the medial wall in NRRU-F01020004.

In dorsal view, a palatal suture is visible as a narrow shelf dorsal to the medial wall, associated with a longitudinal notch, which is situated lateral to the shelf and deepened posteriorly.
This suture is laterally bordered by the bony plate comprising the antorbital fossa. In the left maxilla (NRRU-F01020005), an oval foramen is present laterally adjacent to the bony plate, near the anterior limit of the notch.

The right maxilla (NRRU-F01020004) has four complete alveoli with partial teeth inside and two incomplete alveoli without erupted teeth. Two unerupted teeth are visible in the broken area. Although the left maxilla (NRRU-F01020005) has four alveoli, there are no preserved erupted teeth. All the alveoli, as well as the maxillary teeth, are laterally compressed, anteroposteriorly elongated, and rectangular shaped in ventral view. All the maxillary teeth exhibit the typical shape for carcharodontosaurids, as they are broad in lateral view, slightly recurved, serrated, and transversely thin. Both carinae in all the teeth have denticles, with a density of three denticles per millimeter, as in *Acrocanthosaurus* [53]. Numerous small and non-pronounced marginal enamel wrinkles are present in the distal carinae. In dorsal view of NRRU-

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Fig 4. Left (A–H: NRRU-F01020005) and right (I, J: NRRU-F01020004) maxillae and an in situ maxillary tooth (K; NRRU-F010200040) in dorsal (A, B), medial (C, D), anterior (E), lateral (F, I–K), posterior (G) and alveolar (H) views. The rectangle in I indicates the area magnified in K to show a maxillary tooth. Abbreviations: al, alveolus; aof, antorbital fossa; fo, foramen; gdl, groove for dental lamina; idp, fused interdental plate; mw, medial wall; n, longitudinal notch; p, bony plate; pc, palatal contact; slf, superior labial foramina. Scale bar equals 20 mm for A–J and 10 mm for K.

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F01020004, the second anterior alveolus (the anteriormost one of the complete alveoli) exhibits a replacement tooth adhered to the concave medial side of the root of the erupted tooth.

**Jugal.** There is a nearly complete left jugal (NRRU-F01020006) that shows a laterally compressed and tripartite shape (Fig 5). The ventral margin of this bone is completely straight in lateral view, unlike in other allosauroids, which present distinct shapes such as undulate [43,44] or slightly bowed ventrally [41,54,55].

In lateral view, there is a concave anterodorsal margin in the anterior process to form the posteroventral corner of the antorbital fenestra. Below the antorbital fenestra, although the antorbital fossa is fairly blunt, there is a circular pneumatic foramen that demarcates the posteroventral corner of the fossa on the lateral surface. This foramen corresponds to the jugal pneumatic recess that is also present in other allosauroids, and it has a similar morphology in *Concavenator* [42]. However, it is divided into two parts in *Sinraptor* [44], and it is much narrower in *Acrocanthosaurus* [41] and *Mapusaurus* [54]. The breaks in the central part of the lateral surface of the jugal indicate the presence of an inner cavity posterior to the foramen, a

![Fig 5. Left jugal (NRRU-F01020006) in lateral and medial views. Abbreviations: afe, antorbital fenestra; afo, antorbital fossa; dqjp, dorsal quadratojugal prong; fo, foramen; lc, lacrimal contact; ltf, lateral temporal fenestra; mc, maxilla contact; o, orbit; pc, postorbital contact; pr, pneumatic recess; vqjp, ventral quadratojugal prong. Scale bar equals 20 mm.](https://doi.org/10.1371/journal.pone.0222489.g005)
feature that is also supported by a swelling in the corresponding part of the medial surface. Along the ventral margin in lateral view, there is a narrow groove-like suture for contact with the maxilla in the anterior half of the process. Posterior to this suture, two small foramina and a horizontal ridge are present, the latter running from the anterior end of the groove between quadratojugal prongs. A similar ridge is also seen in *Mapusaurus* and *Tyrannotitan* [55], but it is anterodorsally-oriented toward the ventral margin of the orbit in these species. In medial view, the anterior process has two contact sutures neighboring to the antorbital fenestra, ventrally for the posterior ramus of the maxilla and posteriorly for the descending process of the lacrimal. Both are marked by striations. The posterior part of the anterior process is dorsoventrally tall and has a shallowly concave dorsal margin comprising the ventral margin of the orbit. This is a fairly characteristic condition, given that, in other allosauroids, the orbit excavates the dorsal margin more deeply to reach almost the same level as the ventral margin of the lateral temporal fenestra [41,43,44,56]. A similarly shallow, but strongly narrow concavity in the dorsal margin is also seen in *Monolophosaurus* [57], but it is currently regarded as a basal tetanuran [12].

Posterior to the anterior process, the postorbital process projects dorsally. The anterior margin of the process has a contact suture for the ventral ramus of the postorbital. The suture faces mainly anterolaterally and its ventral half has a dorsally-projecting lamina. In lateral view, the postorbital contact ends at the dorsal margin of the lamina, and thus it is substantially above the ventral rim of the orbit, like in other avetheropods [12,14,47]. In contrast, medial to the lamina, the suture is continuous as a notch and it extends more ventrally up to the base of the postorbital process. A similar notch is also present in *Sinraptor* [44] as the postorbital contact, although it ends high above the ventral margin of the orbit. Posterior to this notch, there is a shallow, dorsoventrally elongate depression.

The posterior process lacks its posterior end and thus it shows the bases of two quadratojugal prongs, which form a tongue-and-groove contact with the anterior ramus of the quadratojugal. The ventral prong is taller than the dorsal prong, which is a similar condition to *Allosaurus* [43], but contrary to most allosauroids [41]. The contact suture for the quadratojugal is also present as the grooves dividing these prongs in both lateral and medial surfaces, which are deeper in the latter. There does not exist an accessory prong between these two prongs, unlike in carcharodontosaurids [41].

**Surangular.** Four partial mandibulae are known for this taxon. Each one of NRRU-F01020007–F01020009 is composed of the articular, prearticular and surangular (Figs 6, 7 and 8), whereas NRRU-F01020010 is composed of the prearticular and surangular. The right surangular is virtually complete in NRRU-F01020008, whereas the left surangular preserves only a posterior part in NRRU-F01020007, F01020009, and F01020010.

The anterior surangular foramen is excavated in the posterior end of the anterior one–third of the surangular, and it is continuous anteriorly with a shallow groove. Anteriorly, the ventral margin of the groove is formed by a finger-like process, which, in other theropods, extends laterally over the lateral surface of the dentary. The flat, anteroventrally-projecting flange (angular process) forms a posterior margin of the external mandibular foramen. There is a wide contact surface for the angular along the ventral margin of the process as a slightly depressed surface with blunt oblique striations. This contact is most clearly observed in NRRU-F01020009 with a prominent step-like dorsal margin, and it is posterodorsally delimited by the prearticular. In the lateral surface of the surangular, the lateral shelf is strongly developed slightly above the midline of the posterior half of the bone. It becomes dorsally higher in its posterior part to form a knob-like process situated anterolateral to the lateral gelenoid. Medial to the lateral shelf, the medial shelf is also well-developed and located more dorsally. Between these shelves, there is a longitudinal and lateromedially wide depression, on
which the *M. adductor mandibulae externus* attaches. Slightly anterior to its posterior end, a blunt longitudinal ridge emerges and divides the depression into two parts in NRRU-F01020008 and F01020009. The medial shelf continues further anteriorly and forms a striated, dorso-medial-facing surface as a suture with the coronoid. In this part, the medial shelf also forms a longitudinal cleft that is continuous with an anterodorsally-directed groove bordering the anteroventral margin of the coronoid suture. The dorsal margin of the coronoid suture is marked by a longitudinal ridge. Posterolaterally, the medial margin of the medial shelf forms a longitudinal ridge projecting dorsally and is continuous with the lateromedial ridge representing the anteromedial margin of the glenoid. The dorsal part of the glenoid forms the lateral part of the glenoid, but it has no contribution to the ridge separating two depressions of the glenoid, unlike in *Sinraptor* [44].

The surangular extends more posteriorly to contribute to the posterolateral end of the retroarticular process. The posterior process of the surangular has a mediodorsally-faced suture for the articular.

Four posterior surangular foramina are preserved beneath the lateral shelf. The most posterior and the biggest one is located anterolaterally and ventral to the glenoid, in the same position as that of *Sinraptor* [44]. This foramen penetrates the bone anteromedially and ends on the posteriormost part of its inner surface (adductor fossa) as a part of possible pneumatic foramina. The second foramen is located more anteriorly, anterolaterally to the knob-like process of the lateral shelf. It penetrates medially or posteromedially into the bone and conjoins with the first foramen. Anteriorly, there are two additional smaller posterior surangular foramina under the marked lateral shelf. The third (posterior) one penetrates the bone with two directions, namely posteromedially and anteromedially, and only the former pierces into the inner surface of the bone. The fourth (anterior) one penetrates only posteromedially and conjoin with the piercing foramen of the third, just before its end. In theropods, only a single foramen or two foramina have been reported, and the latter condition was proposed as a synapomorphy of Allosauroida [47].

The posterior end of the lateral shelf is marked by a deep oval concavity excavating the bone medially. Within this concavity, there are five to seven small foramina separated by septa. This feature has not been reported in other allosauroids and thus could be an autapomorphy for this taxon.

