

SCIENTIFIC REPORTS

Corrected: Author Correction

OPEN

Ceratosaur palaeobiology: new insights on evolution and ecology of the southern rulers

Rafael Delcourt ^{1,2,3}

Ceratosaur theropods ruled the Southern Hemisphere until the end of the Late Cretaceous. However, their origin was earlier, during the Early Jurassic, a fact which allowed the group to reach great morphological diversity. The body plans of the two main branches (Noosauridae and new name Etrigosauria: Ceratosauridae + Abelisauridae) are quite different; nevertheless, they are sister taxa. Abelisaurids have lost the ability to grasp in the most derived taxa, but the reduced forelimb might have had some display function. The ontogenetic changes are well known in *Limusaurus* which lost all their teeth and probably changed the dietary preference at maturity. The results presented here suggest that abelisaurids had different soft tissues on the skull. These tissues might have been associated with evolution of a strong cervicocephalic complex and should have allowed derived taxa (e.g. *Majungasaurus* and *Carnotaurus*) to have low-displacement headbutting matches. The ability to live in different semi-arid environment plus high morphological disparity allowed the ceratosaurs to become an evolutionary success.

Ceratosaurs are theropod dinosaurs known for having extremely reduced forearms and short/deep skulls¹. Although they are not as famous as their distant relatives, the archetypal tyrannosaurs², the ceratosaurs were abundant and well spread out chronospatially through the Mesozoic³ being ecologically important especially in the Southern Hemisphere where most of their remains have been unearthed^{4,5}. As the ceratosaurs were the dominant carnivorous dinosaurs of the southern continents, in diversity and ecology during the Late Cretaceous^{3,4}, they can be considered the tyrannosaurs' counterpart. However, research on ceratosaurs has not received the same attention from non-scientific society and they remain mysterious to the lay public.

The type species of the group, *Ceratosaurus nasicornis*, was described in 1884 from a skull and partial post-cranial skeleton of the Jurassic of USA⁶, but the clade became better understood with *Carnotaurus sastrei*⁷ which has been subject of several palaeobiological studies^{8–11}. In the last three decades the discovery of many species has increased our knowledge of ceratosaurs' phylogeny^{3,12–15}, morphology^{1,12,14,16,17}, biogeography⁴, development^{1,14,18} and behaviour^{8,9}. These studies have shed new light on the Gondwanan tyrants and allowed for an improved understanding of the evolution and life of theropod dinosaurs.

Here I assess the current state of ceratosaur research, focusing on the origin, phylogenetic relationships and biology of this group in Mesozoic ecosystems. Furthermore, I present new information on soft tissue of abelisaurids bringing additional inference of the behaviour and the use of these tissues. Taxonomic comments are made to clarify and interpret the relationships and nomenclatural issues among the taxa.

Results and Discussion

Phylogenetic relationships. Ceratosauria traditionally consists of *Ceratosaurus* and all taxa closer to it than to *Neornithes*¹⁹. However, taxonomy within Ceratosauria has been complicated. Abelisaurids were formally known as Abelisauroidae (=Ceratosauroidae), that comprises *Carnotaurus*, *Noasaurus* and all their most recent common ancestors and all descendants (see below for further discussion). Ceratosauroidae are included in the clade called Averostrans which comprises the taxa related to Ceratosauria and all derived theropods²⁰. Approximately 32 Ceratosauroidae genera are currently known with most of the taxa originating from the Late Cretaceous (Table S1).

¹Universidade Estadual de Campinas (UNICAMP), Instituto de Geociências, Rua Carlos Gomes, 250, 13083-855, Campinas, SP, Brazil. ²Museu Nacional/Universidade Federal do Rio de Janeiro, Departamento de Geologia e Paleontologia, 20940-040, Rio de Janeiro, RJ, Brazil. ³Department of Zoology, Trinity College Dublin, Dublin, 2, Ireland. Correspondence and requests for materials should be addressed to R.D. (email: rafael.delcourt@gmail.com)

Received: 3 October 2017

Accepted: 12 June 2018

Published online: 27 June 2018

Clade	Definition
Etrigansauria (new clade)	the most inclusive clade containing <i>Carnotaurus sastrei</i> and <i>Ceratosaurus nasicornis</i> but not <i>Noasaurus leali</i> . Etrigansauria means “daemon lizard Etrigan”, a daemon from DC Comics mythology.
Ceratosauridae	the most inclusive clade containing <i>Ceratosaurus nasicornis</i> but not <i>Carnotaurus sastrei</i> .
Abelisauridae	the most inclusive clade containing <i>Carnotaurus sastrei</i> but not <i>Ceratosaurus nasicornis</i> .

Table 1. The proposed set of definitions for the ceratosaurian clades.

Ceratosauroida is traditionally divided into two main branches: the Noasauridae and the Abelisauridae²¹ (but see also the last paragraph for new definitions). This classification has been followed in the recent phylogenetic analyses which have revealed more resolution of the relationships within the clades^{3,5,14,15,22}. The relationships between of the two large groups is still being debated; however there are new hypotheses of relationships amongst the noasaurids improving the resolution within the family¹⁴. In the case of abelisaurids, two main branches divide the South American (called Brachyrostra)²² from the European/Indian/Madagascan taxa (previously called Majungasaurinae)⁵. Recent phylogenetic analyses recovered a new clade included in Brachyrostra that comprises the Santonian-Maastrichtian abelisaurids from South America: the Furileusaura^{13,15,23}. Nevertheless the relationships amongst furileusaurians are still debated¹³.

The recent analyses of Wang *et al.*¹⁴ expanded the matrix for phylogenetic relationships of ceratosaurs (744 characters) with dense taxon sampling (198 taxa) including a broad outgroup which better allow to polarize homology statements at the node Ceratosauria. The new hypothesis of Wang *et al.*¹⁴ suggests *Elaphrosaurus bambergi* and *Limusaurus inextricabilis* as sister taxa as recovered by Rauhut and Carrano²⁴. However, in a novel result Wang *et al.*¹⁴ find that *Berberosaurus* basal within Abelisauridae (=new Etrigansauria, see below), and Ceratosauridae is now composed of *Eoabelisaurus* plus *Ceratosaurus* and *Genyodectes serus*. According to Wang *et al.*¹⁴, *Ceratosaurus* is united within non-noasaurid ceratosauroids by the following features: (1) fusion of the quadratojugal and quadrate; (2) posterior extent of the posteroventral process of the dentary directly ventral to the posterodorsal process; (3) parapophyses distinctly below the level of the diapophyses in posterior dorsal vertebrae; (4) contact of the pubis and ischial obturator process and (5) transverse infrapopliteal ridge between the medial and lateral femoral condyles. Additionally, *Dahalokely tokana* is recovered as a majungasaurini instead of within Noasauridae as proposed by Farke and Sertich²⁵ and Tortosa *et al.*⁵ or within Brachyrostra as suggested by Delcourt¹³ and Filippi *et al.*¹⁵. This new hypothesis suggests that the origin of ceratosauroids and its two main branches are older than previously thought, with an African origin, decreasing the length of previous ghost lineages.

Nevertheless, the inclusion of Ceratosauridae in Abelisauridae as proposed by Wang *et al.*¹⁴ has important taxonomic implications and some clade definitions must to be done. According to the International Code of Zoological Nomenclature (ICZN)²⁶, the family name Ceratosauridae has priority over Abelisauridae because the first was coined in 1884 by Marsh⁶ and the second was coined in 1985 by Bonaparte and Novas²⁷. Additionally, according to the Principle of Coordination of ICZN²⁶ “a name established for a taxon at any rank in the family group is deemed to have been simultaneously established for nominal taxa at all other ranks in the family group”. It means that once Ceratosauridae is nested in Abelisauroida, the superfamily Ceratosauroida is the synonym senior to Abelisauroida and the synonym junior must be replaced. The definition of Ceratosauroida here follows the suggestion of Wilson *et al.*²⁸ for Abelisauroida: the clade is composed by *Carnotaurus*, *Noasaurus* and all their most recent common ancestors and all descendants (also including Ceratosauridae). If the phylogenetic hypothesis of Wang *et al.*¹⁴ is correct, I propose a new clade to include Ceratosauridae and Abelisauridae as well as new definitions for these two families (Table 1):

Also, it is worth noting that the subfamily Majungasaurinae⁵ in the topology of Wang *et al.*¹⁴ should be considered a tribe and called Majungasaurini because is inserted in the subfamily Carnotaurinae. This taxonomic change helps to clarify the relationships among Ceratosauroida and satisfies the nomenclature requirements (Fig. 1). Therefore, in the present contribution I will follow the Wang *et al.*¹⁴ phylogenetic results. All the phylogenetic definitions used here are in the Supplementary Materials.

