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ARTICLE

Abelisauroidea (Theropoda, Dinosauria) from Africa: a review of the fossil record

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Abstract. The Continental African abelisauroid theropod dinosaur fossil record from the Jurassic-Cretaceous periods is becoming increasingly better understood, and offers great insight into the evolution and biogeography of this long-lived group of carnivores. Abelisauroidea is among the most familiar groups of theropod dinosaurs from Gondwana, with fossil records in South America, Australia, India and Africa, along with Europe. The objective of the present study is to review the fossil record of abelisauroids in continental Africa. Based on the literature and records from the online databases "The Paleobiology Database" and "The Theropod Database", we review the distribution of these theropods in Africa and comment on their evolution. The African continent is a major region of importance when it comes to 26 Abelisauroidea fossil findings, including records of both major subdivisions of the clade: the Abelisauridae and Noasauridae families. The oldest Abelisauroidea fossil record found in Africa dates from the Late Jurassic, while the final records date from the end of the Cretaceous. This indicates that clade was the longest surviving lineage of the large theropods of Africa, and they filled a variety of ecological roles, including apex predators, at the end of the Cretaceous, when tyrannosaurids occupied similar niches in the northern continents.

Keywords. Abelisauroidea; Abelisauridae; Noasauridae; Africa; Fossil; Record.

INTRODUCTION

The Abelisauroidea – the group including the mid-to-large-bodied abelisaurids and the smaller, fast-running noasaurids – are among the most diverse and abundant carnivorous dinosaurs (Theropoda) from the Southern Hemisphere. Their fossils have been found in every modern continent that was once part of Gondwana, with a few records also in Europe (Le Loeuff & Buffetaut, 1991; Tortosa *et al.,* 2014; Hendrickx & Mateus, 2014). The first fossils of abelisaurids from Continental Africa were found at the beginning of the 20th century, and the noasaurid *Elaphrosaurus* from Tanzania was named as a new species in 1920 (Janensch, 1920), although it was not recognized as an abelisaur at the time (Rauhut & Carrano, 2016). Much later, Sereno *et al.* (1996) described and named the putative noasaurid *Deltadromeus* from Morocco, although it was also not recognized as an abelisaur at the time. Since then, many new fossils from Continental Africa have been discovered, and in the mid-2000s some of these were finally recognized as belonging to abelisaurs, particularly abelisaurids. These included the new species *Rugops, Kryptops, Chenanisaurus,* and *Afromimus* (Sereno *et al.,* 2004; Sereno & Brusatte, 2008; Longrich *et al.,* 2017: Sereno, 2017). Although the currently recognized diversity of African abelisaurid species is not as high as it is in South America (Bonaparte & Powell, 1980; Bonaparte & Novas, 1985; Bonaparte, 1985; Bonaparte, 1991; Coria & Salgado, 1998; Coria *et al.,* 2002; Kellner & Campos, 2002; Calvo *et al.,* 2004; Canale *et al.,* 2009; Gianechini *et al.,* 2015, 2021; Filippi *et al.,* 2016; Langer *et al.,* 2019; Cerroni *et al.,* 2020; Aranciaga-Rolando *et al.,* 2021; Méndez *et al.,* 2021; Ortiz David *et al.,* 2021), Africa can now join South America as an area of particular importance for understanding abelisaur diversity and evolution, and thus for understanding what these theropods reveal about dinosaur evolution, distribution, and extinction more broadly.

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The objective of this paper is to review the records of Abelisauroidea in Continental Africa based on the most recent discoveries and to discuss the distribution of these animals on Africa during the Jurassic and Cretaceous.

METHODS

As a basis for this paper, we performed a bibliographic survey to gather information about Abelisauroidea records in Africa. The online platforms The Paleobiology Database (https://paleobiodb.org/#) and Theropod database (https://www.theropoddatabase.com) were the main databases used for the survey. The search carried out on "The Paleobiology Database" used the keyword engine of the website, and the keywords used were "Abelisauroidea", "Abelisauridae", and "Noasauridae". The website "Theropod database" was also searched to ensure greater coverage of the literature. Content in this database is searched through directories; thus, we accessed the "Abelisauroidea" directory to collect bibliographic data. All data were entered and organized in spreadsheets of the software Microsoft Office Excel 2016. In addition, for analytical purposes, we use the recent phylogeny of Abelisauroidea proposed by Baiano *et al.,* 2021 to discuss the nomenclature, taxonomy, and evolution of abelisauroids (Fig. 1).