In the anterior view of NRRU-F01020009, there are four small pits ventrally along the anterolateral margin of the glenoid, but they are clearly absent in a smaller specimen (NRRU-F01020008). Lateroventral to these pits, there is a large, mediolaterally-elongated pneumatic foramen on the posteriormost part of the adductor fossa. This foramen penetrates the surangular posteriorly and is separated by dorsoventrally-orientated septa. Laterally, the foramen widens and is continuous with the first and second posterior surangular foramina. Although this foramen is visible in all the available surangular materials, the septa are apparently absent in the smallest specimen (NRRU-F01020010). In NRRU-F01020008, the surangular forms an oval fossa at the...
middle of the glenoid along the suture line with the articular. Although the glenoid is also well preserved in NRRU-F01020010, the fossa is absent. The absence of these characters in smaller specimens indicate some ontogenetic variations within the surangular.

**Prearticular.** Each of the four posterior mandibles (NRRU-F01020007–F01020010) contains a part of the prearticular, but it is best preserved in NRRU-F01020007 (Fig 8). Each
prearticular is preserved in contact with the surangular and, if present, the articular in the medial side of the mandible. Only the thick posterior part of the prearticular is preserved. This
posterior part is broadly expanded to underlie the articular to cover its ventral margin and the hooked postadductor process of the surangular. The preserved prearticular is anteriorly extended, forming the ventral margin of the mandible.

In lateral view, anterior to the level of the posterior surangular foramen, the ventral margin of this bone becomes bowed ventrally. On the dorsal margin of the anterior part of this bone, there is a longitudinal ridge projecting laterally. When in articulation with the surangular, the ridge makes a long and narrow groove rather than a normal suture line. Below or anterior to this ridge, the lateral aspect of this bone forms a concave surface, possibly for the contact with the angular. The posterior part of this bone swells medially and becomes Y-shaped in medial view due to a prominent notch at the middle of its posterodorsal margin. There are three open foramina in the medial aspect of the prearticular. The posterior one is formed at the notch of the articular-prearticular suture (see Articular below). The middle one is seen only in NRRU-F01020009 (the largest specimen among the four), and it is situated anterior to the posterior one. The anteriormost one is seen in both NRRU-F01020007 and F01020009, situated at the dorsal margin of the posterior part of the prearticular, just below the anterior margin of the suture with the articular, also described in Acrocanthosaurus [41].

**Articular.** Three articulars (NRRU-F01020007–F01020009) are preserved in articulation with the surangular and the prearticular (Figs 6–8). The anterior margin is delimited by a marked ridge of the surangular, as in other Tetanurae [12]. In dorsal view, the articular is as wide as long, with a depressed and strongly wide glenoid region. The glenoid region is not separated in the lateral and medial glenoid fossae by a sharp ridge, like Allosaurus [58] or Sinraptor [44]. However, this interglenoid ridge is also greatly reduced in Mapusaurus and low in Acrocanthosaurus [41]. There is a tall and slightly sharp spine, forming the posterior margin of the glenoid. This spine is smaller and less developed than in carcharodontosaurids such as Acrocanthosaurus or Mapusaurus, but it is similarly developed as in non-carcharodontosaurid allosauroids like Sinraptor or Allosaurus. Posterior to this spine, there is a laterally-oriented groove, which divides the retroarticular process from the spine. This groove is possibly homologous to that observed in Tyrannosaurus [59] and Murusraptor, in the latter of which the groove is recognized as the insertion of M. depressor mandibulae [22]. The semicircular retroarticular process is lateromedially wide and has a concave bowl-like attachment surface facing posterodorsally. A posteriorly-oriented retroarticular process has been proposed as a synapomorphy of Avetheropoda [12,60] or a synapomorphy of Allosauria [12]. However, a posterodorsally inclined retroarticular process is also defined in Acrocanthosaurus [41].

In medial view, there are two prominent foramina in NRRU-F01020007, F01020009, and F01020010. The first one is below the approximate middle of the medial glenoid, formed together with the notch of the posterodorsal margin of the prearticular. This foramen is not seen in other allosauroids, so this seems to be a diagnostic feature for this taxon. The second one is the foramen posterior chorda tympani located immediately below the posterior margin of the medial glenoid. This foramen is smaller than those of Sinraptor [44] and Acrocanthosaurus [41]. The medial surface of the articular presents a projection that envelopes this foramen.

**Cervical vertebra.** One complete and two incomplete cervical vertebrae are known for this taxon (Fig 9). NRRU-F01020011 is an almost complete cervical vertebra, most likely to be the 3rd in comparison with Allosaurus [43], mainly based on a quite short distance between parapophysis and diapophysis and the extent of the anterior projection of the prezygapophysis. NRRU-F01020012 and F01020013 are basically similar to NRRU-F01020011 and have laterally wide centra and relatively flat anterior surfaces, being likely to be the successive cervical vertebrae, namely, in 4th to 6th position. The anteroposteriorly short centra also support that these are not the longer posterior vertebra from the 6th position, like in Neotheropoda [61].
Fig 9. Cervical vertebrae, NRRU-F01020011 (A–E), F01020012 (F–H), and F01020013 (I) in anterior (A), left lateral (B, F), ventral (C), dorsal (D), posterior (C, G), and right lateral (H, I) views. Uncolored casts of each specimen are used for B–E, G and H. Abbreviations: acdl, anterior centrodiapophyseal.
The centrum is opisthocoelous and is invaded bilaterally by a pneumatic foramen on its anterior part. In the 3rd cervical, the anterior articular surface is circular in anterior view and convex, but its ventral half is more flattened than the dorsal half. In the following cervical vertebrae, the anterior surface is laterally elongate, and the opisthocoelic condition is very reduced, like in Sinraptor (IVPP V10600), and completely unlike the developed hemispherical condition (“ball and socket”) in derived carcharodontosaurs [55]. The well-excavated posterior surface is offset strongly ventrally relative to the anterior surface and elongated laterally to show an elliptical outline posteriorly, except for its dorsal part where the rim is slightly concave anteriorly. The parapophysis strongly projects laterally from the anteroventral corner of the centrum so that it almost reaches the lateroventral margin of the anterior surface in lateral view. The parapophyseal facet is convex in NRRU-F01020011 and F01020013, whereas it is flat in NRRU-F01020012. In the 3rd cervical, the ventral surface of the centrum is almost flat, except for a laterally-oriented ridge between both parapophyses and a blunt median keel in its anterior two-thirds. The following cervical vertebrae have a completely flat ventral surface without the median keel, whereas the lateral ridge between parapophyses is present as a ventral margin of the anterior surface.

The centrum is camerate due to the division in several huge camerae by septa, as proposed by Britt [62]. This structure is best observed in NRRU-F01020012. In posteromedial view, the lateral wall of the internal cavity of the centrum is penetrated by the pneumatic foramen occupying its posterodorsal margin. The rest of the lateral wall is excavated by several fossae. They are directed anteriorly in the area anterior–anteroventral to the opening and directed posteriorly in the area posterior–posteroveltral to the opening. Additionally, a laterally-oriented foramen is present anterodorsal to the opening. Anterior to the large internal cavity, another small cavity, with several laterally-oriented foramina, is present inside the anterior articular surface. Dorsal to the internal centrum cavity, another cavity that opens dorsally toward the infrapostzygapophyseal fossa is present.

The pneumatic foramen is better developed on the left side than on the right side in NRRU-F01020011. The anterior and dorsal margins of the pneumatic foramen are marked by an anterodorsally-bowed lamina which extends from the posterovelventral margin of the centrodiapophyseal fossa to the anterodorsal margin of the parapophysis. The pneumatic foramen deepens anteriorly and splits into two, dorsal and ventral, fossae separated by a thick, anterodorsally-directed septum, as in Aerosteon [21]. The dorsal fossa of the pneumatic foramen is narrow and deep anteriorly and becomes broader and shallower posteriorly. The anterior part of the dorsal fossa opens medially into the internal chamber of the centrum, at least, in the subsequent cervical vertebrae, whereas the condition is unknown in the 3rd cervical because of the extreme narrowness of the corresponding part. The ventral fossa is almost elliptical, and it is further divided into two parts, the one excavates anteromedially toward the anterior surface and the other anterovelventrally into the parapophysis. The posterior and medial margins of the ventral fossa are marked by a posteromedially-bowed lamina that extends from the ventral margin of the septum between the fossae to the posterodorsal margin of the parapophyseal facet. A similar fossa is observed in Condorraptor [63] and Sinraptor [44], in which the pneumatic foramen is located posterodorsal and dorsomedial to the parapophysis, respectively.
The prezygapophysis is projecting anterodorsally and supported lateroventrally by the prezygodiapophyseal lamina, and medioventrally by a blunt centroprezygapophyseal lamina. Between these laminae, the prezygocentrodiapophyseal fossa is present and has a foramen that is small, laterally narrow, and located near the base of the centerodiapophyseal lamina. The ventral margin of this foramen is also preserved in the broken neural arch of the following cervical vertebrae. This foramen opens into a large pneumatic cavity within the prezygapophysis that is visible in the broken right side. The tab-like prezygapophyseal facet faces dorsally but somewhat inclines anteromedially as in *Sinraptor* [44], and unlike in *Allosaurus* [43]. The anterior margins of the left and right prezygapophyseal facets are medially continuous as thin laminae and they meet at their medial ends to form the V-shaped base of the spinoprezygapophyseal fossa. This fossa deepens medially, and the deepest part has a rugosity that indicates an attachment of the interspinal ligament.