The origin of Ceratosauroida is subject of debate concerning the time of the basal-most taxa. Although its origin has been recovered to the Early/Late Cretaceous (Aptian/Cenomanian, between 126–93.9 My)^{3,5,15,25}, some authors suggest it could be earlier, originating in the Early Pliensbachian/Toarcian, between 191–174 My (Early Jurassic)^{14,29} or Aalenian/Bajacian (Middle Jurassic)¹². These differences hinge on the position of *Berberosaurus liassicus* (Pliensbachian/Toarcian), a ceratosaurian from Morocco known by a partial postcranial skeleton²⁹ and the position of *Eoabelisaurus mefi* (Aalenian/Bajacian) a medium-sized etrigansaurian from Argentina known by an almost complete skeleton¹². Depending on the position of these taxa, the origin of Ceratosauroida is younger or older. In some analyses, *Berberosaurus* is considered as a basal ceratosaurian^{12,13}, a neoceratosaurian⁵, a basal abelisauroid²⁹ or sister-taxon of cornisauria¹⁴. The topology of *Eoabelisaurus* is also controversial, falling out as basal within Ceratosauroida^{5,13}, Abelisauridae¹² or within Ceratosauridae¹⁴.

Ceratosaur anatomy. Ceratosauroida probably has most disparity (morphological variety) of any major theropod group³⁰. They could be omnivorous/herbivorous such as in *Limusaurus*¹⁴, have horns as in *Ceratosaurus*, *Carnotaurus* and *Majungasaurus crenatissimus* or have extreme reduced forelimbs as in *Majungasaurus*, *Aucasaurus garridoi* and *Carnotaurus*³¹. However, the body plans of the main branches (Noasauridae and Etrigansauria) remain respectively similar within each group (Fig. 2).

Noasaurids tends to be smaller and more gracile than etrigansaurians¹ with a long neck, small heads, and larger forearms^{32–34}. Although the morphology of noasaurids differs substantially from those etrigansaurians, the

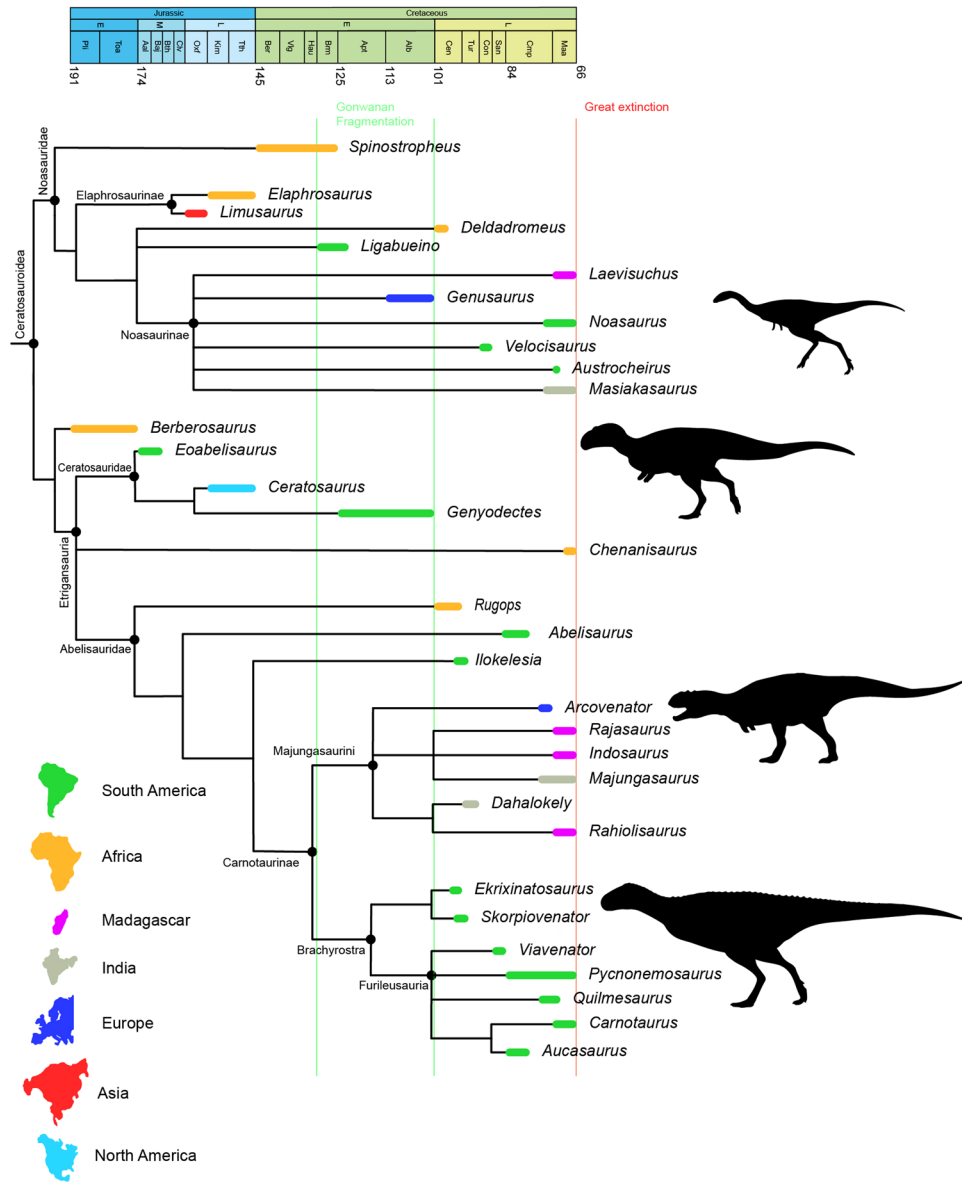


Figure 1. The hypothetical phylogenetic relationships of ceratosaurs based on current topologies. The main source is from Wang *et al.*¹⁵. The phylogenetic position of *Chenanisaurus* is from Longrich *et al.*²⁴ and the *Ligabueino*, *Austrocheirus*, Majungasaurinae and Brachyrostra are from Filippi *et al.*¹⁶.

ilium of Noosaurinae (subfamily included in Noosauridae) is as low as in Carnotaurinae (subfamily included in Abelisauridae) despite the fact that these two groups are not closely related. The skull of noosaurids are long and low compared to those of abelisaurids^{17,33}. Interestingly, even among noosaurids the morphology of the skull varies substantially. The skull of *Limusaurus* becomes toothless through ontogeny, likely to meet a change in diet (see below)¹⁴, whereas the skull of *Masiakasaurus knopfleri* presents strong procumbent dentitions which probably indicate additional divergence from the typical theropod diet³⁵. The forearms of noosaurids are poorly known, but as in other ceratosauroids the humerus, radius and ulna are more reduced distally than proximally suggesting that the reduction may have occurred in a modular fashion, from the distal to proximal across the phylogeny¹². However, the humeri of noosaurids are slenderer than those of abelisaurids (Fig. 3A).

The body plan of etrigansaurians strongly differs from other theropods, and their morphology is more thoroughly known than that of noosaurids^{1,4}. Whereas the noosaurids have long skulls, the etrigansaurians have strong and deep skulls, especially those of Brachyrostra which also showed encroachment of the postorbital into the orbit, just beneath the eye²². The skull of abelisaurids became shorter and more rugose in more derived taxa. *Ceratosaurus*, *Eoabelisaurus*, and possibly *Genyodectes* have longer skulls compared to those of abelisaurids. The skull's shortening and deepening started in abelisaurid basal forms, such as the Aptian-Albian *Kryptops palaios* and the Cenomanian *Rugops primus*, both from Niger^{36,37}, and reached its extremity in the Carnotaurinae taxa. The skull of *Carnotaurus* is exaggeratedly short and deep compared with those other taxa of the same clade. The skull of *Abelisaurus* was largely reconstructed in the snout as well as in the posterior area^{1,3,38}, and taphonomic