The data compiled in our spreadsheet includes: i) the authors who described the fossils; ii) the date when the description was made; iii) the described materials (type, number of specimens, state of preservation, and a short description of the material); iv) the geological setting of each material; v) the age of the material; and vi) the locality of each record.

Institutional abbreviations: CMN (former NMC): Canadian Museum of Nature, Ottawa, Canada; MHNM: Muséum d'Histoire Naturelle de Marrakech, Marrakech, Morocco; GZG: Geowissenschaftliches Zentrum, Universität Göttingen, Göttingen, Germany; MB: Museum für Naturkunde, Berlin, Germany; MGGC: Museo Geologico Giovanni Capellini, Bologna, Italy; MGUP: Museo di Geologia e Paleontologia, "Gaetano Giorgio Gemmellaro", Università degli Studi di Palermo, Palermo, Italy; MNN: Musée National Boubou Hama, Niamey, Niger; MPCM: Museo della Rocca di Monfalcone, Monfalcone, Italy; MPUR NS: Museo Universitario di Scienze della Terra, Sapienza Università di Roma, Rome, Italy; NMB: Staatliche Naturhistorische Museum, Braunschweig, Germany; OCP Group: Office Chérifien des Phosphates, Khouribga, Morocco; OLPH, Olphin collection, Museo di Geologia e Paleontologia, "Gaetano Giorgio Gemmellaro," Università degli Studi di Palermo, Palermo, Italy; ONM: Office National des Mines, Tunis, Tunisia; PRC.NF: Libyan Petroleum Institute, Tripoli, Lybia; ROM: Royal Ontario Museum, Toronto, Canada; SGM: Ministère de l'Énergie, des Mines et des Énergies renouvelables, Rabat, Morocco. UCPC: University of Chicago Paleontology Collection, Chicago, USA; WDC: Wyoming Dinosaur Center, Thermopolis, Wyoming, USA.

RESULTS AND DISCUSSION

Currently, records of abelisauroids in mainland Africa come from eight countries, with the largest collection from Morocco. Tunisia has so far yielded a small sample of teeth. The record in Libya consists of parts of vertebrae and part two fossils of legs. Egypt has produced only one tooth crown, and a femur that has been lost. Abelisauroids from Kenya and Zimbabwe have not yet been formally described, but the materials from Kenya are promising and may belong to two new taxa. From Niger, three species of unequivocal abelisauroid have been described, along with at least two problematic taxa. Africa's oldest abelisauroid records come from Middle Jurassic Tendaguru Formation from Tanzania (Fig. 2).

Madagascar also has yielded many records of Abelisauroidea, including two well-known species (*Majungasaurus crenatissimus, Masiakasaurus knopfleri*). We will not consider these records in this manuscript, instead focusing on fossils from continental Africa because they have not yet received a detailed review.

Niger

***Kryptops palaios* Sereno & Brusatte, 2008** – *Kryptops palaios* comes from the Elrhaz Formation (Aptian-Albian), in the region of "Gadoufaoua", in the western part of the Ténéré Desert, Republic of Niger.

The holotype MNN GAD1-1 comprises a left maxilla with teeth. Sereno & Brusatte (2008) included several partial vertebrae and ribs (MNN GAD1-3 to GAD1-8) and an articulated pelvic girdle and sacrum (MNN GAD1-2) in the holotype specimen, but the postcrania was shown by Carrano *et al.* (2012) to belong to a non-abelisaurid theropod, most likely a carcharodontosaurid. We agree with this assessment. Therefore, these bones are no longer considered part of the *Kryptops* holotype.