The diapophysis is projected strongly ventrally and slightly posterolaterally, as in the 3\textsuperscript{rd} cervical of *Allosaurus* [43], and it has a ventrally-facing flat facet. In lateral view, the anterior and posterior margins are demarcated by the anterodorsally-inclined prezygodiapophyseal lamina and the subvertically oriented postzygodiapophyseal lamina, both of which make the diapophysis being subtriangular, as seen in some carcharodontosaurs [13]. The centrodiapophyseal laminae are inclined anteriorly with the anterior lamina directed dorsally and the posterior lamina directed anterodorsally in their basal part, as in the anterior cervical vertebrae of other allosauroids. The posterior centrodiapophyseal lamina is thicker and longer than the anterior. The centrodiapophyseal fossa is present between these laminae with several deeper fossae inside. At least in the medial part, the fossa is larger on the right side than on the left, contrary to the condition of the pneumatic foramen. The medial part is wide and has a circular outline on the right side, whereas it is narrow and triangular and is ventrally bordered by the dorsal rim of the pneumatic foramen on the left side. The lateral part of the centrodiapophyseal fossa extends until the ventral margin of the diapophyseal facet.

The postzygapophyses projects laterally and slightly posteriorly from the base of the neural spine. The postzygapophyseal facet faces lateroventrally and slightly posteriorly. The facet is elongated ventromedially to the level slightly above the neural canal, as in the anterior cervical vertebrae of other allosauroids. The ventral margin of the facet is supported by a short, vertical lamina demarcating the lateral margin of the neural canal. Posterior margins of the left and right facets ventrally emerge as fairly thin laminae and meet at their medioventral ends to form a V-shaped hypophene that delimits the base of the spinopostzygapophyseal fossa. The posterodorsal margins of both postzygapophyses also demarcate the dorsal margin of the spinopostzygapophyseal fossa, except for its mediadorsal part, in which the fossa is continuous as a groove on the posterior surface of the neural spine. This fossa medially deepens and has a rugosity indicating an attachment of the interspinal ligament as in the spinoprezygapophyseal fossa. The postzygocentrodiapophyseal fossa is present between the postzygodiapophyseal lamina and the anteroventral margin of the postzygapophysis, and above the posterior centrodiapophyseal lamina. This fossa is the largest pneumatic fossa in the cervical vertebra. The fossa invades the neural arch dorsomedially and has a deeper dorsomedial part distinguished by a step-like lateroventral margin, as in *Sinraptor* (IVPP V10600). The epipophysis is present as a mound-like swelling on the dorsal surface of the postzygapophysis, unlike a large posteriorly-oriented projection of *Sinraptor* [44], *Concavenator* [64], *Tyrannotitan* [55], *Mapusaurus* (MCF-PVPH 108.90), and other theropods such as ceratosaurids [12].

The neural spine is laterally thin and plate-like and seems to be projected purely dorsally. The anterior and posterior surfaces are narrow, but they have longitudinal grooves continuous to the spinopre- and spinopostzygapophyseal fossae, respectively. The base of the neural spine
is invaded by pneumatic foramina bilaterally in NRRU-F01020011 and F01020013 and the left side is larger than the right, as in the pneumatic foramen in NRRU-F01020011.

**Posterior dorsal vertebrae.** Three posterior dorsal vertebrae are known for this taxon (Fig 10). NRRU-F01020015 and F01020016 only preserve the centrum and the neural spine, respectively. NRRU-F01020014 is more complete than the other two, lacking the anterodorsal part of the neural spine, transverse processes, and parapophyses. Both NRRU-F01020014 and F01020015 are slightly distorted to offset the posterior surface to the left side relative to the anterior surface, but they are still parallel to each other. Compared with *Allosaurus* [43], the absence of pneumatic foramina, the strong constriction of the centrum, and the absence of a parapophysis in the mid-height of the centrum indicate that NRRU-F01020014 and F01020015 are posterior vertebrae from the 7th. Judging from the dorsal margin perpendicular to both anterior and posterior margins, NRRU-F01020016 is a thin, plate-like spine projecting almost completely dorsally like in NRRU-F01020014 and the posterior dorsal vertebrae from the 8th of *Allosaurus* and *Sinraptor*.

The centrum is higher than transversally wide in both anterior and posterior views. In NRRU-F01020015, the centrum is platycoelous with flat anterior and slightly concave posterior surfaces. In contrast, the anterior surface is slightly concave, and thus, the centrum is amphicoelous in NRRU-F01020014. In lateral view, the centrum is as high as long in NRRU-F01020014 and F01020015. Both the anterior and posterior surfaces exhibit a dorso-ventrally-elongated elliptical outline, but their dorsal margin is excavated by the ventral margin of the neural canal. In both materials, the posterior surface is facing slightly more ventrally than the anterior. The mid-section of the centrum is strongly constricted, in such a way that it is hourglass-shaped (constriction *sensu* Carrano et al. [12]). This constriction, which has been previously proposed as a synapomorphy of Metriacanthosauridae [61], is an unambiguous synapomorphy of Allosauroida present only in their posterior dorsal vertebrae [12]. The ventral surface has a sharp midline ridge, as in 6th and 7th dorsal vertebrae of *Neovenator*, although it is not well developed as the ventral keel (hypapophyses) of the anterior elements in other theropods. The centrum lacks pneumatic foramina on both lateral surfaces, unlike carcharodontosaurids and *Neovenator* [65], which have pneumatic foramina in all dorsal vertebrae, including the posterior.

The prezygapophysis projects anteriorly from the base of the neural spine and its facet faces dorsally. The margin between the neural spine and the prezygapophysis is marked by a small foramen. Both prezygapophyses are closely located to each other to form a narrow cleft, the hypantrum. The hypantrum emerges beneath the prezygapophyses in anterior view and become slightly broader as it approaches its ventral margin. The prezygocentrodiapophyseal fossa, which is best preserved on the right side of NRRU-F01020014, is deeply excavated, as in other avetheropods [12]. The outline of the fossa is marked dorsally by a horizontally-oriented prezygodiapophyseal lamina and by an anterodorsally-directed centroprezygapophyseal lamina. The posterodorsal and posteroventral margins of this fossa are marked by thin broken walls of the bone indicating the presence of thin laminae. A short posterodorsally-oriented lamina extending from the anterodorsal margin of the lateral surface of the centrum supports the parapophysis, as in the 10th of *Sinraptor* [44].

Posterodorsal to the prezygocentrodiapophyseal fossa, there is another large pneumatic foramen composing the centrodiaaphyseal fossa at the base of the transverse process. This fossa is surrounded by a thin broken section, except for its ventral margin that is marked by a posteriorly oriented lamina. The deepest part of the centrodiaaphyseal fossa is continuous to the inner cavity of the neural arch, as in the prezygocentrodiaaphyseal fossa.

The postzygapophyses project slightly posteriorly from the base of the neural spine, and their facet faces ventrally. The facet lacks flange-like lateral extensions unlike that of
neovenatorids [14]. The posterior margins of postzygapophyses meet at their medial ends to form the ventral border of the spinopostzygapophyseal fossa. Ventral to this junction, the sheet-like hyposphene extends ventrally with parallel lateral edges, unlike the ventrolaterally divergent triangular shape in other theropods. This parallel condition has been defined as a synapomorphy of Carcharodontosauridae [12]. However, other allosauroids also have this parallel hyposphene, such as some vertebrae of *Allosaurus* (UMNH-VP 9029, 9060, 10111; BYU 17532, 9063), *Neovenator* (MIWG 6348; BMNH R10001), and *Murusraptor* (MCF-PVPH-411). The hyposphene lacks a step-like ridge running posterodorsally from the dorsal border of the neural canal to the posterior edge of the postzygapophyses, as in some megalosauroids and megaraptorans [12,63].

Between the articular surfaces of postzygapophysis and hyposphene, the postzygocentropophyseal fossa is excavated and opens into a huge cavity inside the neural arch, which is also continuous with other major fossae in the neural arch. The lateral margin of the postzygocentropophyseal fossa forms a thin lamina that composes the ventral part of the posterior centropophyseal lamina.

The neural spine is plate-like, and it is higher than anteroposteriorly wide in lateral view. In dorsal view, the spine is a transversally thin sheet, unlike the I-beam cross-sectioned neuraphysis of the derived carcharodontosaurids [66]. In NRRU-F01020014, the spine projects almost perpendicularly to the anteroposterior axis of the centrum as in the 9th dorsal vertebra of *Sinraptor* [44]. Ventrally, perpendicular flanges on the lateral margins emerge on the anterior and posterior surfaces of the neural spine. The spinoprezygapophyseal and spinopostzygapophyseal fossae are present between these flanges. A pronounced roughness representing interspinous ligament metaplastic scars is present within these fossae, and it is dorsally continuous with other major fossae in the neural arch. The lateral margin of the postzygocentropophyseal fossa forms a thin lamina that composes the ventral part of the posterior centropophyseal lamina.