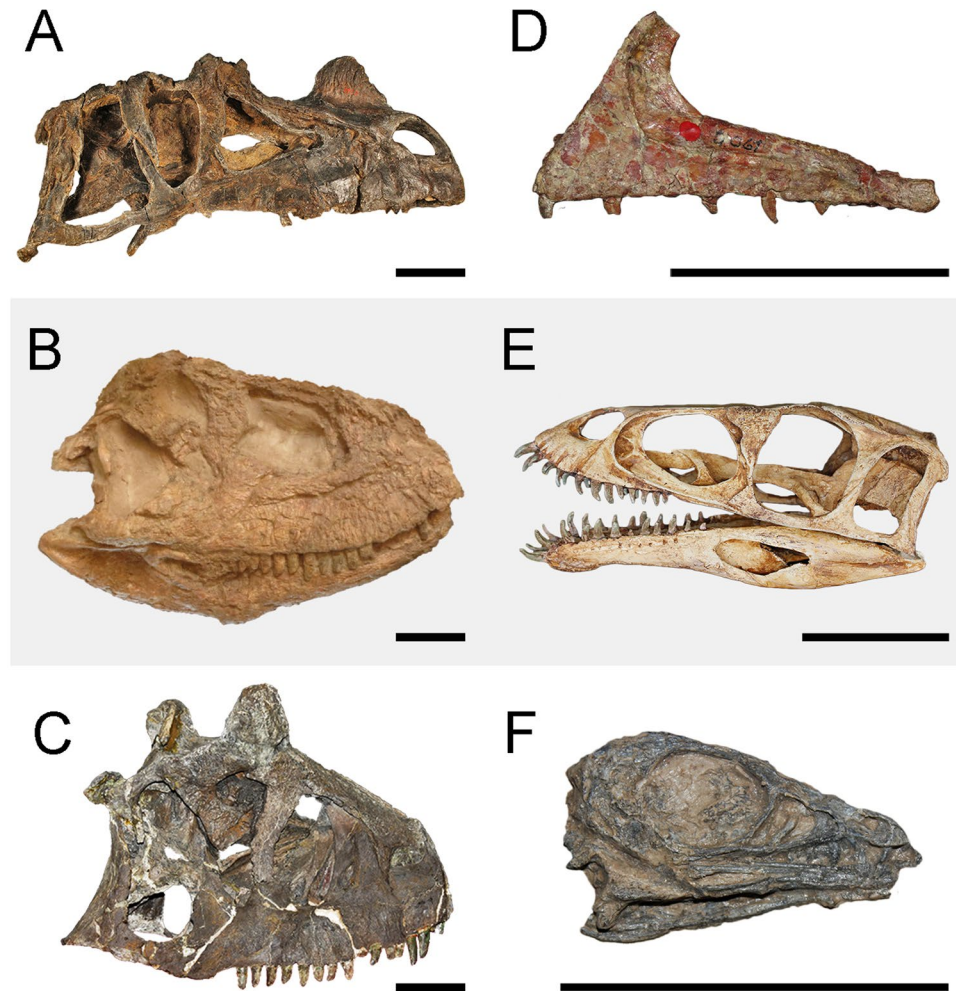


Figure 2. The anatomy of ceratosaur, showing the variety of cranial morphology in the group. Right lateral side of the skulls of (A) *Ceratosaurus* (USNM 4735), (B) *Skorpiovenator* (MMCH-PV 48) and (C) *Carnotaurus* (MACN-CH 894) (scale bar: 10 cm). Left maxilla of (D) *Noosaurus* (PVL 4061; Fundación Miguel Lillo, Tucumán, Argentina); reconstruction of the skull of (E) *Masiakasaurus* and left lateral side of the skull of (F) *Limusaurus* (IVPP 20093 V; Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China) (scales bar: 5 cm).

distortion has modified the proportions and several contacts between elements are missing such as the jugal articulations^{3,38}. Therefore, as previously suggested³⁸, *Abelisaurus* should have had a shorter skull than was previously reconstructed and frequently reproduced resembling those of Carnotaurinae (e.g. *Majungasaurus*) instead of *Ceratosaurus* (as suggested by Bonaparte and Novas²⁷).

Regarding the basal abelisaurids, *Kryptops* was diagnosed based on a left maxilla, several partial vertebrae and ribs and an articulated pelvic girdle and sacrum³⁶. However, as noted by Novas *et al.*⁴ and Carrano *et al.*³⁹, the pelvic girdle and sacrum of *Kryptops* were found “eroded and free of the rock some 15 meters distant” and have more shared features with tetanurans than abelisaurids. The vertebral non-sacral remains also share features with ceratosaurians as well as tetanurans³⁶. The maxilla is also incomplete and with only a general diagnosis possible (e.g. external texture on the maxilla, which is composed of short linear grooves that are also shared with *Majungasaurus* and *Rugops*). The only autapomorphy is a secondary wall in the anteroventral corner of the orbital fossa obscuring it and that has a scalloped and fluted dorsal margin³⁶. Therefore, as the holotype of *Kryptops* is a miscellany of materials belonging to different groups with just one autapomorphy supporting the species, this taxon might have been considered as *nomen dubium* rather than a valid taxon. The postcranial skeleton probably has a phylogenetic relationship with carcharodontosaurids instead of abelisaurids as suggested by Novas *et al.*⁴ and Carrano *et al.*³⁹.

Abelisaurids has strongly reduced forearms without grasping ability⁴⁰ (Fig. 3B). According to Agnolin and Chiarelli⁴⁰, abelisaurids probably also lacked forearm mobility. However, recent analyses on *Majungasaurus* musculature suggest that, although much reduced, abelisaurids did not lose full mobility of the forelimb, and may have used it for intraspecific display⁴¹. Some taxa such as *Aucasaurus*, *Majungasaurus* and *Carnotaurus* may have lost the ungual of the digits I and IV^{31,40,42} whereas the ceratosaurid *Eoabelisaurus* has strongly reduced the manual unguals¹². The digit IV is fused to the metacarpal in *Majungasaurus* and *Aucasaurus* precluding mobility.

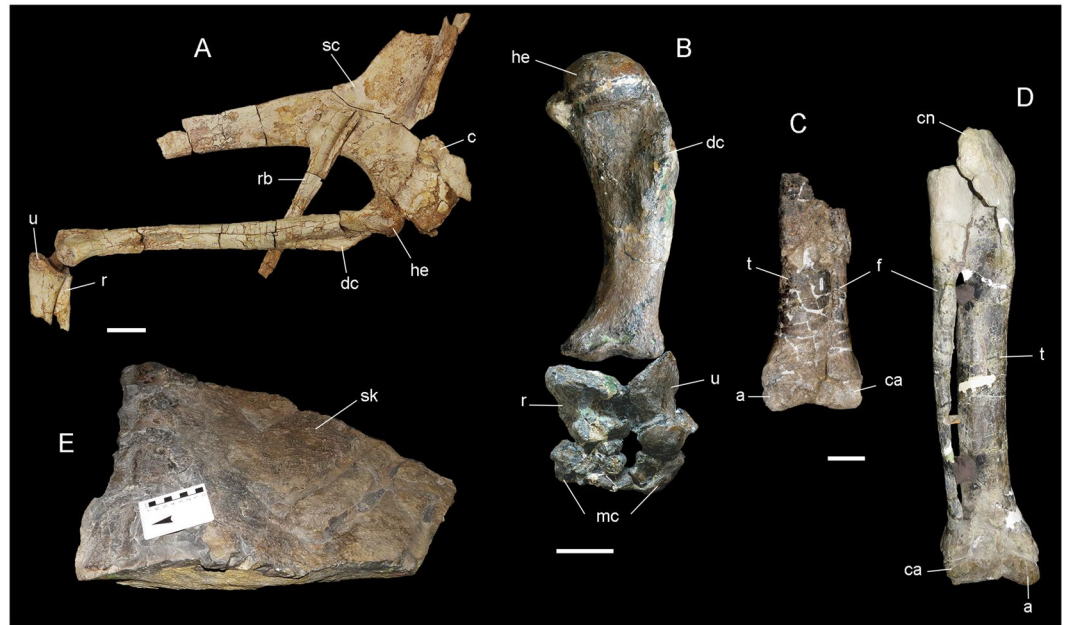


Figure 3. Limbs elements and skin impression of ceratosaurs. **(A)** Pectoral and forelimb of *Deltadromeus* (SGM-Din 2; Ministère de l'Énergie et des Mines, Rabat, Morocco); **(B)** forelimb of *Carnotaurus* (MACN-CH 894); **(C)** distal articulated tibia, fibula, astragalus and calcaneum of *Eoabelisaurus* (MPEF-Pv 3990; Museo Paleontológico 'Egidio Feruglio', Trelew, Argentina); **(D)** articulated tibia, fibula, astragalus and calcaneum of *Xenotarsosaurus* (UNPSJB PV 194/1; Universidad Nacional de la Patagonia 'San Juan Bosco', Chubut, Argentina) and **(E)** caudal skin impression of *Carnotaurus* (MACN-CH 894). Scale bar: 5 cm. Abbreviations: a, astragalus; c, coracoid; ca, calcaneum; cn, cnemial crest; dc, deltopectoral crest; f, fibula; he, humeral head; mc, metacarpals; r, radio; rb, rib; sc, scapula; sk, skin impression; t, tibia; u, ulna.

Extreme reduction also reduced autonomy of all digits due to the extreme reduction, although the hemispherical humeral head and distal radius and ulna suggests that the shoulder and the wrist had a large range of motion^{38,41}. However, as pointed by Gianechini *et al.*³⁸ the range of motion of the humerus should have been higher in latero-medially (i.e. abduction-adduction) than in anteroposteriorly (i.e. flexion-extension) because the development of the dorsal and ventral rim of the glenoid fossa reduced anteroposteriorly movements. Also, is worth noting that the large scapulocoracoids and reduced forelimbs in ceratosaurs might be related to a close developmental association between scapular blade and the axial skeleton, holding the shoulder girdle to the axial skeleton and for mobility of the girdle and the ribcage^{38,41,43}. Those muscles attached to the neck could have had an important role in feeding as in extant crocodiles (e.g. muscle *levator scapulae* which is an effective abductor of the neck and hence the head)^{41,44}.

The hindlimbs of ceratosaurs are different in the two main branches. In noasaurids, the hindlimbs are more slender than the etrigansaurians; however this is due to the overall size of individuals of the groups¹. Abelisaurids' hindlimbs and caudal vertebrae suggest that these taxa, specially the brachyrostrans, may have had powerful cursorial abilities. The tibia have well developed dorsal anterior projection (cnemial crest) onto which the main knee extensor muscles are inserted (i.e. *iliotibiales*)⁴⁵. The large size of the cnemial crest and its dorsal inclination suggest that some ankle extensors and digital flexors muscles were large, increasing their force-producing capability. Additionally, the dorsal inclination of the transverse processes in the caudal vertebrae suggests that the muscle *caudofemoralis longus*, the main femur extensor, may have been larger than in other theropods contributing to the cursorial ability¹⁰. Also, the presence of accessory articulations in caudal vertebrae (hyposphene-hypantrum) apart of the inclined transverse processes, increases the tail rigidity^{10,46} and may have enhanced overall speed and acceleration¹⁰. However, acceleration might have been more impressive than top speed. When preserved, feet of some abelisaurids are short (e.g. *Majungasaurus*)⁴⁷, indicating low tangential velocity at the ankle. The type of *Carnotaurus* lacks feet and the distal portion of the epipodials, even though it is often reconstructed as having gracile legs and feet¹⁷.