***Rugops primus* Sereno, Wilson & Conrad, 2004** – *Rugops primus* is from the Echkar Formation (Cenomanian), which outcrops near Abangharit, in the Republic of Niger. *Rugops* was described based on the specimen MNN IGU1, a partially complete cranium. Before the description of *Rugops,* abelisaurids were not clearly known from Africa, and it was often argued that they may have never lived on the continent. *Rugops,* therefore, was the first named species, and first well-preserved specimen, of a genuine abelisaurid described from continental Africa (Sereno *et al.,* 2004).

***Afromimus tenerensis* Sereno, 2017** – *Afromimus* comes from the Elrhaz Formation (Aptian-Albian), in the region of "Gadoufaoua", Ténéré Desert, Niger Republic. The holotype MNBH GAD112 is a fragmentary, possibly adult individual and includes a dorsal rib fragment, seven partial mid and distal caudal vertebrae, two partial chevrons, a tibia and incomplete fibula partially coossified with the astragalocalcaneum, and three partial pedal phalanges including an ungual. In the study that described

Afromimus tenerensis Sereno (2017) originally identified it as an ornithomimosaur, a type of derived theropod more closely related to birds than were abelisaurids. However, Sereno (2017) also noted features in MNBH GAD112 that are shared with abelisauroids. Because on these resemblances, Cerroni *et al.* (2019) compared *Afromimus* with Abelisauroidea in detail and performed an extensive phylogenetic analysis. This resulted in the assignment of *Afromimus* to Abelisauroidea and possibly to Noasauridae, although its fragmentary condition precludes a confident referral to the latter family.

Undescribed abelisaur (Sereno *et al.,* 2004) – This material is from the Elrhaz Formation (Aptian-Albian), in the region of "Gadoufaoua", in the western part of the Ténéré Desert, Republic of Niger. The specimen was reported as