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Middle caudal vertebra. A caudal vertebra (NRRU-F01020017) lacking the right prezygapophysis and both transverse processes is known for this taxon (Fig 10). The presence of an anterior and posterior ramus of the neural spine and its height, as well as the presence of a small transverse process, indicate that this vertebra could be around the 25th middle caudal vertebra, comparing with *Allosaurus* [43]. The spool-shaped centrum has a triangular anterior surface with a ventral apex and a sub-rectangular posterior surface. Both surfaces are as wide as high, and slightly concave. The ventral portion of the posterior surface is beveled strongly anteriorly for articulation with the chevron. Ventrally, the centrum is pinched as a blunt longitudinal keel, and it slightly widens and flattens near the chevron articulation.

The neural arch is dorsoventrally thin and anteroposteriorly elongate. The prezygapophysis is projected further anteriorly than the anterior surface of the centrum, and its facet is dorsomedially oriented. The transverse processes are incomplete, but they are situated below the
level of the dorsal margin of the centrum and they are anteroposteriorly narrow, as in 22nd–
25th caudal vertebrae of Allosaurus. The postzygapophyses are posteriorly projected from the
base of the neural spine, but do not extend the posterior end of the centrum. The articular
facet is oriented laterally and slightly ventrally. The neural spine is split into anterior and pos-
terior processes, the last one is not dorsally high. The spinoprezygapophyseal fossa is reduced
to a small circular recess that penetrates the anterior surface of the base of the neural spine as
in the middle caudal vertebrae of Neovenator [45]. The neural spine is present as an anteropos-
teriorly long and laterally narrow sheet. The dorsal margin of the neural spine is concave at its
middle part in lateral view. Anterior and posterior to this concavity, the broken bases of the
anterior spur and the rod-like process are present, as in the mid-caudal vertebrae of other allo-
sauroids [67].

Manual ungual. NRRU-F01020018 is a manual ungual lacking only its proximal and dis-
tal ends (Fig 11). The preserved proximoventral margin exhibits an anterior end of the flexor
tubercle. As seen in megaraptorids, the ungual is mediolaterally thin and dorsoventrally low
even in the part near the proximal end. The ungual is not strongly recurved, unlike those of
some allosauroids such as Allosaurus (UMNH-VP 9718), Concavenator (MCCM-LH 6666),
Fukuiraptor (FPDM-V43), and Saurophaganax (OMNH 780). Some derived carcharodontosa-
saurids, such as Mapusaurus (MCF-PVPH 108.14) and Acrocanthosaurus (NCSM 14345),
have less recurved unguals, and they are transversally broad, unlike in Siamraptor. Both medial
and lateral surfaces have a single vascular groove along the ventral margin in a fixed distance.

Ischium. A proximal portion of the right ischium (NRRU-F01020020) is preserved, lack-
ing most of the shaft and the articulation for the pubis (Fig 11). In the proximal portion, the
lateral surface is flat or slightly convex, whereas the medial surface is shallowly concave. The
iliac peduncle flares laterally at its dorsal margin. In proximal view, although the posteromedial
part of the contact surface for the ilium is rugose because of the erosion, the remaining part
exhibits a flat surface, like in other basal allosauroids (e.g., Allosaurus and Sinraptor) and
unlike the peg-and-socket articulation in abelisaurids, a neovenatorid Siats meekerorum [68]
and carcharodontosaurids [12,69]. Anterior to the iliac contact, there is a blunt ridge oriented
anterolaterally, which makes two shallow concavities between the iliac and pubic peduncles in
the acetabular surface. In lateral view, the base of the pubic peduncle also has a blunt ridge ori-
ented horizontally, just above the midline of the peduncle. The posterior margin of the iliac
peduncle is almost straight and directed anteroventrally, so that the posteriorly-directed flange
is absent like in basal allosauroids and Neovenator, unlike Allosaurus and carcharodontosaur-
ids [11]. Between the iliac peduncle and the shaft of the bone, there is a rugose swelling on the
lateral surface, the ischial tuberosity, which indicates the attachment of M. flexor tibialis inter-
nus [70,71]. The ischial tuberosity is reduced to a slight rugosity in allosauroids such as Neove-
nator, Allosaurus, Concavenator, and Acrocanthosaurus, among other theropods [45,70,72]. In
Siamraptor this scar is slightly more marked, even more than in Siamotyrannus (PW9-1).
Although the obturator process is also broken at its base, the proximal and distal obturator
notches are present, separating the process from the pubic peduncle and the shaft, respectively.
At the level of the ventral end of the obturator process, the posterior margin of the proximal
shaft exhibits a beginning of a distinct crest, which seems to be as those observed in Sinraptor
and other metriacanthosaurids [44] but not in Allosaurus (BYU 12906, 16942; UMNH-VP
9505, 20726) and Acrocanthosaurus (NCSM 14345).

The distal part of the ischium (NRRU-F01020019), which probably belongs to the same
bone as the proximal part (NRRU-F01020020), has convex lateral and flat medial surfaces (Fig
11). In lateral view, a blunt longitudinal ridge runs along the midline of the shaft. Distally, the
posterior margin of the shaft forms a thin, flange-like projection, which makes the area poste-
rior to the longitudinal ridge slightly broader than the anterior area. The distal end is only
slightly flared anteroposteriorly, as in *Allosaurus*. The medial surface has well-developed stria-
tions except for its proximal part, in which the surface becomes smooth and swells medially.
There is no sign of fusion with the opposite ischium.

**Tibia.** Only the distal part of the tibia (NRRU-F01020021) is preserved (Fig 11). The shaft
is almost straight, mediolaterally wider than anteroposteriorly thick, and mostly flat anteriorly
and convex posteriorly, in the preserved distal portion. Distally, the shaft is expanded trans-
versely. On the anterior aspect of this expansion, there is a contact for the ascending process
of the astragalus that is represented by a triangular, slightly concave surface. Its proximomedial
margin (suprastragalar buttress) is represented by an oblique blunt ridge, as seen in *Acro-
canthosaurus*, *Mapusaurus*, and *Neovenator*, unlike the step-like ridge seen in more basal allo-
sauroids such as *Allosaurus* [43] and metriacanthosaurids [44,73]. The lateral malleolus is
larger and projecting farther distally than the medial malleolus, as in *Acrocanthosaurus* [66], *Mapusaurus* [54], and *Neovenator* [45]. The lateral margin of the lateral malleolus is straight and directed distolaterally as in *Australovenator* [74] and *Mapusaurus* [54], unlike the rounded one seen in other allosauroids [12]. The medial malleolus projects medially at the same degree as *Allosaurus* [43], *Neovenator* [45], and *Concavenator* [72], unlike the more medially projecting one in *Acrocanthosaurus* [66]. The medial margin of the medial malleolus is rounded and has a blunt apex at its middle part as in *Allosaurus* [43] and *Concavenator* [72]. This apex is more prominent in *Acrocanthosaurus* [66], although is absent in *Neovenator* [45] and *Sinraptor* [44]. Posteriorly, the medial malleolus has a flat, postero-medially-faced surface. On the postero-distal margin, there is a notch just medial to its midline, as seen in metriachanthosaurids [44,73].

**Pedal phalanx IV-1.** NRRU-F01020022 is somewhat deformed (Fig 11). The proximal articular surface is a single shallow concavity, indicating the articulation with a ball-shaped distal surface of the metatarsal IV as in other theropods. In dorsal view, there is a depression just proximal to the distal articular surface (hyperextensor pit). More proximal to that, a small nutrient foramen penetrates the bone distoventrally. The medial collateral ligament fossa is much deeper and more ventral situated than the lateral one. In ventral view, there is a narrow, longitudinal depression at its proximolateral end, as well as a nutrient foramen just proximal to the distal articular surface.

**Discussion**

**Phylogenetic analysis**

Several phylogenetic matrices have been used in order to study the phylogenetic relationships of theropod in recent years (e.g. [1,11,12,14,47,67,75–78]). Focusing on the basal Tetanurae, two data matrices are widely recognized as the main ones on the discussion of the alternative distributions of allosauroids, related to the intense debate about the position of Megaraptora. Therefore, we have tested the datasets proposed by Carrano et al. [12] and Porfiri et al. [13] (modified from Novas et al. [76]) in order to establish the phylogenetic relationships of *Siamraptor*. The data matrix of Carrano et al. [12] consists of 361 characters and 62 taxa, and the one of Porfiri et al. [13] is performed by 284 characters and 46 taxa. There are no modifications of these matrices, except for one character in Carrano et al. [12] (ch.132), in which one additional state of character has been added to include the condition in *Siamraptor* (See S1 Appendix).