Etrigansaurian soft tissue. The etrigansaurians also are well known by their rugosities and projections from the skull elements³. Carcharodontosaurid theropods have rugosities in lateral skull bones as well, but the morphology is different⁴⁸ and leads to misinterpretations of the group⁴⁹. Although abelisaurids have strong rugose skulls, the textures are variable throughout the skull⁴⁸. The texturization of the skull happened independently from the projections. For example, the skull of *Ceratops* is diagnosed by having a rounded midline horn core on the fused nasals³ and horn cores forming a dorsal crest on the lacrimals⁵⁰, although the skull is otherwise smooth⁴⁸. On the other hand, the skull of *Skorpiovenator bustingorryi* is strongly texturized but without any projections²². The skull roof in abelisaurids is thick but this feature varies among the species⁴⁸. Both majungosaurini *Majungasaurus* and *Rajasaurus normandensis* have a single medial horn formed by the frontal and frontal/nasal, respectively^{28,48},

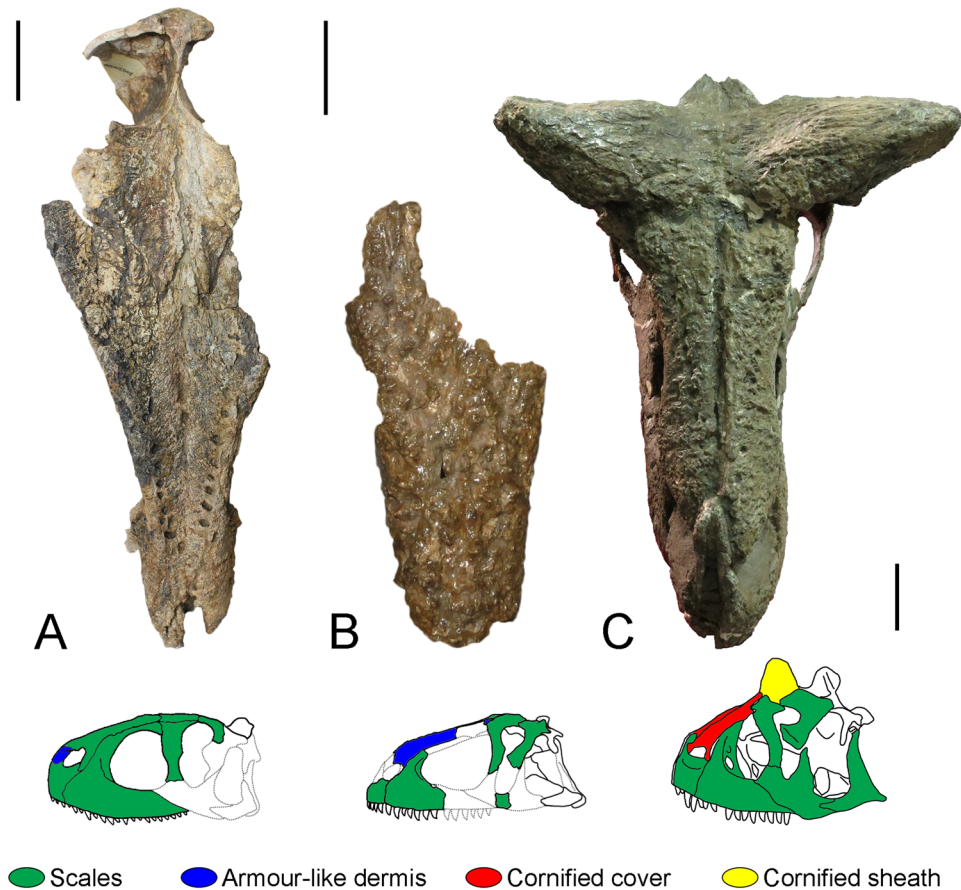


Figure 4. Skin structures inferred for abelisaurids. Dorsal surface of the skull of (A) *Rugops* (MNN IGU1), (C) *Carnotaurus* (MACN-CH 894) and dorsal surface of the fused nasal of (B) *Abelisaurus* (MPCA 11908). Scales bar: 5 cm.

whereas the brachyrostran *Carnotaurus* has two frontal horns laterally oriented¹⁷, *Aucasaurus* has the lateral margins of frontal elevated in the orbital region, and *Viavenator exxoni* has almost flattened frontals⁵¹. The flattened frontals of *Ekrixinatosaurus novasi*⁵² and probably of *Skorpiovenator* suggest the basal position of these two taxa in relation to *Furileusaura* as proposed by Filippi *et al.*¹⁵.

The rugosities in abelisaurids resulted from a mineralization processes with specializations in the overlying dermis, such that the mineralized tissue includes the irregular surface texture representing mineralization of the bone's periosteum, overlying dermal fibers or combination of the two, characterizing the metaplastic ossification⁴⁸. The sculpture of lateral bones (e.g. maxilla, jugal, quadratojugal, dentary) presents a higher percentage of tangential vascular canals and grooves, whereas the dorsal roofing elements (e.g. frontal, dorsal postorbital and lacrimal, nasal, nasal process of the premaxilla) tend to have more projecting, tuberculate and/or cauliflower-like texture that combine with the vascular canals and grooves (Figs 4 and 5A,B)⁴⁸. Sampson and Witmer⁴⁸ have suggested that abelisaurids might have had more robust skulls than other theropods due to the high skull's mineralization. Following the results of Hieronymus *et al.*⁵³ for inference of soft tissues in Centrosaurine and Carr *et al.*⁵⁴ for Tyrannosauridae, it is possible to assess the superficial cranial soft tissues of abelisaurids. These tissues show a hierarchy of textures which became more complex towards the phylogeny.

The basal abelisaurid *Rugops* has the dorsal surface of nasals with a row of seven pits, visible sutures between them and hummocky rugose surface which is also present in the dorsal surface of frontal, prefrontal lacrimal and maxilla (Figs 4A and 5C). These features are correlated with overlying scales as observed in living crocodiles and reptiles⁵³. On the other hand, the anterior-most snout has a different texture compared to other categories of soft tissue. The nasal articulation processes of premaxilla and the anterior processes of nasal, show a papillate texture indicating the presence of armour-like dermis as suggested by Hieronymus *et al.*⁵³. The presence of these tissues suggests that *Rugops* had, at least two categories of tissues covering the surface of the skull. Interestingly, the type of *Rugops* could be a subadult individual due to its small size, incomplete fusion between the nasals and the presence of the fenestra between the prefrontal, frontal, postorbital and lacrimal³. As the rugosities tend to increase during ontogeny¹⁸, the armour-like dermis could reach a larger surface if *Rugops* grew up and developed more papillate texture.

Abelisaurus, as other abelisaurids, have a lateral cranium surface (e.g. maxilla) with dense tangentially arranged grooves suggesting it was covered by large scales or scutes, as suggested by Sampson and Witmer⁴⁸ and Hieronymus *et al.*⁵³ (Figs 4B and 5D). However, the nasal of *Abelisaurus* differs from that of *Rugops* being