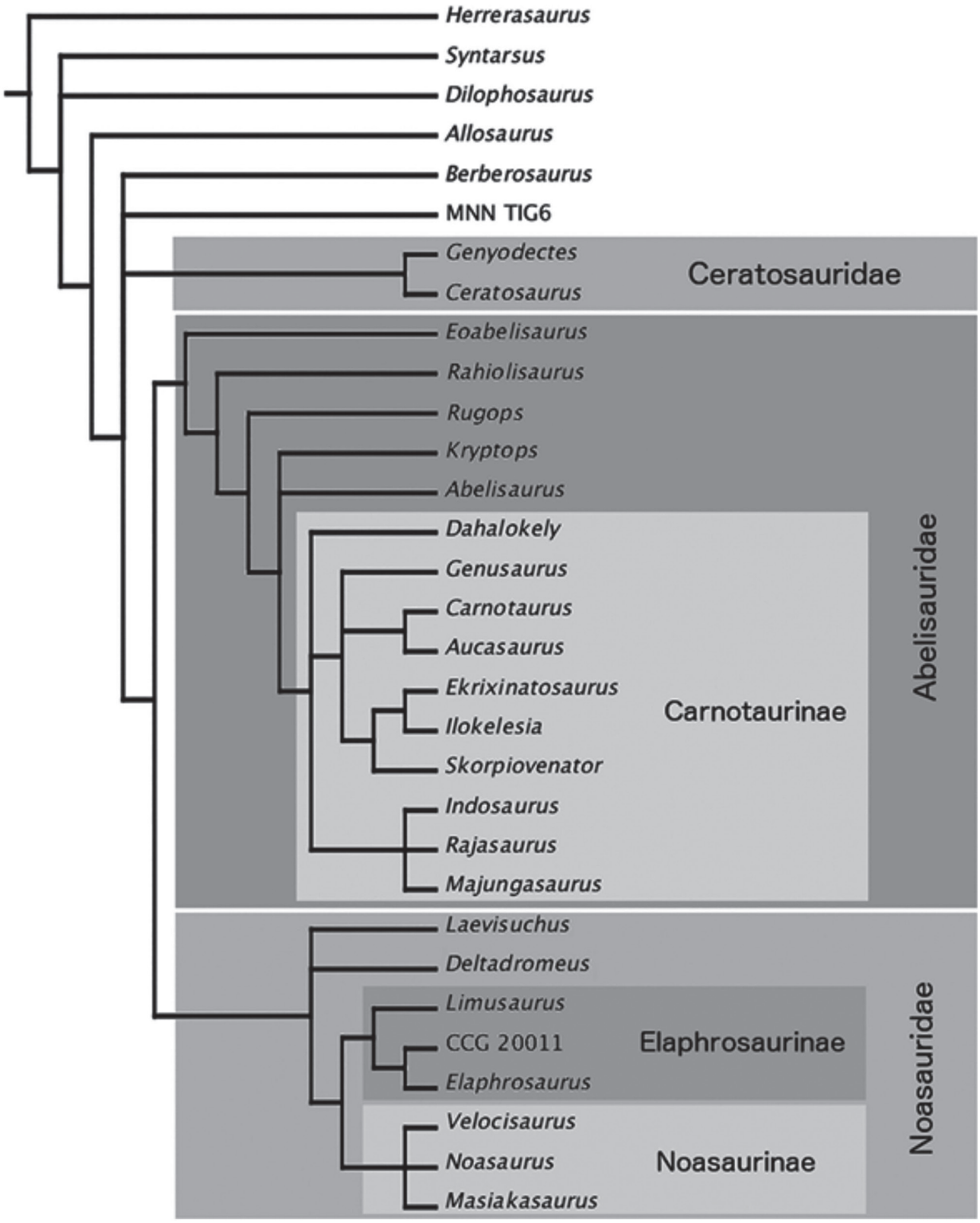

Figure 1. Abelisauroidea phylogeny (modified from Baiano *et al.,* 2021).

an almost complete articulated skeleton, possibly one of the most complete noasaurids ever found (Sereno *et al.*, 2004; Sereno & Brusatte, 2008; Sereno, 2010, 2017; Keillor, 2010). Although it has been mentioned in some papers and briefly described in abstracts and conference proceedings, it has yet to be formally described or named.

Tunisia

Abelisauridae indet (Fanti *et al.*, 2014) – MGGC 21889 is a fragment of a left dentary without associated teeth. The fossil comes from the Oum ed Diab Member (Aptian-Albian) of the Ain el Guettar Formation, which crops out in the Tataouine Basin in southern Tunisia.

Abelisauridae indet (Fanti *et al.*, 2014) – ONM TM 02 is a small fragment of a left dentary without associated teeth. The material is from the Oum ed Diab Member (Aptian-Albian) of the Ain el Guettar Formation, which crops out in the Tataouine Basin in southern Tunisia.

Abelisauroidea indet (Fanti *et al.*, 2014) – Recently, Fanti *et al.* (2014) described a number of theropod teeth from the Tataouine Basin, but there is no precise information about the origin of each specimen. Nevertheless, it is known that these fossils were collected in the Oum ed Diab and Chenini Members (Aptian-Albian) of the Ain el Guettar Formation. The abelisauroid teeth from the Tatatouine Basin belong to five dental morphotypes: Morphotype 1 (2 teeth); Morphotype 2 (13 teeth); Morphotype 6 (9 teeth); Morphotype 7 (2 teeth); Morphotype 8 (4 teeth).

Libya

Abelisauroidea indet (Smith *et al.*, 2010) – PRC.NF.1.21 includes two incomplete dorsal vertebrae, a centrum of a proximal caudal vertebra, the caudal part of a neural arch, the distal part of a right femur, and a well preserved right tibia. The fossils are from the town of Nalut, in Libya, about 30 km east of the border with Tunisia, where the Cabao Formation (Aptian) crops out.