The matrices were managed using Mesquite 3.01 [79]. Subsequently, these matrices were imported into TNT 1.5 [80] in order to perform a heuristic tree search and find the most parsimonious trees (MPTs). The heuristic tree search used the New Technology algorithms: sectorial searches, ratchet, tree-drifting, and tree fusing, using the default settings for all of them. These algorithms were applied to new searched trees using the driven search with a stabilization of the consensus twice with a factor of 25. Subsequently, the results were exposed to the branch-swapping algorithm of tree bisection reconnection (TBR). The character was ordered only in Porfiri et al. [13], as indicated in their methodology. The MPTs found from both iterations were examined under the strict consensus, and the consistency index (CI) and retention index (RI) were obtained using the "stats.run" script of TNT. The branch support was tested using the methodology proposed by Goloboff et al. [81] to calculate Bremer Support values and the resampling methods bootstrap and jackknife (under default settings). Additionally, in order to find "wildcards" taxa, a reduced consensus tree was performed using the agreement subtrees method. In addition, pruned trees were carried out, calculating pruning up to five taxa.
The heuristic tree search using the data matrix based on Carrano et al. [12] produced 972 MPTs of 1016 steps, with a consistency index of 0.416 and a retention index of 0.695 (Fig 12). *Siamraptor* is nested within Allosauria in the strict consensus as a more derived position than Allosauridae (*Allosaurus + Saurophaganax* sensu Carrano et al. [12]) and as the most basal taxon of Carcharodontosauria (the most inclusive clade including Neovenatoridae and Carcharodontosauridae and excluding Allosauridae sensu Benson et al. [14]). The reduced tree in Allosauroidea reduced Metriacanthosaurinae (sensu [12]) to *Y. hepingensis* and *S. dongi* and Carcharodontosaurinae to *Tyrannotitan* and *Mapusaurus*. However, the pruning analysis indicated that only pruning *Streptospondylus* improves Megalosauria node but pruning the rest of “wildcard” taxa does not improve the results. The position of the *Siamraptor* was not affected by both the reduced and pruned trees.

*Siamraptor* presents four allosauroid synapomorphies in this phylogenetic analysis: (1) a projected medial edge of the mandibular glenoid [ch.133 (1)], (2) a pneumatic foramen on the posterior rim of the antorbital fossa of jugal [ch.52 (1)] (see discussion below), (3) an expanded prezygocentrodiapophysal fossa in dorsal vertebrae [ch.182 (1)]; and (4) a strong constriction in the posterior dorsal vertebrae centrum (hourglass-shaped) [ch.194 (1)]. *Siamraptor* has the following synapomorphy of Allosauria: the presence of fused paradental plates in the maxilla, without replacement grooves and forming a continuous medial lamina [ch.138 (1)]. *Siamraptor* shares with the members of Carcharodontosauria: (1) the presence of two pneumatic foramina oriented anteroventral-posterodorsally in cervical vertebrae [ch.169 (1)], (2) a parallel and sheet-like hyposphene lamina (although this feature is also observed in other allosauroids, as previously mentioned in the description) [ch.187 (1)]; and (3) a reduced and oblique ridge of suprastragalar buttress for the astragalus in the anterior surface of the tibia (shared with *Neovenator* and Carcharodontosauridae, but transformed in a bluntly rounded vertical and medial ridge in megaraptorans [12]) [ch.322 (3)]. Finally, some diagnostic features are obtained based on this phylogenetic analysis: (1) the presence of more than two posterior surangular foramina (an autapomorphy among theropods) [Modified ch. 132 (2)], (2) the presence of marginal enamel wrinkles (shared with Carcharodontosauridae in this phylogeny, although this character actually has a high level of homoplasy because it turns up several times in the Averostra lineage [42]) [ch.143 (2)]; and (3) the flat anterior surfaces of the presacral vertebrae, in contrast to the convex condition in Tetanurae (an autapomorphy among tetanurans) [ch. 156 (0)]. Some symplesiomorphies are determined based on the results of this phylogenetic analysis, such as the postero- and dorally-oriented attachment surface of the retroarticular process, which is posteriorly-oriented in Allosauria (except in *Acrocanthosaurus* sensu [41]) [ch.137 (0)]; and the low and blunt epipophyses, as in *Allosaurus* but different in other allosauroids [ch.177 (0)].

In the data matrix of [13], the results of the heuristic search showed 138 MPTs of 932 steps of length, with CI of 0.371 and RI of 0.664 (Fig 13). *Siamraptor* occupies a similar position within Allosauroida as in the results obtained in the analysis using the data matrix of [12]. In the strict consensus, the position of *Siamraptor* is more derived than *Allosaurus*, rather nested in a basal polytomy within Carcharodontosauria with *Eocarcharia, Concavenator*, and *Neovenator*. This result is obtained mainly by the position of megaraptorids nested in Tyrannosauridea, unlike the one nested in Allosauroida in the analysis that follows [12]. The polytomy in the base of Carcharodontosauria is solved in the reduced tree, pruning *Eocarcharia, Concavenator*, and *Neovenator*. These specimens, not observed in this agreement subtree, were added one by one to check their phylogenetic position related to *Siamraptor*. However, each taxon included was positioned in the same polytomy. In the reduced tree, *Carcharodontosaurus saharicus* is also pruned from Carcharodontosauridae, and Megaraptora is composed by
Fig 12. Strict consensus of the phylogenetic analysis based on Carrano et al. [12] matrix. The numbers at the top of the nodes indicate Bremmer support, those at the bottom are bootstraps and jackknife branch support, respectively. 

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Fig 13. Strict consensus of the phylogenetic analysis based on Porfiri et al. [13] matrix. The numbers at the top of the nodes indicate Bremmer support, those at the bottom are bootstraps and jackknife branch support, respectively. 

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Megaraptor and Eotyrannus. The pruned analysis indicated that any pruning taxa does not improve the topology of the trees.

Only one allosauroid synapomorphy is present in Siamraptor according to this analysis: the presence of the prezygoepipophyseal lamina, a ridge splitting the lateral surface of the neural arch of the cervical vertebra into two [ch.103 (1)]. This feature is also observed in megaraptorids but [13] coded a new character state as a deeper condition for this group. Siamraptor shares two features with other members of Allosauria: (1) enamel wrinkles near the denticles [ch.1 (1)]; and (2) a strong medial expansion of the distal medial malleolus [ch.190 (1)]. Based on this analysis, the diagnostic features of Siamraptor proposed are: (1) a sub-rectangular alveolar contour of the maxilla, also shared with Mapusaurus, Megalosaurus, Tanycolagreus, and Eotyrannus [ch.9 (1)]; (2) a slightly opisthocoelous condition in cervical vertebrae (an autapomorphy of the node of Megalosauroidea+Neotetanurae sensu [13], shared with Ceratosaurus, Piatnitzkysaurus, and Dilong [ch.97 (0)]); (3) the presence of a hyposphene-hypantrum accessory articulation in cervical vertebrae (an autapomorphy among allosauroids, shared with some carcharodontosaurids) [ch.102 (1)], and (4) a subvertical posterior dorsal neural spine (an autapomorphy among allosauroids) [ch. 108 (0)].

Although both analyses differ in the position of Megaraptora (Megalapartoridae sensu [13]), the position of Siamraptor as a member of Carcharodontosauria is unambiguously supported by both results.

Remarks on the allosauroid anatomy

**Skull anatomy.** The tetanuran condition of Siamraptor is unambiguous, based on two skull synapomorphies of this group. The presence of a jugal pneumatic foramen has been considered as a tetanuran synapomorphy [56,60]. However, some coelurosaurians appear to lack this structure [82], and it is identified as an allosauroid synapomorphy [12]. Although the morphology and development of this foramen vary within the tetanuran clade, its position in the antorbital fossa of the jugal in Siamraptor allows homologizing it to the one described by Sereno et al. [56,60]. Moreover, the presence of a well-developed antorbital fossa in the jugal is a feature shared with some tetanurans [12,67]. In lateral view of the jugal, the ventral margin of the postorbital contact ends above the ventral margin of the orbit in Siamraptor. The postorbital contact ends substantially above the ventral margin of the orbit in Avetheropoda [12,14,47]. Besides this lateral contact, the ventral portion of the postorbital also wraps around onto the medial surface and is inserted on a marked notch of the jugal in Siamraptor. This notch on the medial surface is also observed in Sinaraptor [44] and some specimens of Allosaurus (e.g. UMNH-VP 9085), in which the ventral end of this medial contact notch is also substantially above the ventral margin of the orbit in Sinaraptor and Allosaurus. In Siamraptor, although the lateral surface indicates a dorsally situated end of the postorbital ventral tip, this medial notch runs through the postorbital process down below the orbit, similar to non-avetheropodan theropods such as Torvosaurus (“Edmarka rex” by [83]; juvenile of Torvosaurus by [12]).

The descriptions of several complete allosauroid skulls in recent years (e.g. [41,42,44]) have enabled us to improve the knowledge of the cranial osteology of this widely known theropod group. The presence of two posterior surangular foramina is observed in Allosaurus [47] and Sinaraptor [44], and it has been proposed as a synapomorphy of Allosauroidea that was reverted to the primitive condition in Carcharodontosauridae [47]. However, the basal carcharodontosaurid Concavenator also presents two foramina [42], and only Acrocanthosaurus lacks the second posterior surangular foramen within Allosauroidea. Siamraptor shows an unusual feature relative to the number of posterior foramina in the surangular, due to the presence of four of
them. Within Allosauroida, the skull of *Siamraptor* shows more similarities with members of Allosauria than with basal allosaurids such as metriacanthosaurs. For instance, *Siamraptor* has a well-developed maxillary process in the premaxilla that does not project beyond the posterior margin of the bone, whereas it does in *Sinraptor* [44].