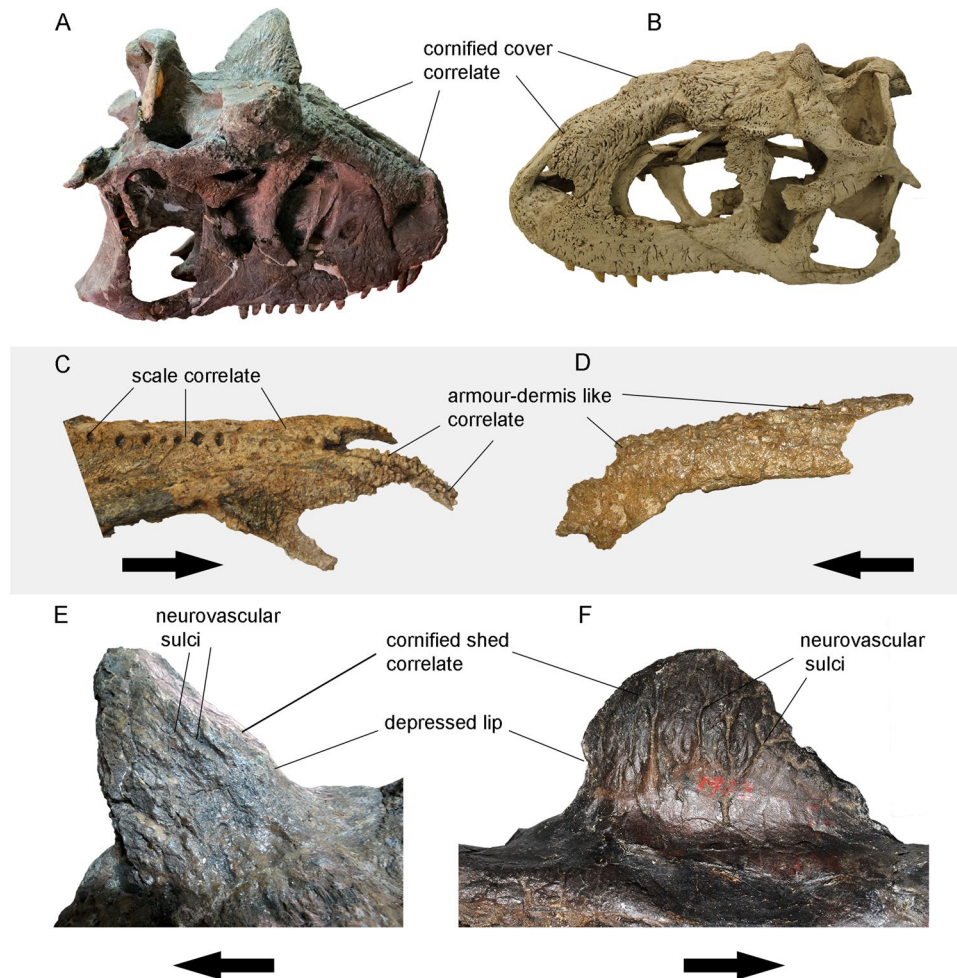


Figure 5. Details of the skin structures inferred for abelisaurids. Right side of the skull of (A) *Carnotaurus* (MACN-CH 894) and left side of the skull of (B) *Majungasaurus* (FMNH PR 2100 – cast), both in dorsolateral view. Right side of the nasal of (C) *Rugops* (MNN IGU1) and left side of the nasal of *Abelisaurus* (MPCA 11908), both in dorsolateral view. Detail of the right frontal horn of (E) *Carnotaurus* (MACN-CH 894) and left side of nasal horn of (F) *Ceratosaurus* (USNM 4735). Arrowhead pointing rostrally without scale.

extremely rugose with bone lobules across its surface. This texture is associated with armour-like dermis⁵³, as seen in the anterior snout of *Rugops* (Fig. 5C)

The dorsal surface of carnosaurine skulls (nasal, frontal, dorsal lacrimal and dorsal postorbital) have coarse pitting and grooving on bone surfaces suggesting that these were covered by cornified tissue, being an osteological correlate with the cornified cover seen on muskoxen, centrosaurine dinosaurs⁵³, and tyrannosaurids⁵⁴ (Figs 4C and 5A,B). However, it is improbable that abelisaurids had projections higher than the frontal horns. This category of tissue increased the toughness of the head roof, which also might have had an important ecological function as discussed below.

The horns of *Carnotaurus* and *Ceratosaurus* would have been more extended than the preserved fossil and covered with cornified sheath, indicated by neurovascular grooves, depressed lip and less rugosity than the other bones surfaces as suggested by the results of Hieronymus *et al.*⁵³ (Fig. 5E and F). Although the horn cores of *Carnotaurus* are more rugose than those of *Ceratosaurus*, ventral to the depressed lip the frontals are markedly lesser rugose. The single horn of *Majungasaurus* and *Rajasaurus* do not have the depressed lip seen in *Carnotaurus* and *Ceratosaurus*, suggesting that they were covered by cornified tissue without dorsal extension.

The only preserved soft tissues so far belongs to *Carnotaurus* and correspond to the anterior cervical region associated with cervical ribs, the shoulder region, thorax and tail¹⁷. The skin impressions present conical protuberances and there is no evidence for filaments or feathers (Fig. 3E). So far, the tubular filaments and feathers are only known in tetanuran theropods^{55,56}.

Regarding the bone histology, some analyses also shed some light to the development of ceratosaurs as well as palaeoenvironment^{14,57–59}. For example, the robustness of *Masiakasaurus*, once believed as different morphs (robust and gracile)⁶⁰, might be considered to be developmental feature instead of dimorphism⁵⁷, as also shown in allometric analyses¹. Additionally, the slow growth of the same species can be related to the low resources of Maevarano Formation^{57,61}.



Figure 6. Hypothetical reconstruction of two abelisaurids showing the soft tissues on the head inferred from osteological morphology of the skull. On the top, *Carnotaurus*; on the bottom, *Pycnonemosaurus*. Art by Maurilio Oliveira.

Ceratosaur ontogeny. Ontogenetic traits are difficult to interpret in fossils, sometimes leading to misunderstanding in taxonomy^{3,62,63}. In the case of abelisaurids, just a few species are known from certain ontogenetic series, such as *Limusaurus*, *Ceratosaurus* and *Majungasaurus*^{3,14,18}. Also, there are some specimens of *Masiakasaurus* of different sizes³³ with inference on ontogeny from bone histological analyses⁵⁷.

The ontogenetic series of *Ceratosaurus* is still unclear. Madsen and Welles⁵⁰ described two different species of *Ceratosaurus* (*C. magnicornis* and *C. dentisulcatus*) based on cranial and post-cranial associated elements. Nevertheless, Rauhut⁶⁴ suggests that the diagnosis of these species are subjective and there might have been just one species of *Ceratosaurus* in Morrison Formation. Carrano and Sampson³, following Rauhut⁶⁴, also argued that these two species have size-based diagnosis suggesting that they might be different ontogenetic specimens from *Ceratosaurus*. Although there are other materials attributed to *Ceratosaurus*³, no study was conducted to discuss the ontogenetic traits so far.

The series of *Limusaurus* shows at least 78 ontogenetic modifications through the growth from the analyses of 19 specimens¹⁴. Delcourt³⁰ reported the loss of teeth in mature individuals, while most juveniles had toothed jaws, the skull also becomes longer through ontogeny. In a parallel and broader study, Wang *et al.*¹⁴ also reported several changes including the formation of a beak after birth. The amount of modifications in *Limusaurus* ontogeny and the presence of gastroliths in the abdominal region also suggest that this species change ontogenetically dietary preferences from omnivory to herbivory^{14,32}.

The ontogeny of *Majungasaurus* was assessed by Ratsimbaholison *et al.*¹⁸ using mainly landmark-based approaches in the skull and in some isolated cranial elements (premaxilla, maxilla, lacrimal, postorbital, jugal, quadrate, dentary and surangular). The authors suggested that the ontogenetic changes include: the skull becomes deeper, the orbit becomes smaller, the sutures among the bones become more complex, and the texture of lateral bones increase¹⁸. In this study, the postcranial elements were not assessed.

Histological analyses suggest that *Masiakasaurus*⁵⁷ and small abelisaurid theropods⁵⁸ had a cyclical growth strategy as well as slowdown growing. However, in larger taxa, such as *Aucasaurus*, the growth rate tend to be higher than in smaller forms⁵⁸.

Apart from these studies, some inferences about ontogenetic stages were made based on fusion of bones. For example the types of *Xenotarsosaurus bonapartei*, *Euabelisaurus*, and *Aucasaurus* are considered mature

individuals because they have a fused tibia and astragalus^{12,42} (Fig. 3C and D), whereas the type of *Rugops* has been suggested as being an immature individual based on the fusion of the cranial elements³ (see above). The type of *Pycnonemosaurus nevesi*, despite being considered the largest abelisaurid so far¹, is considered a subadult specimen¹³ based on the presence of caudal vertebrae with unfused arches and centra as well as tibia. However, determining the maturity of a specimen based only on the fusion of arches with centrum is not safe because these elements are size-independent⁶⁵.

Ceratosaur behaviour. Ceratosaur behaviour can be inferred from several studies on anatomy^{4,40,48} and biomechanics^{8,9,66}. Also, the new information on soft tissue presented here (see above), suggest a behavioural pattern in abelisaurids as discussed below.

Gregarious behaviour is difficult to deduce; however small species found associated in the same assemblage localities, such as *Masiakasaurus*³³ and *Limusaurus*¹⁴, suggest that they might have lived together. In the case of *Majungasaurus*, several specimens were found associated, but some materials (ribs, chevron, neural spines, transverse processes and neural arches) have teeth marks made by its conspecifics suggesting that this species had cannibalistic behaviour⁶¹. This behaviour can be explained by the resource scarcity in the Maevarano Formation during the Late Cretaceous that was semi-arid⁶¹.

Going through the new information of soft tissues of abelisaurids shown here (above), it is possible to infer that this clade might have had some intraspecific headbutting behaviour at least in carnosaurine taxa (as suggested for *Carnotaurus*⁸ and *Majungasaurus*⁶⁷). The presence of cornified cover on the skull, that was inferred for *Carnotaurus* and *Majungasaurus*, has been related to headbutting behaviour in extant taxa (e.g. *Ovibos moschatus*, *Syncerus caffer* and *Buceros vigil*) as well as extinct (e.g. *Pachyrhinosaurus*, *Achelousaurus horneri*⁵³ and *Stegoceras validum*⁶⁸). Nevertheless, differing from those that engage in violent headbutting and have deep cancellous bone⁶⁸ (which carnosaurine lack), the carnosaurine might have used the head in low-motion headbutting and shoving matches at low speeds (as marine iguana *Amblyrhynchus cristatus*⁶⁹) or engaged giraffe-like strikes to each other's neck and flanks⁶⁷. The giraffe-like strikes have been proposed for *Majungasaurus*⁶⁷ due to the presence of tall, rugose nasals, struts within sinuses and a unicorn-like projection of the frontals^{48,67}, although stresses. Also, the mechanical analyses of *Carnotaurus* skull performed by Mazzetta *et al.*⁹ support the low-motion headbutting in this taxa. Furthermore, the presence of well-developed occipital region (e.g. nuchal crest)⁴⁸ associated with large epiphysis and neural spines in the cervical vertebra increasing the neck musculature^{70,71} strongly suggest that the cervicocephalic complex (head and neck) withstood high stress. Indeed, the well-developed epiphyses indicate a good leverage for intervertebral dorsiflexion by the muscle *transversospinalis cervicis* and the origin of a strong muscle *complexus*, a head dorsoflexor⁷². As similar features on neck and skull are spread throughout the carnosaurine abelisaurids, all the taxa belonging to this clade may have had similar behaviour in territoriality or mating matches for instance. It is worth noting that cranio-facial biting was reported for non-avian theropods^{73–75}. This behaviour could have had several possible reasons, including territoriality, courtship/mating, play, predation/cannibalism, intrapack dominance and subadult dispersal⁷⁴. In the case of carnosaurine, the headbutting and/or giraffe-like strikes could also have been added to the behavioural repertoire for any reasons above.