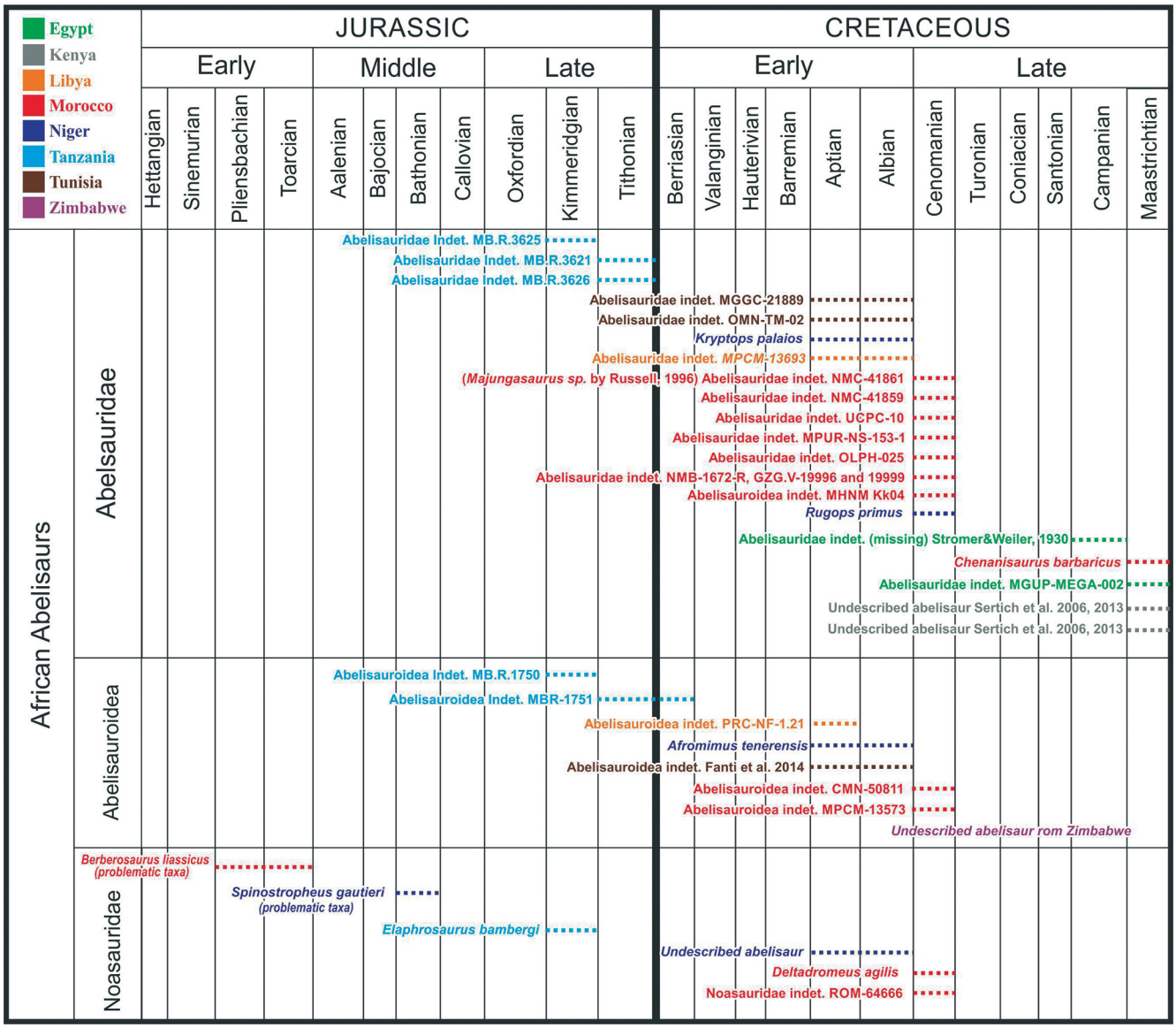

Figure 2. Map of the Continental Africa and Arabian Peninsula and the African countries that have abelisaur records.

Abelisauridae indet. (Smith & Della Vecchia, 2006) – MPCM 13693 is a tooth crown from the sandstones of the Cabao Formation (Aptian-Albian) found in a quarry nearby Nalut, western Jabal Nafusah, Libya.