Although the premaxilla with four teeth is the primitive condition for Theropoda [67], this number is variable in several groups of theropods. For example, *Allosaurus* and *Neovenator* have five premaxillary teeth [43,65]. Within Allosauroida, derived carcharodontosaurids show a plesiomorphic condition that is the presence of only four teeth [11,41]. This condition is unknown in basal carcharodontosaurs due to the absent or incomplete premaxilla in *Eocarcharia* [51] and *Concavenator* [42]. The phylogenetic position in both analyses of *Siamraptor* indicates that the presence of five premaxillary teeth is a parallelism between *Allosaurus* and *Neovenator*, and that the rest of Allosauroida present the primitive condition. Regarding the premaxilla and maxilla, the interdental plates are fused to form a continuous medial lamina without replacement grooves in *Siamraptor*. This feature has been previously proposed as a synapomorphy of Allosauridae and Carcharodontosauridae [48]. However, other allosaurians also have a continuous medial lamina in the parodontal region, such as *Neovenator* [45] and *Fukuiraptor* [23]. Therefore, [12] proposed this feature as a synapomorphy of Allosauria. On the other hand, [13] coded separated interdental plates in *Allosaurus*, although several specimens of *Allosaurus* present this continuous lamina (UMNH-VP 5316, 9168, 9229).

Several carcharodontosaurian features are absent in the skull of *Siamraptor* despite its position as a basal taxon of this more exclusive group. For instance, the ventral portion of the anterior margin of its premaxilla is almost vertically oriented as in basal allosaurids like *Allosaurus* (e.g. BYU 1068; UMNH-VP 6500, 6502, 9248, 9250) and *Sinraptor* [44]. This condition is distinct from the slightly posterodorsally oriented anterior margin in carcharodontosaurs such as *Neovenator* (MIWG 6348) and *Acrocanthosaurus* (NCSM 14345), and thus is proposed as a synapomorphy of Carcharodontosauria within Allosauroida [11]. This feature is also observed in other theropods such as *Torvosaurus* (BYU 4882; [84]). Within Carcharodontosauridae, the interdental plates in the maxilla are more than twice deeper than anteroposterior wide [11]. Although the interdental plates of *Siamraptor* are deep with respect to their anteroposterior width, their proportions are between 1.19 and 0.96, so they are distinct from the carcharodontosaurid condition. Of course, it is necessary to take account of the absence of the most anterior regions of both maxillae, because the depth of those unknown parodontal plates could be even bigger. In *Siamraptor*, the lateral surface of the maxilla is smooth and lacks a strong external sculpturing by groove foramina like in other allosaurids and basal carcharodontosaurids [41,42], unlike in Carcharodontosaurinae [11]. Another absence of derived carcharodontosaurid feature is observed in the orbital margin of the jugal, which is angled posterodorsally in *Siamraptor* whereas is mostly vertically oriented in Carcharodontosaurinae [12]. Meanwhile, the jugal presents a horizontal ridge along its ventral margin in order to contact with the maxilla in *Siamraptor*, and an additional prominent horizontal ridge running from the notch of the quadratojugal processes towards anteriorly throughout the area below the postorbital process. A ridge similar to the latter has also been reported and interpreted as an insertion area for the M. pterygoideus ventralis in carcharodontosaurids such as *Mapusaurus* and *Tyrannotitan* [55], but it is anterodorsally-oriented in these derived carcharodontosaurids. In addition, the jugal of *Siamraptor* presents two ventral foramina posterior to the maxillary contact. Nutrient foramina in the lateral surface of the jugal have been noticed in *Allosaurus fragilis* [43,85] and are observed in the skull of *Allosaurus fragilis* (DINO 2560) in the same position as in *Siamraptor*.

**Axial anatomy.** The prezygapophyses of cervical vertebrae in *Siamraptor* are displaced laterally away from centrum, and the distance between them in each vertebra is wider than the
width of the neural canal, a condition that is shared with both abelisaurids [12,69] and tetanurans [12].

Among tetanurans, Siamraptor shows several features shared with Allosauroida and other more exclusive clades. The hyposphene extends ventrally as a sheet with parallel lateral edges in Siamraptor. This parallel condition has been defined as a synapomorphy of Carcharodontosauridae [47] and Abelisauridae [12], different from the ventrolaterally divergent triangular shape in many other theropods. However, as abovementioned, other allosauroids also have this parallel and vertical hyposphene laminae in dorsal vertebrae, thus, this condition should be considered as a synapomorphy of Allosauroida, although it is also observed in some tyrannosauroids [13]. As in Allosauria, Siamraptor has the primitive tetanuran condition in the mid-caudal vertebrae, a short rod-like and posteriorly inclined neural spine [67]. This condition contrasts with the morphology observed in metriachantosaurids, which have broadly rectangular and sheet-like neural spine [67].

Siamraptor occupies a basal position in Carcharodontosauria as a sister taxon of Neovenatoridae and Carcharodontosauridae. The relationship with these more exclusive clades is based on the sharing of several features with other carcharodontosaurian taxa, such as the presence of two pneumatic foramina in cervical vertebra and a well-developed and subvertically oriented postzygodiapophyseal lamina. The presence of two pneumatic foramina in the cervical centrum is a derived condition in Theropoda [86]. Furthermore, the presence of two antero-posteriorly elongated pneumatic foramina located behind the parapophyses and separated by a thin lamina is a feature observed in Carcharodontosauria, as in neovenatorids such as Neovenator [45] and Aerosteon [21] and derived carcharodontosaurids like Giganotosaurus or Tyrannotitan [55]. The pneumatic foramina of Siamraptor are not split by a thin oblique sheet of bone as in Tyrannotitan and other carcharodontosaurids [55], but both pneumatic foramina are separated by a septum that is more similar to that observed in Aerosteon [21]. Regarding the postzygodiapophyseal lamina, it is well developed and subvertically oriented, the diaphysis being extensive and subtriangular in lateral view in the Siamraptor, like in other carcharodontosaurians, except Neovenator and Acrocanthosaurus [13].

Despite these shared features with other carcharodontosaurians, Siamraptor lacks pneumatic foramina in the posterior dorsal vertebrae as in most non-carcharodontosaurians. The pneumatic foramina are present in all dorsal vertebrae and some caudal vertebrae in Carcharodontosauria except Concavenator [64]. Moreover, the camerate condition is visible in Siamraptor due to the presence of cavities consisting of several large chambers that are not further subdivided [62]. This type of internal pneumatic cavities is present in most tetanurans but is distinct from those camellate-type vertebrae of derived carcharodontosaurids and other carcharodontosaurians [45,58]. Moreover, derived carcharodontosaurids like Tyrannotitan (MPEF-PV 1157) and Giganotosaurus (MUCP-Ch 1) have a strong opisthocoelic condition in the cervical vertebrae. However, the cervical vertebrae of Siamraptor have an almost flat anterior articular surface, even more than those observed in Allosaurus (e.g. UMNH-VP 8348, 8352, 8487); and rather similar to the cervical vertebrae of Sinraptor [44].

The basal position within Allosauria is also supported by the offset in the positions of the articular surfaces of the cervical vertebrae. In Siamraptor, the posterior articular surface is strongly ventrally projected with respect to the anterior one. Although this condition of the cervical vertebrae is commonly seen in Dinosauria [87], among allosauroids this condition is only observed in basal allosaurians such as Allosaurus (UMNH-VP 8352, 8487, 8519, 10192) and some neovenatorids [45,88]. The offset is substantially reduced in the cervical centra of carcharodontosaurids [11,56].

Some symplesiomorphic conditions shared with other allosauroids are observed in the axial skeleton of Siamraptor, including the cervical epipophyses and the dorsal neural spines. A long
cervical epipophysis was proposed as a synapomorphy of Carcharodontosaridae [55]; however, this feature is also well developed in other carcharodontosaurs like Neovenator [45], other allosauroids like metriacanthosaurs [44], and other theropods like ceratosauroids [69], indicating a long epipophysis as a derived condition in theropods. Therefore, Siamraptor shows a primitive condition due to the short epipophyses in its cervical vertebrae, a symplesiomorphy also observed in Allosaurus. Although not complete, Siamraptor also shows a primitive condition in the dorsal neural spine of the dorsal vertebra due to its vertical orientation, unlike the anteriorly-inclined neural spine in some allosauroids [58].

Appendicular anatomy. Two tetanuran conditions of the ischium are observed in Siamraptor. One of them is a reduction of the antitrochanter in the ischium. Conversely, the primitive condition in theropods is the presence of a large and well-developed antitrochanter in the ischium [61,89,90]. In addition, although the ischial obturator process is not complete, a ventral notch seems to be developed in Siamraptor. The presence of this notch is another tetanuran synapomorphy [60].

The suprastragalar buttress for the astragalus is oblique in Siamraptor like in other tetanurans, but it is more reduced and rounded, like in some carcharodontosaurs such as Neovenator and derived carcharodontosaurs [12]. However, this morphology is distinct from megaraptorans in that it is transformed into a vertical ridge on the medial side [12]. Another feature in the tibia of Siamraptor that is shared with other carcharodontosaurs is the strong distal extension of the lateral malleolus beyond the medial malleolus. This condition differs from those observed in Allosaurus and primitive allosauroids, in which the distal extension of the lateral malleolus is absent or indistinct [11]. Within Carcharodontosaura, Siamraptor has a medially oriented medial malleolus of the tibia as in Carcharodontosauridae [47].

Regardless of the controversial phylogenetic position of Megaraptora in Allosauroidea [14] or Tyrannosauroidea [13], Siamraptor presents a feature in the manual ungual that is similar to megaraptorans. This feature is based on a new character [14] about the proximal height and width ratio of the manual unguals. The transversally narrow condition, observed in some megaraptorans and coelurosaurians, was defined with a ratio of 2.4, in contrast to the 2.0 ratio of the other theropods as the basal condition. Despite a slight incompleteness of the proximal end, the ratio is 2.26 in the manual ungual of Siamraptor, showing at least an intermediate state between the megaraptoran condition and the primitive condition for theropods.