The low-motion headbutting behaviour also may have been present or began in more basal taxa such as *Rugops* and *Abelisaurus* in parallel with the development of scales and armour-like dermis on the dorsal cranium (e.g. nasal). For example, the dorsal surface of marine iguana skull has hummocky rugosities⁵³ as in *Rugops*, suggesting that this structure associated with armour-like dermis might have allowed the abelisaurid a similar behaviour (i.e. low-motion headbutting). This hypothesis of low-motion headbutting developing through the phylogeny in abelisaurids can be tested if a species with similar skull showed *Rugops* hummocky rugosities plus well-developed cervical epiphyses and neural spine and if it was found in Early Cretaceous beds (e.g. Aptian). If the headbutting was not developed in this taxon, certainly the development of armour-like dermis and later cornified cover on the skull in more derived abelisaurids might have allowed for this behaviour. It is worth noting that the giraffe-like strikes seem to be more complex than the iguana-like low-motion headbutting because the first requires more complex development of the skull, as seen in *Majungasaurus*⁶⁷, than in *Rugops*. Therefore, carnosaurine could potentially have adopted both combat styles. The possibilities of these behaviours in abelisaurids are testable with quantitative biomechanical methods^{8,9,67} and could be assessed in the future.

Biomechanical studies on the skull of abelisaurids have suggested that they had cranial mechanical advantage similar to allosaurs (e.g. *Allosaurus fragilis* and *Carcharodontosaurus saharicus*)⁶⁶ and similar bite force (e.g. *Carnotaurus*: 3,341 Newtons⁹; *Allosaurus*: 3,573 Newtons⁷⁶). These results mean that these two groups had high efficient mechanical advantage, but a bite force not as strong as that of *Tyrannosaurus*^{9,66}.

According to the analyses of Therrien *et al.*⁷⁷, carnosaurines (e.g. *Majungasaurus* and *Carnotaurus*) might have been ambush predators attacking large prey. Additionally, Sampson and Witmer⁴⁸ have suggested that *Majungasaurus*, and possibly other carnosaurines, were “adapted for a mode of predation that entailed relatively few, penetrating bites accompanied by powerful neck retraction, as well as bite-and-hold behaviour”. This predatory behaviour is consistent with results on skull biomechanics^{9,66} as well as neck analyses^{69,70}.

The development of advantageous features (e.g. large muscles for cursorial abilities)¹⁰ plus the increase the body size towards the phylogeny¹ granted abelisaurids the opportunity to succeed the carcharodontosaurids as main predators in the Southern Hemisphere after their extinction in Turonian^{49,78}. Interestingly, these two groups share dentary^{22,49} and skull advantage mechanics⁶⁶ that might have helped the extinction of carcharodontosaurids through ecological interactions¹ when this group was becoming rare in the Cenomanian, possibly due to climate changes (i.e. changing in the mean temperatures and floral compositions)⁷⁹. Therefore, it is reasonable to suggest that the latest abelisaurids (carnosaurine) were tyrannosaurid counterparts since the former were dominant in Southern Hemisphere³ and the latter in Northern Hemisphere².

Ceratosaur biogeography. The new phylogenetic analyses presented by Wang *et al.*¹⁴ suggest that Ceratosauroida was present in North America (*Ceratosaurus*) and Asia (*Limusaurus*, also suggested by Rauhut and Carrano²⁴), instead just in South America, Europe, Africa, India and Madagascar^{4,5}. However, Ceratosauroida originated in Africa²⁹ and the taxonomic diversity spread during the Middle Jurassic to North America, Europe, Asia, Africa, South America and Madagascar (Fig. 1). Australia and Antarctica do not have ceratosaur remains so far⁴, nevertheless it is possible that this group was present there and future discoveries can change this scenario.

The division of the main branches of Ceratosauroida (Noasauridae and Etrigosauria) happened in the Early Jurassic^{14,29} just after the origin of this group. The latest ceratosauroids, from the Aptian³⁶, were restricted to Southern Hemisphere and Europe⁵. However, during the Barremian to Santonian Gondwana remained isolated from Laurasia when the fauna could acquire a wide geographic distribution across the southern landmass; relating to Europe in Campanian-Maastrichtian rather than Asiamerica^{4,80}. The presence of the European majungasaurini *Arcovenator escotae* corroborates this biogeographic hypothesis⁵ whereas the European noasaurid *Genusaurus sisteronis* from Aptian^{14,81} would have to be considered a relic from the early origin of noasaurids.

It seems the abelisaurids body size increases along the phylogeny¹; however, the new phylogenetic analyses presented by Wang *et al.*¹⁴ suggest a large abelisaur (i.e. *Abelisaurus*) in the base of the clade. Also, there is a new evidence that abelisaurids reached medium/large sizes (between 5.6 and 7.6 m long, based on a partial tibia) from Berriasian-Valanginian of South America⁸². Nevertheless, the largest species were restricted to South America and Africa so far^{1,23,83}. This is because insular environments, such as Late Cretaceous of Europe⁵ and Madagascar, supports smaller fauna than continental landmass. Finally, the ability to live in semi-arid palaeoenvironment with low resources, such as those of *Majungasaurus* and *Pycnonemosaurus*^{61,84}, and the high disparity of the group facilitated the evolutionary success of ceratosauroids during this time (Fig. 6).

Methods

The information presented here includes several studies on ceratosauroids anatomy, phylogeny and biomechanics (see References). The soft tissues inference made are based on methods and results presented by Carr *et al.* and Hieronymus *et al.*^{48,49}. Additionally, I examined first-hand the materials of *Abelisaurus comahuensis* (MPCA 11098; Museo Provincial 'Carlos Ameghino', Cipolletti, Argentina), *Kryptops palaios* (MNN GAD1-1; Musée National du Niger, Niamey, Niger), *Aucasaurus garridoi* (MCF-PVPH-236; Museo Municipal 'Carmen Fuñes', Plaza Huinul, Argentina), *Carnotaurus sastrei* (MACN-CH 894; Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina), *Rugops primus* (MNN IGU1), *Ekrixinatossaurus novasi* (MUCPv-294; Museo de Geología y Paleontología, Lago Barreales, Argentina), *Skorpiovenator bustingorryi* (MMCH-PV 48; Museo Municipal Ernesto Bachman, Villa El Chocon, Argentina), *Majungasaurus crenatissimus* (cast; FMNH PR 2100; Field Museum of Natural History, Chicago, USA), *Ceratosaurus nasicornis* (USNM 4735; National Museum of Natural History, Washington, USA) for morphological comparison to infer the soft tissues.