Morocco

Abelisauridae indet (Russell, 1996) – NMC 4186 is a fragment of right dentary without teeth. This bone was assigned to *Majungasaurus* sp. by Russell (1996), but the description does not clarify exactly what features are shared between the Moroccan specimen and *M. crenatissimus* from Madagascar. Therefore, we will treat NMC 41861 as Abelisauridae indet. The bone is from the Kem Kem beds of the Late Cretaceous (Cenomanian). There is incomplete information regarding the exact locality where this specimen was collected, and it possibly comes from southern Morocco.

Abelisauridae indet (Russell, 1996) – NMC 41859 is from the Cenomanian Kem Kem beds. There is little information about the exact locality where this material was collected and it probably comes from southern Morocco. This specimen is a fragment of a right dentary.

Abelisauroidea indet (Russell, 1996) – CMN 50811 is from the Cenomanian Kem Kem beds. The specimen is a centrum of a cervical vertebra, which is hourglass-shaped. It was initially described by Russell (1996) along with a second cervical vertebra (CMN 50810).

Both were referred to as "Bone 'Taxon' B", identified as an indeterminate small theropod. Recently, McFeeters (2013) revised these specimens and suggested that both cervical vertebrae of "Bone 'Taxon' B" belonged to two different individuals. Thus, CMN 50811 possibly belongs to an abelisaur closely related to noasaurids, and CMN 50810 is another theropod with uncertain phylogenetic affinities. Chiarenza & Cau (2016) suggested that another specimen, "Bone 'Taxon' C" CMN 50403 (Russell, 1996), shares affinities with the vertebral material of the indeterminate abelisauroid PRC.NF.1.21 from Libya (see above; Smith *et al.,* 2010).

Abelisauridae indet (Mahler, 2005) – UCPC-10 is from the Kem Kem beds of the Upper Cretaceous (Cenomanian) and was collected by locals from the region of Erfoud, western Morocco. The material is a fragment of a right maxilla and according to Mahler (2005) exhibits characters that are diagnostic of Abelisauridae.

Abelisauridae indet (Porchetti *et al.,* 2011) – The specimens MPUR NS153-1 and MPUR NS153-2 are from the Cenomanian Kem Kem beds and were found in Hammada des Kem Kem, next to the Begaa village, about 10 km northeast of Taouz, Morocco. Both specimens are incomplete main bodies of left maxillae.

Abelisauridae indet. (Chiarenza & Cau, 2016) – OLPH 025 is from the Cenomanian Kem Kem beds and was collected next to the Moroccan-Algerian border, in southern Taouz, Errachidia Province, in the region of Meknès-Tafilalt, Morocco. The fossil is a proximal portion of a right femur.

Noasauridae indet. (Evans *et al.,* 2015) – ROM 64666 is from the Cenomanian Kem Kem beds and was collected next to Jebel Beg'aa (southeast Taouz, Errachidia Province), in the region of Meknès-Tafilalt, Morocco. The specimen is an almost complete and well-preserved left femur, in which only small parts of the proximal and distal ends are worn by abrasion.

Abelisauroidea indet (Novas *et al.,* 2005) – MPCM 13573 is from the Cenomanian Kem Kem beds. It possibly comes from the region of Tafilalt, in the northern region of the Sahara Desert, Morocco. The specimen is an ungual phalanx, probably from the fourth digit of the left foot.

Abelisauridae indet (Richter *et al.,* 2013) – The specimens NMB-1672-R, GZG.V.19996, and GZG.V.19999 are three well-preserved teeth from the Cenomanian Kem Kem beds of Morocco. In a recent study, Richter *et al.* (2013) found that these specimens closely resemble abelisaur teeth.

Abelisauroidea indet. (Zitouni *et al.,* 2019) – This fossil was found in the Aferdou region, near the locality of Gara Sbaâ, and belongs the Kem Kem Beds (Cenomanian) of Morocco. The specimen MHNM KK04 is a highly fractured and fragile right ilium.

***Chenanisaurus barbaricus* Longrich, Pereda-Suberbiola, Jalil, Khaldoune & Jourani, 2017** – The holotype of this species is from the region of Sidi Chennane. Although the specimen was not collected by the authors who described it, the pale white color of the bone and the color of the associated matrix are consistent with the preservation of other materials found in the Sidi Chennane locality.