Although Siamraptor shares several appendicular features with the lineage of carcharodontosaurs, this new taxon also shows differences against the members of more exclusive clades. For instance, a peg-and-socket-like iliac articulation in the ischium is a synapomorphy of Carcharodontosauridae [12], and it is also observed in the neovenatorid Siats meekerorum [68] and some abelisauroids [69]. Siamraptor differs from this derived condition because it presents a flat surface, like most theropods.

Some primitive conditions are observed in the ischium of Siamraptor, such as the absence of a posteriorly-oriented flange in the iliac peduncle, which is a feature observed in Allosaurus and Carcharodontosauridae [11]. In addition, the distal end of the ischium is rounded or slightly expanded. This feature is considered as a primitive condition in Theropoda [67] that is also retained in tetanurans and tapered distally into a point in coelurosaurians [67,69]. The rounded distal end of the ischium of Siamraptor is distinct from the well-developed and expanded ischial boot observed in some carcharodontosaurs such as Neovenator [45] and Concavenator [72] as well as other allosauroids like Yangchuanosaurus [91]. Despite these primitive features in the ischium, a metriacanthosaurid condition is present in the tibia. The notch observed in the medial part of the posterodistal margin in Siamraptor seems to be homologous to the deep pit for the articulation with the astragalus described in Sinraptor [44], and observed in a metriacanthosaurid theropod from Thailand [73].
Comparison with Asian allosauroids. Allosauroidea is widely represented in Asia by several taxa, especially by members of Metriacanthosauridae and Carcharodontosauria. These clades were the apex predators from Late Jurassic to mid-Cretaceous [5]. Siamraptor is proposed here as a new Asian allosauroid from the Early Cretaceous of Thailand, which belongs to the less inclusive clade Allosauria (Allosauridae + Carcharodontosauria sensu [12]).

The Early Cretaceous of Thailand has also yielded other allosauroids, Siamotyrannus isanensis [7] and an isolated small fragment of an indeterminate carcharodontosaurid. Originally, Siamotyrannus was defined as a primitive member of Tyrannosauroidea [7]. However, subsequent studies have reinterpreted this taxon as a member of Allosauroidea (e.g. [1,11]) and the phylogenetic analysis of Carrano et al. [12] proposed it as a member of Metriacanthosauridae. Siamotyrannus (PW9-1) is represented by a pelvic girdle, the last dorsal vertebra, a sacrum and anterior caudal vertebrae in articulation. Therefore, Siamraptor shares only the ischium and the posterior dorsal vertebra with Siamotyrannus. Even though several parts are missing, such as the obturator process in both taxa, the mid-shaft in Siamraptor and the distal end in Siamotyrannus, the ischium can be compared in several points. For instance, the ischium of Siamraptor shares a symplesiomorphy with the most primitive allosauroids including Siamotyrannus, namely, the absence of a posteriorly oriented flange in the iliac peduncle. On the other hand, the pubic peduncle of Siamotyrannus is anteriorly elongated, which makes the acetabulum concavity wider than in Siamraptor. Moreover, the proximal end of Siamotyrannus is dorsoventrally shorter than the one in Siamraptor. The proximal obturator notch is dorsoventrally narrow in Siamotyrannus, distinct from that of Siamraptor, in which the notch is widely opened dorsoventrally. A diagnostic feature is a curved shaft of the ischium [7], which seems to be straight in Siamraptor. The distinct crest along the posterior margin of the ischial shaft is present in Siamotyrannus (PW9-1), as in other metriacanthosaurids [44,91–93] except Metriacanthosaurus (Fig 16 in [94]). In Siamraptor, only the proximal end of this crest is observed in the proximal shaft, and it is clearly absent in the distal part, so it seems to be smaller than those of metriacanthosaurids. In Siamotyrannus, only the centrum of the posterior dorsal vertebra is preserved and exhibits the hourglass-shape, as seen in Siamraptor and other allosauroids. The pneumatic foramen is absent in both taxa, as in other basal allosauroids. Regarding the other allosauroid of Thailand, a fragmentary and non-diagnostic maxilla is reported as an indeterminate carcharodontosaur from the Barremian Sao Khua Formation [25]. This maxilla represents a posterior part of the right maxilla; for that reason, it is possible to compare it with Siamraptor. Both specimens have several common features with carcharodontosaurians in their maxillae: fused interdental plates forming a single lamina with faint suture lines; tall interdental plates that increase in height towards the anterior end; the presence of the groove for the dental lamina; and a swollen medial wall dorsal to the groove for the dental lamina. There are only two differences between both specimens: in Siamraptor, the maxillary alveoli are more rectangular and lateromedially compressed in ventral view, and the superior labial foramina are much smaller and they are more open laterally than ventrally. The fragmentary nature of Sao Khua carcharodontosaur makes further comparison difficult, but it is not ruled out that both specimens could be related to each other in spite of the temporary discordance.

Other Asian metriacanthosaurids are Yangchuanosaurus shangyouensis [95] (including Y. magnus, sensu Carrano et al. [12]), ‘Y.’ hepingensis Gao [96], ‘Szechuanosaurus’ zigongensis Gao [91] (Y. zigongensis sensu Carrano et al. [12]), and Sinraptor dongi, all from the Late Jurassic of China. The distal end of the ischium is separated in Siamraptor as in most tetanurans; however, it is fused in Metriacanthosauridae [12,92]. The epipophyses of the cervical vertebrae are extremely elongated and robust in metriacanthosaurids such as Sinraptor [44], Y. shangyouensis [92] and Shidaisaurus [93], distinct from the blunt and reduced epipophyses of the
cervical vertebra seen in *Siamraptor* and *Allosaurus* (e.g. UMNH-VP 8348, 8352, 10192; BYU 12023). A single pneumatic foramen excavates the cervical centrum of *Sinraptor* [44], ‘Y.’ *hepingensis* [96], ‘S.’ *zigongensis* [91], in contrast to the two anteroposteriorly elongated pneumatic foramina developed in the cervical vertebrae of *Siamraptor*. In dorsal vertebrae, the hypopshene lamina diverges ventrolaterally in *Sinraptor* [44] and other metriacanthosaurids [12], distinct from the vertical and parallel hypopshene of *Siamraptor*. Despite the abovementioned differences against metriacanthosaurids, *Siamraptor* also shares some similar features with some of them. For instance, a posterodorsally oriented retroarticular process in the artic- ular is seen in *Sinraptor* and *Y. shangyouensis* [12], although *Acrocanthosaurus* also presents this character [41]. Moreover, a vertical dorsal neural spine is shared with *Y. shangyouensis* [92] and, as discussed above, a deep medial pit in the posterodistal end of the tibiae is shared by *Siamraptor*, *Sinraptor*, and a metriacanthosaurid from Thailand [73].

*Kelmayisaurus petrolicus* [97] is another allosaurid from the Early Cretaceous of China that has been identified as a carcharodontosaurid [24]. There is only one autapomorphy for *Kelmayisaurus* in the dentary, so that the absence of the dentary in *Siamraptor* makes it difficult to carry out comparisons that allow determining a synonymy between both taxa. Contrarily, both specimens have fragments of the maxilla. Even though the parts preserved in those fragments do not correspond with each other, it is possible to compare several characteristics. The alveoli of *Kelmayisaurus* are oval [24] in contrast to the rectangular ones in *Siamraptor*. Furthermore, *Kelmayisaurus* (IVPP 4022) lacks the strongly marked medial wall over the interdental plates seen in *Siamraptor*, although the maxilla of the former is heavily abraded [24].

The mid-Cretaceous is represented by the carcharodontosaurid *Shaochilong maortuensis* [98] and the neovenatorid *Chilantaisaurus tashuikouensis* [99]. Regarding the first taxon, only the maxilla and the caudal vertebra are comparable with *Siamraptor*. The maxilla of *Shaochilong* is complete and it is characterized by two autapomorphies: the paradental groove is absent; therefore, the interdental plates and the medial wall are not clearly separated; and the interdental plates are excavated by several dorsoventrally-oriented grooves [5]. *Siamraptor* lacks those dorsoventrally-oriented grooves, although they are more anteriorly located in *Shaochilong*. The most striking difference is the absence of a clearly distinct medial wall in the maxilla, because *Siamraptor* has a well-developed and strongly marked ridge in both the dorsal and ventral margins of the medial wall. The teeth are also different, *Siamraptor* presents teeth mesiodistally thicker and more labiolingually compressed. Moreover, *Shaochilong* seems to lack marginal undulations, distinct from those observed in *Siamraptor*. The middle caudal vertebra is known for both taxa. *Siamraptor* shows anteriorly projected prezygapophyses, unlike the short ones that barely reach the anterior border of the centrum in *Shaochilong*. Conversely, the postzygapophyses are strongly projected in *Shaochilong*, further posterior to the centrum, unlike the shortly projected ones in *Siamraptor*.

*Chilantaisaurus* and *Siamraptor* can be compared only on the distal end of the tibia. The main difference is the astragalar buttress, which is a robust longitudinal ridge along the medial margin of the tibia in *Chilantaisaurus* [6], and a reduced proximolaterally-oriented ridge in *Siamraptor*.