References

- Grillo, O. N. & Delcourt, R. Allometry and body length of abelisauroid theropods: *Pycnonemosaurus nevesi* is the new king. *Cretac. Res.* **69**, 71–89 (2017).
- Brusatte, S. L. *et al.* Tyrannosaur Paleobiology: New Research on Ancient Exemplar Organisms. *Science* (80) **329**, 1481–1485 (2010).
- Carrano, M. T. & Sampson, S. D. The Phylogeny of Ceratosauria (Dinosauria: Theropoda). *J. Syst. Palaeontol.* **6**, 183–236 (2008).
- Novas, F. E., Agnolín, F. L., Ezcurra, M. D., Porfiri, J. & Canale, J. I. Evolution of the carnivorous dinosaurs during the Cretaceous: The evidence from Patagonia. *Cretac. Res.* **45**, 174–215 (2013).
- Tortosa, T. *et al.* A new abelisauroid dinosaur from the Late Cretaceous of southern France: Palaeobiogeographical implications. *Ann. Paleontol.* **100**, 63–86 (2014).
- Marsh, O. C. Principal characters of American Jurassic dinosaurs, Part VIII, The Order Theropoda. *Am. J. Sci.* **27**, 329–340 (1884).
- Bonaparte, J. F. A horned Cretaceous carnosaur from Patagonia. *National Geographic Research* **1**, 149–151 (1985).
- Mazzetta, G. V., Fariña, R. A. & Vizcaíno, S. F. On the palaeobiology of the South American horned theropod *Carnotaurus sastrei* Bonaparte. *Gaia Ecol. Perspect. Sci. Soc.* **192**, 185–192 (1998).
- Mazzetta, G. V., Cisilino, A. P., Blanco, R. E. & Calvo, N. Cranial mechanics and functional interpretation of the horned carnivorous dinosaur *Carnotaurus sastrei*. *J. Vertebr. Paleontol.* **29**, 822–830 (2009).
- Persons IV, W. S. & Currie, P. J. Dinosaur speed demon: The caudal musculature of *Carnotaurus sastrei* and implications for the evolution of South American abelisauroids. *PLoS One* **6**, e25763 (2011).
- Paulina Carabajal, A. The Braincase Anatomy of *Carnotaurus sastrei* (Theropoda: Abelisauroidea) from the Upper Cretaceous of Patagonia. *J. Vertebr. Paleontol.* **31**, 378–386 (2011).
- Pol, D. & Rauhut, O. W. M. A Middle Jurassic abelisauroid from Patagonia and the early diversification of theropod dinosaurs. *Proc. R. Soc. B Biol. Sci.* **279**, 1–6 (2012).
- Delcourt, R. Revised morphology of *Pycnonemosaurus nevesi* Kellner & Campos, 2002 (Theropoda: Abelisauroidea) and its phylogenetic relationships. *Zootaxa* **4276**, 1–45 (2017).
- Wang, S. *et al.* Extreme Ontogenetic Changes in a Ceratosaurian Theropod. *Curr. Biol.* **27**, 144–148 (2017).
- Filippi, L. S., Méndez, A. H., Juárez Valieri, R. D. & Garrido, A. C. A new brachyrostran with hypertrophied axial structures reveals an unexpected radiation of latest Cretaceous abelisauroids. *Cretac. Res.* **61**, 209–219 (2016).
- Ruiz, J., Torices, A., Serrano, H. & López, V. The hand structure of *Carnotaurus sastrei* (Theropoda, Abelisauroidea): Implications for hand diversity and evolution in abelisauroids. *Palaeontology* **54**, 1271–1277 (2011).
- Bonaparte, J. F., Novas, F. E. & Coria, R. A. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. *Nat. Hist. Museum Los Angeles Cty. Contrib. to Sci.* 1–42 (1990).
- Ratsimbaholison, N., Felice, R. & O'Connor, P. Ontogenetic changes in the craniomandibular skeleton of abelisauroid dinosaur *Majungasaurus crenatissimus* from the Late Cretaceous of Madagascar. *Acta Palaeontol. Pol.* **61**, 281–292 (2016).
- Padian, K., Hutchinson, J. R. & Holtz, T. R. Phylogenetic definitions and nomenclature of the major taxonomic categories of the carnivorous Dinosauria (Theropoda). *J. Vertebr. Paleontol.* **19**, 69–80 (1999).
- Ezcurra, M. D. A review of the systematic position of the dinosauriform archosaur *Eucoelophysis baldwini* Sullivan & Lucas, 1999 from the Upper Triassic of New Mexico, USA. *Geodiversitas* **28**, 649–684 (2006).
- Bonaparte, J. F. The Gondwanian theropod families Abelisauroidea and Noasauridae. *Hist. Biol.* **5**, 1–25 (1991).

22. Canale, J. I., Scanferla, C. A., Agnolin, F. L. & Novas, F. E. New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisauroid theropods. *Naturwissenschaften* **96**, 409–14 (2009).
23. Longrich, N. R., Pereda-Suberbiola, X., Jalil, N.-E., Khaldoune, F. & Jourani, E. An abelisauroid from the latest Cretaceous (late Maastrichtian) of Morocco, North Africa. *Cretac. Res.* **76**, 40–52 (2017).
24. Rauhut, O. W. M. & Carrano, M. T. The theropod dinosaur *Elaphrosaurus bambergi* Janensch, 1920, from the Late Jurassic of Tendaguru, Tanzania. *Zool. J. Linn. Soc.*, <https://doi.org/10.1111/zoj.12425> (2016).
25. Farke, A. A. & Sertich, J. J. W. An Abelisauroid Theropod Dinosaur from the Turonian of Madagascar. *PLoS ONE* **8** (2013).
26. Ride, W. & others. *International code of zoological nomenclature*. (International Trust for Zoological Nomenclature, 1999).
27. Bonaparte, J. & Novas, F. *Abelisaaurus comahuensis* n. gen. n. sp. Carnosauria del cretácico superior de Patagonia. *Ameghiniana* **21**, 259–265 (1985).
28. Wilson, J. A. *et al.* A new abelisauroid (Dinosauria, Theropoda) from the Lameta Formation (Cretaceous, Maastrichtian) of India. *Contributions of the Museum of Paleontology* **31**, 1–42 (2003).
29. Allain, R. *et al.* An abelisauroid (Dinosauria: Theropoda) from the Early Jurassic of the High Atlas Mountains, Morocco, and the radiation of ceratosaurs. *J. Vertebr. Paleontol.* **27**, 610–624 (2007).
30. Delcourt, R. Evolução morfológica de Ceratosauria e Tyrannosauroida (Dinosauria: Theropoda). (Universidade de São Paulo, 2016).
31. Burch, S. H. & Carrano, M. T. An articulated pectoral girdle and forelimb of the abelisauroid theropod *Majungasaurus crenatissimus* from the Late Cretaceous of Madagascar. *J. Vertebr. Paleontol.* **32**, 1–16 (2012).
32. Xu, X. *et al.* A Jurassic ceratosaur from China helps clarify avian digital homologies. *Nature* **459**, 940–4 (2009).
33. Carrano, M. T., Loewen, M. A. & Sertich, J. J. W. New materials of *Masiakasaurus knopfleri* Sampson, Carrano, and Forster, 2001, and implications for the morphology of the Noasauridae (Theropoda: Ceratosauria). *Smithson. Contrib. to Paleobiol.* **95**, 1–53 (2011).
34. Lockley, M., Kurihara, R. & Mitchell, L. In *Tyrannosaurus rex, the tyrant king* (eds Larson, P. L. & Carpenter, K.) 130–164 (Indiana University Press, 2008).
35. Sampson, S. D., Carrano, M. T. & Forster, C. A. A bizarre predatory dinosaur from the Late Cretaceous of Madagascar. *Nature* **409**, 504–6 (2001).
36. Sereno, P. C. & Brusatte, S. L. Basal Abelisauroid and Carcharodontosaurid Theropods from the Lower Cretaceous Elrhaz Formation of Niger. *Acta Palaeontol. Pol.* **53**, 15–46 (2008).
37. Sereno, P. C., Wilson, J. A. & Conrad, J. L. New dinosaurs link southern landmasses in the Mid-Cretaceous. *Proc. Biol. Sci.* **271**, 1325–1330 (2004).
38. Gianechini, F. A. *et al.* New abelisauroid remains from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. *Cretac. Res.* **54**, 1–16 (2015).
39. Carrano, M. T., Benson, R. B. J. & Sampson, S. D. The phylogeny of Tetanurae (Dinosauria: Theropoda). *J. Syst. Palaeontol.* **10**, 211–300 (2012).
40. Agnolin, F. L. & Chiarelli, P. The position of the claws in Noasauridae (Dinosauria: Abelisauroidea) and its implications for abelisauroid manus evolution. *Palaontologische Zeitschrift* **84**, 293–300 (2010).
41. Burch, S. H. Myology of the forelimb of *Majungasaurus crenatissimus* (Theropoda, Abelisauroidea) and the morphological consequences of extreme limb reduction. *J. Anat.* **231**, 515–531 (2017).
42. Coria, R. A., Chiappe, L. M. & Dingus, L. A new close relative of *Carnotaurus sastrei* Bonaparte 1985 (Theropoda: Abelisauroidea) from the Late Cretaceous of Patagonia. *J. Vertebr. Paleontol.* **22**, 460–465 (2002).
43. Senter, P. & Parrish, J. M. Forelimb function in the theropod dinosaur *Carnotaurus sastrei*, and its behavioral implications. *PaleoBios* **26**, 7–17 (2006).
44. Meers, M. B. Crocodylian forelimb musculature and its relevance to Archosauria. *Anat. Rec. A. Discov. Mol. Cell. Evol. Biol.* **274**, 891–916 (2003).
45. Romer, A. S. Crocodylian pelvic muscles and their avian and reptilian homologues. *Bull. Am. Museum Nat. Hist.* **48**, 533–552 (1923).
46. Méndez, A. H. The caudal vertebral series in abelisauroid dinosaurs. *Acta Palaeontol. Pol.* **59**, 99–107 (2014).
47. Carrano, M. T. The Appendicular Skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauroidea) From the Late Cretaceous of Madagascar. *J. Vertebr. Paleontol.* **27**, 163–179 (2007).
48. Sampson, S. D. & Witmer, L. M. Craniofacial Anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauroidea) From the Late Cretaceous of Madagascar. *J. Vertebr. Paleontol.* **27**, 32–102 (2007).
49. Delcourt, R. & Grillo, O. N. Reassessment of a fragmentary maxilla attributed to Carcharodontosauridae from Presidente Prudente Formation, Brazil. *Cretac. Res.* **84**, 515–524 (2018).
50. Madsen, J. & Welles, S. *Ceratosaurs* (Dinosauria, Theropoda): a revised osteology. *Area* **2** (2000).
51. Filippi, L. S., Méndez, A. H., Gianechini, F. A., Juárez Valieri, R. D. & Garrido, A. C. Osteology of *Viavenator exxoni* (Abelisauroidea; Furileosauria) from the Bajo de la Carpa Formation, NW Patagonia, Argentina. *Cretac. Res.* **83**, 95–119 (2018).
52. Calvo, J. O., Rubilar-Rogers, D. & Moreno, K. A new Abelisauroidea (Dinosauria: Theropoda) from northwest Patagonia. *Ameghiniana* **41**, 555–563 (2004).
53. Hieronymus, T. L., Witmer, L. M., Tanke, D. H. & Currie, P. J. The facial integument of centrosaurine ceratopsids: morphological and histological correlates of novel skin structures. *Anat. Rec. (Hoboken)* **292**, 1370–96 (2009).
54. Carr, T. D., Varricchio, D. J., Sedlmayr, J. C., Roberts, E. M. & Moore, J. R. A new tyrannosaur with evidence for anagenesis and crocodile-like facial sensory system. *Sci. Rep.* **7**, 44942 (2017).
55. Ortega, F., Escaso, F. & Sanz, J. L. A bizarre, humped Carcharodontosauria (Theropoda) from the Lower Cretaceous of Spain. *Nature* **467**, 203–206 (2010).
56. Rauhut, O. W. M., Foth, C., Tischlinger, H. & Norell, M. A. Exceptionally preserved juvenile megalosauroid theropod dinosaur with filamentous integument from the Late Jurassic of Germany. *Proc. Natl. Acad. Sci.* **109**, 11746–11751 (2012).
57. Lee, A. H. & O'Connor, P. M. Bone histology confirms determinate growth and small body size in the noasaurid theropod *Masiakasaurus knopfleri*. *J. Vertebr. Paleontol.* **33**, 865–876 (2013).
58. Canale, J. I., Cerda, I., Novas, F. E. & Haluza, A. Small-sized abelisauroid (Theropoda: Ceratosauria) remains from the Upper Cretaceous of northwest Patagonia, Argentina. *Cretac. Res.* **62**, 18–28 (2016).
59. Evans, D. C., Barrett, P. M., Brink, K. S. & Carrano, M. T. Osteology and bone microstructure of new, small theropod dinosaur material from the early Late Cretaceous of Morocco. *Gondwana Res.* **27**, 1034–1041 (2015).
60. Carrano, M. T., Sampson, S. D. & Forster, C. A. The osteology of *Masiakasaurus knopfleri*, a Small Abelisauroid (Dinosauria: Theropoda) From the Late Cretaceous of Madagascar. *J. Vertebr. Paleontol.* **22**, 510–534 (2002).
61. Rogers, R. R., Krause, D. W., Rogers, K. C., Rasoamimanana, A. H. & Rahantarisoa, L. Paleoenvironment and paleoecology of *Majungasaurus crenatissimus* (Theropoda: Abelisauroidea) from the Late Cretaceous of Madagascar. *J. Vertebr. Paleontol.* **27**, 21–31 (2007).
62. Carr, T. D. Craniofacial Ontogeny in Tyrannosauridae (Dinosauria, Coelurosauria). *J. Vertebr. Paleontol.* **19**, 497–520 (1999).
63. Fowler, D. W., Woodward, H. N., Freedman, E. A., Larson, P. L. & Horner, J. R. Reanalysis of ‘*Raptorex kriegsteini*’: A juvenile tyrannosaurid dinosaur from Mongolia. *PLoS One* **6**, e21376 (2011).
64. Rauhut, O. W. M. The interrelationships and evolution of basal theropod dinosaurs. *Spec. Pap. Palaeontol.* **69**, 1–213 (2003).
65. Brochu, C. A. Closure of neurocentral sutures during crocodylian ontogeny: implications for maturity assessment in fossil archosaurs. *J. Vertebr. Paleontol.* **16**, 49–62 (1996).