The specimens are described as coming from Couche III of the Ouled Abdoun Basin (Maastrichtian). *Chenanisaurus* was described based on the specimen OCP DEK-GE 772, an anterior fragment of the left dentary. In addition, there are two other specimens: OCP DEK-GE 457 and OCP DEK-GE 458, which are two well-preserved teeth. The well-preserved maxillary tooth WDC-CCPM-005 described by Buffetaut *et al.* (2005) likely comes from Couche III of the Ouled Abdoun Basin (Maastrichtian). This tooth was identified as belonging to an abelisaurid. Later, Longrich *et al.* (2017) indicated that this tooth belongs specifically to *C. barbaricus*.

Egypt

Abelisauridae indet. (Stromer & Weiler, 1930) – This specimen is a proximal portion of a tibia found in the Nubian Sandstone (Campanian) of Egypt. The tibia, which was destroyed in World War II, showed abelisaurian affinities (Buffetaut *et al.,* 2005).

Abelisauridae indet. (Gemmellaro, 1921) – MGUP MEGA002 is a tooth crown from the Duwi Formation (Maastrichtian), which outcrops near Idfu, in the Nile Valley, Egypt. The specimen was originally referred (Gemmellaro, 1921) to *"Megalosaurus" crenatissimus,* an abelisaurid that is now well-known from the Late Cretaceous of Madagascar and is now called *Majungasaurus crenatissimus* (Krause *et al.,* 2007). The Duwi specimen remained unmentioned for decades in the scientific literature. During the 1990s, this specimen was mentioned by Sampson *et al.* (1996) and more recently its phylogenetic affinities were evaluated, which supported the assignment of MEGA002 to Abelisauridae indet. (Smith & Lamanna, 2006).

Kenya

Undescribed Abelisauridae (Sertich *et al.,* 2013) – this record refers to a possible giant abelisaurid that was more than 11 meters long (Sertich *et al.,* 2006, 2013). The material includes part of a skull, and axial and appendicular skeleton elements. This theropod is from the Lapurr Mountains, in the sandstones referred to as the "Turkana Grits" (Maastrichtian), Kenya (Fig. 9). This potential new species has only been mentioned in conference abstracts and has yet to be fully described or named in the literature. A second abelisaurid taxon was also apparently found in the Lapurr Mountain, in the "Turkana Grits" sandstones (Maastrichtian) of Kenya (Sertich *et al.,* 2006). However, there is, as of yet, no clear information about which specimens belong to this taxon. In the original report, the authors only comment that the "dental and axial materials suggest the presence of two abelisaurid theropods, a large one and another giant one".

Zimbabwe

Undescribed Abelisauroidea (Woolley *et al.,* 2015) – Woolley *et al.* (2015) recently mentioned the existence of fossils (teeth and vertebrae) that would indicate the presence of at least one middle-sized abelisauroid taxon in the Gokwe Formation (Cretaceous) (Fig. 10), Zimbabwe. This specimen has only been mentioned in conference proceedings and has not yet been fully described or named in the literature.

Tanzania

***Elaphrosaurus bambergi* Janensch, 1920** – *E. bambergi* is from the Middle Dinosaur Member of the Tendaguru Formation (Kimmeridgian), that crops out north of Tendaguru Hill, Tanzania (Fig. 3). *Elaphrosaurus* was described based on a well-preserved postcranial skeleton. The holotype, MB R 4960, was described by Janensch (1920, 1925) and includes 16 presacral vertebrae, 6 sacral vertebrae, 18 caudal vertebrae, a middle caudal chevron, a left humerus, both ilia, the left pubis, both ischia, the left femur, a tibia, a fibula, an astragalus-calcaneum, the left metatarsals II and III, the proximal part of metatarsal IV, and three pedal phalanges. Rauhut & Carrano (2016) reviewed the material described by Janensch (1929) and pointed out that Janensch described a left and a right scapulocoracoid, a right metacarpal II, and a left metacarpal IV (HMN R dd 4960.35, 4960.36) that were found in the same locality as the holotype and, therefore, most likely belonged to the same individual. Thus, Rauhut & Carrano (2016) suggested that this material should be included as part of the holotype of *Elaphrosaurus,* a suggestion made by Sereno (2004) and Carrano & Sampson (2008) as well.