*Fukuiraptor kitadaniensis* [23] is the only allosaurid known from the Early Cretaceous Japan. It can be compared with *Siamraptor* on the maxilla, cervical and dorsal centrum, and the ischium. In dorsal view, the bony plate comprising the antorbital fossa is thick in *Fukuiraptor* (FPDM-V43) in contrast to that of *Siamraptor*. In lateral view, the superior labial foramina are present as a row just below the ventral rim of the antorbital fossa, whereas they are located along the ventral margin of the lateral surface in *Siamraptor*. Moreover, the area ventral to the antorbital fossa is dorsoventrally narrower than in *Siamraptor*. The medial wall is
dorsoventrally narrower than that of Siamraptor. The pneumatic foramina of the cervical vertebra are developed but not extremely, unlike Siamraptor. The centrum is anteroposteriorly elongate, in contrast to the short one of Siamraptor. The ventral surface is concave between the parapophyses whereas it is almost flat in Siamraptor. a step-like lateroventral margin of the postzygocentrodiapophyseal fossa is absent, unlike Siamraptor. On the dorsal centrum, although that of Fukuiraptor also seems to belong to the posterior dorsal vertebra in comparison with Allosaurus, the ventral surface is smoothly rounded and lacks the midline ridge, which is present in Siamraptor.

**Skeletal pneumaticity compared with Aerosteon and Murusraptor**

Pneumaticity in bones, especially in axial elements, has evolved independently in sauropodomorphs and basal theropods [21]. This pneumaticity is represented by several distinct structures like pneumatic foramina and pneumatopores in several saurischian taxa in the fossil record (e.g. [21,22,100,101]).

*Siamraptor* is characterized by cranial and axial bones that are remarkably pneumatic. This pneumaticity is comparable with those observed in other two allosauroids, Aerosteon and Murusraptor, although both taxa could have another phylogenetical interpretation as tyrannosauroinds (see “Phylogenetic analysis”).

The surangulars of Siamraptor show multiple striking foramina, some of them could be related with an unusual surangular pneumaticity. The most striking feature is the presence of large, smooth-walled external openings separated by septa in the posterior part of the surangular, which are observable in anterior view, and the presence of an oval concavity posterior to the lateral shelf. The pneumaticity in the mandible is also reported in Murusraptor and derived tyrannosauroids. The articular of Murusraptor is strongly pneumatized, but the condition is unknown in the surangular [22]. Gold et al [102] argued that the surangular pneumaticity is unusual in theropods, but it is described in derived tyrannosauroids which share several characteristics with that observed in Siamraptor as follows: 1) the pneumaticity in Siamraptor and derived tyrannosauroids, such as Tyrannosaurus, is extremely related to the posterior area of the surangular, close to the articular. 2) although, as mentioned by these authors, the surangular foramina are not necessarily referred to a pneumatic opening, the authors also suggested that the enlargement of the surangular foramen of derived tyrannosauroids could be associated to the surangular pneumaticity. In Siamraptor, there is not a strongly enlarged surangular foramen, but there is a striking increase in the number of these foramina and, even, the posterior-most one is slightly wide compared to those in other allosauroids.

The axial pneumaticity is the most developed of the Siamraptor features. The centrum of the cervical vertebrae is strongly excavated by pneumatic foramina that penetrate through the lateral surfaces broadly, separated by septa as those observed in the mid cervical centra of Aerosteon [21]. There are also camerate structures within the centrum, with huge camerae separated by septa; and other smaller and oval camerae penetrating the neural arch. Wedel [103] proposed that the large camerae in a camerate structure may bifurcate to produce successive generations of smaller camerae. The centrum of some vertebrae of Murusraptor has also this camerate structure [22], distinct from the camellate structure proposed in Aerosteon [21] and in other carcharodontosauria (e.g. Brusatte et al., 2008). In the anterior cervical vertebra of Siamraptor, there is a small foramen within the prezygocentrodiapophyseal fossa. This type of pneumatopores invading the neural arch through the vertebral fossa is also observed in cervical and dorsal vertebrae of Aerosteon (MCNA-PV-3137) and Murusraptor (MCF-PVPH-411, [22]). Moreover, the centrodiapophyseal and postzygocentrodiapophyseal fossae in the cervical and dorsal vertebrae of Siamraptor are extremely excavated and they connect with the huge
internal camerae of the neural arch. Based on the Pneumaticity Profile of the neural arch [104], the presence of these foramina or fossae that connect with the internal camerae are an unambiguous sign of pneumaticity. In the neural spine of cervical and dorsal vertebrae of *Siamraptor*, it is also observed that a pair of pneumatopores pierce the base of the spine bilaterally. Similar pneumatopores are also present in the atlas of *Aerosteon* [21] and in the caudal vertebra of *Murusraptor* (MCF-PVPH-411), and its presence also indicates the formation of an air sac in the base of the neural spine. Finally, the neural spine filled by a huge lumen is slightly similar to that described in *Aerosteon* [21], although it is shorter than the latter due to the development of a strong metaplastic scar. The axial pneumaticity is attributed to cervical, thoracic or abdominal air sacs in non-avian saurischian dinosaurs like in living birds [21,105,106]. The pneumaticity observed in the surangular, articular, and axial skeleton of *Siamraptor* is only superficially described so far; for that reason, further studies about the pneumatization of this theropod, using a CT scan, should be performed in order to evaluate the pneumatized structures.

**Paleobiogeographic implications**

The major clades of Allosauroidea seem to have widely global distributions with few time intervals where samples of allosauroids are known [14]. Metriacanthosauridae, the most basal clade within Allosauroidea [12], is represented mostly by Asian taxa, except *Metriacanthosaurus* from the Late Jurassic of England [107]. Allosauridae, the sister taxon of Carcharodontosauria [12], is composed of *Allosaurus + Saurophaganax*, both from the Upper Jurassic of USA, and the genus *Allosaurus* also have representatives from the Lusitanian Basin in Portugal. Most genera known from the Lusitanian Basin record have closely related taxa in the Morrison Formation record, although some taxa closely related to those of North America have been reinterpreted as independent Portuguese species, as is the case of *Allosaurus europaeus* [108]. This reinterpretation implies an emerging vicariant evolution of the Late Jurassic theropod faunas [26]. Carcharodontosauria is composed of two more exclusive clades, Neovenatoridae and Carcharodontosauridae, and both clades have Asian representatives. Neovenatoridae comprises two Asian taxa, *Fukuiraptor* from the Lower Cretaceous of Japan and *Chilantaisaurus* from the mid-Upper Cretaceous of China. Carcharodontosauridae also comprises two taxa from China, namely *Kelmayisaurus* from the Lower Cretaceous and *Shaochilong* from the mid-Upper Cretaceous. However, representatives of both clades were more widely distributed in Laurasia landmasses during the Early and mid-Cretaceous (e.g. [23,56,65,68,74,75]), and mostly distributed in Gondwana during the Late Cretaceous (e.g. [22,48,54,55,109]). The earliest carcharodontosaurian from Laurasia was recently reported from fragmentary material from the Upper Jurassic of the Lusitanian Basin, Portugal [26]. The presence of these taxa in Gondwana and Laurasia during the Upper Jurassic implies that this group was early spread in both landmasses. Under this scenario, the presence of a new basal carcharodontosaurian from the Lower Cretaceous of Thailand supports an extension of the record in the Laurasian landmasses during the earliest stage of the evolutionary history of this clade. An early widely distribution of the most exclusive clade Carcharodontosauridae has been previously suggested [110]. Posteriorly, a near-cosmopolitan distribution is achieved by major allosauroids clades [14]. This broad geographical distribution occurred in other major theropod clades, early in their geological history [12]. The most recent studies propose a model of distribution of late Mesozoic taxa that supports these previous hypotheses [27, 30]. The network models [28] show a cosmopolitan distribution of theropod taxa through mid-Mesozoic, including Early Cretaceous, where there were huge fauna interchanges between America, Asia, and Europe. The results concur with the possibility of full network connectivity between Laurasian landmasses.
Persisting up until Berriasian–Barremian, results also detected by Ezcurra and Agnolin [20]. This situation matches with the high distribution of Carcharodontosauria during the Late Jurassic and Early Cretaceous, with the presence of basal members of this clade in Europe and Asia.

Conclusions

A new carcharodontosaurian theropod, *Siamraptor suwati*, is described based on isolated cranial and postcranial remains from the Lower Cretaceous Khok Kruat Formation. *Siamraptor* is diagnosed by eight characters in cranial and axial elements, and it also exhibits several carcharodontosaurian synapomorphies such as two pneumatic foramina oriented anteroventral–postero-dorsally in cervical vertebrae, a parallel and sheet-like hyposphene lamina, and a reduced and oblique ridge of suprastragalar buttress for the astragalus in the tibia. *Siamraptor* is also characterized by remarkable pneumaticity in cranial and axial bones, which is comparable with those observed in several other carcharodontosaurs, although those taxa could have another phylogenetical interpretation as tyrannosaurs. Both phylogenetic analyses using two independent datasets locate *Siamraptor* as the most basal member of Carcharodontosauria, which also means that this taxon is the first definitive carcharodontosaurian theropod from Southeast Asia. The presence of *Siamraptor* in this area indicates an extension of the record in the Laurasian landmasses during the earliest stage of the evolutionary history of Carcharodontosauria.

Supporting information

S1 Appendix. Phylogenetic and data matrices information.

(DOCX)

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