66. Sakamoto, M. Jaw biomechanics and the evolution of biting performance in theropod dinosaurs. *Proc. Biol. Sci.* **277**, 3327–3333 (2010).
67. Snively, E., Cotton, J. R., Witmer, L., Ridgely, R. & Theodor, J. Finite Element Comparison of Cranial Sinus Function in the Dinosaur *Majungasaurus* and Head-Clubbing Giraffes. In ASME 2011 Summer Bioengineering Conference 1075–1076 (2011).
68. Snively, E. & Theodor, J. M. Common Functional Correlates of Head-Strike Behavior in the Pachycephalosaur *Stegoceras validum* (Ornithischia, Dinosauria) and Combative Artiodactyls. *PLoS One* **6**, e21422 (2011).
69. Carpenter, C. C. Aggression and social structure in iguanid lizards. In *Lizard ecology: A symposium* 87–105 (1967).
70. Méndez, A. H. The cervical vertebrae of the Late Cretaceous abelisaurid dinosaur *Carnotaurus sastrei*. *Acta Palaeontol. Pol.* **59**, 569–579 (2014).
71. O'Connor, P. M. The postcranial axial skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *J. Vertebr. Paleontol.* **27**, 127–163 (2007).
72. Snively, E. Neck Musculoskeletal Function in the Tyrannosauridae (Theropoda, Coelurosauria): Implications for Feeding Dynamics. (University of Calgary, 2006).
73. Peterson, J. E., Henderson, M. D., Scherer, R. P. & Vittore, C. P. Face biting on a juvenile tyrannosaurid and behavioral implications. *Palaio* **24**, 780–784 (2009).
74. Tanke, D. H. & Currie, P. J. Head-biting behavior in theropod dinosaurs: Paleopathological evidence. *Gaia Ecol. Perspect. Sci. Soc.* **184**, 167–184 (1998).
75. Hone, D. W. E. & Tanke, D. H. Pre- and postmortem tyrannosaurid bite marks on the remains of *Daspletosaurus* (Tyrannosaurinae: Theropoda) from Dinosaur Provincial Park, Alberta, Canada. *PeerJ* **3**, e885 (2015).
76. Rayfield, E. J. *et al.* Cranial design and function in a large theropod dinosaur. *Nature* **409**, 1033–7 (2001).
77. Therrien, F., Henderson, D. M. & Ruff, C. B. In *The carnivorous dinosaurs* (ed. Carpenter, K.) 179–237 (Indiana University Press Indianapolis, Indiana, 2005).
78. Novas, F. E., de Valais, S., Vickers-Rich, P. & Rich, T. A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. *Naturwissenschaften* **92**, 226–230 (2005).
79. Coria, R. A. & Salgado, L. Mid-Cretaceous turnover of saurischian dinosaur communities: evidence from the Neuquen Basin. *Geol. Soc. London, Spec. Publ.* **252**, 317–327 (2005).
80. Ezcurra, M. D. & Agnolín, F. L. A new global palaeobiogeographical model for the late mesozoic and early tertiary. *Syst. Biol.* **61**, 553–566 (2012).
81. Accarie, H. *et al.* Découverte d'un dinosaure théropode nouveau (*Genusaurus susteronis* ng. n. sp.) dans l'Albien marin de Sisteron (Alpes de Haute-Provence, France) et extension au Crétacé inférieur de la lignée cérosaurienne. *Comptes rendus l'Académie des Sci. Série 2. Sci. la terre des planètes* **320**, 327–334 (1995).
82. Canale, J. I., Apesteguía, S., Gallina, P. A., Gianechini, F. A. & Haluza, A. The oldest theropods from the Neuquén Basin: Predatory dinosaur diversity from the Bajada Colorada Formation (Lower Cretaceous: Berriasian–Valanginian), Neuquén, Argentina. *Cretac. Res.* **71**, 63–78 (2017).
83. Chiarenza, A. A. & Cau, A. A large abelisaurid (Dinosauria, Theropoda) from Morocco and comments on the Cenomanian theropods from North Africa. *PeerJ* **4**, e1754 (2016).
84. Bittencourt, J. S. & Langer, M. C. Mesozoic dinosaurs from Brazil and their biogeographic implications. *An. Acad. Bras. Cienc.* **83**, 23–60 (2011).

Acknowledgements

I would like to thank Paul Sereno and Bob Masek (University of Chicago), David Bohaska (National Museum of Natural History), Juan Porfiri and Doménica Santos (Museo de Ciencias Naturales de la Universidad Nacional del Comahue), Peter Makovicky and William Simpson (Field Museum of Natural History), Rubén Barbieri (Museo Provincial Carlos Ameghino), Rubén Martínez (Universidad Nacional de la Patagonia San Juan Bosco), Rodolfo Coria (Museo Municipal Carmen Fuñes), Juan Canale (Museo Municipal Ernesto Bachmann), Alejandro Kramarz and Federico Agnolín (Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'), Eduardo Ruigómez (Museo Paleontológico 'Egidio Feruglio') and Xu Xing and Zheng Fang (Institute of Vertebrate Paleontology and Paleoanthropology) for providing access to their respective palaeontological collections. I thank Maurilio Oliveira for providing the Fig. 6. I also thank Ulisses Caramaschi and Borja Holgado (Museo Nacional) for important comments on nomenclature and phylogenetic definitions. I thank Gwendoline Deslyper (Trinity College Dublin) and Nadine Douglas (University College Dublin) for reviewing the English language. Also, I thank Fundação de Amparo à Pesquisa do Estado de São Paulo and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior for their financial support (FAPESP 2012/09370-2; CAPES - PNPd).

Author Contributions

R.D. collected and analysed the data and wrote the manuscript.

Additional Information

Supplementary information accompanies this paper at <https://doi.org/10.1038/s41598-018-28154-x>.

Competing Interests: The author declares no competing interests.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2018