?Abelisauridae indet (Janensch, 1925) – MB.R.3625 is a left tibia from the Middle Dinosaur Member of the Tendaguru Formation (Kimmeridgian). Rauhut (2011) suggested that this fossil is possibly from an abelisaurid.

Abelisauroidea indet (Janensch, 1925) – MB.R.1750 is a tibia described by Janensch (1925) as "Coelurosaurier B". Rauhut (2005) reviewed this fossil and indicated that it likely belonged to a small abelisauroid. The specimen is from the St locality from the Middle Dinosaur Member (Kimmeridgian) of Tendaguru, Tanzania.

?Abelisauridae indet (Janensch, 1925) – MB R 3621 is a well-preserved right femur from the TL locality of the Upper Dinosaur Member (Tithonian) of the Tendaguru Formation. Janensch argued that this fossil exhibits many characters that indicate a relationship with Ceratosauria. A more recent review (Rauhut, 2011) highlighted abelisaurid characters, so that it probably belongs to an indeterminate Abelisauridae.

?Abelisauridae indet (Janensch, 1925) – MB R 3626 is a well preserved right tibia from the TL locality of the

Figure 3. Africa abelisauroid record distribution from Late Jurassic to Late Cretaceous, ages from Cohen *et al.* (2020).

Upper Dinosaur Member (Tithonian) of the Tendaguru Formation. Janensch (1925) indicated that this fossil shows ceratosaurian characters. Recently, a review of this specimen (among others) argued that it has abelisaurian affinities (Rauhut, 2011).

Abelisauroidea indet (Janensch, 1925) – MB.R.1751 is a tibia described by Janensch (1925) as "Coelurosaurier C". Rauhut (2005) reviewed the material and suggested that it might belong to a small abelisauroid. The specimen was found in the locality from the Upper Dinosaur Member (Tithonian/Berriasian) of Tendaguru, Tanzania.

Problematic taxa

***Berberosaurus liassicus* Allain, Tykoski, Aquesbi, Jalil & Monbaron, 2007** – *B. liassicus* is from the upper layers of the continental series of Toundoute, which is Early Jurassic (Pliensbachian-Toarcian) in age, in the region of Douar de Tazouda, near the Toundoute village, High Atlas, Ouarzazate Province, Morocco. *Berberosaurus* was described based on postcranial material that includes a cervical vertebra (MHNM-Pt9), the anterior part of a sacrum (MHNM-Pt23), a second left metacarpal (MHNM-Pt22), a right femur (MHNM-Pt19), the proximal end of a left tibia (MHNM-Pt21), the distal end of a right tibia (MHNM-Pt16), and a left fibula (MHNM-Pt20).

Allain *et al.* (2007) considered *B. liassicus* to be a basal abelisauroid. The authors also indicated that the material shows some affinities with Noasauridae. However, later studies suggested that this theropod was a basal ceratosaur (Carrano & Sampson, 2008; Ezcurra *et al.,* 2010). A more recent study (Rauhut & Carrano, 2016) presented two main hypotheses regarding this taxon: *B. liassicus* may be a basal ceratosaur or a member of the more derived Ceratosauridae.

***Deltadromeus agilis* Sereno, Dutheil, Larochene, Larsson, Lyon, Magwene, Sidor, Varricchio & Wilson, 1996** – This taxon was collected in the Kem Kem region, southeastern Morocco, and was found in the lower layers (Cenomanian) of the Kem Kem beds. The holotype, SGM Din-2, is an incomplete postcranial skeleton that includes at least a cervical rib, anterior dorsal neural arches, two dorsal ribs, two gastralia, four anterior caudal neural spines, eighteen middle to posterior caudal vertebrae, five chevrons, partial scapulocoracoid, humerus, proximal radius, proximal ulna, an impression of part of a left iliac lamina, ischial shaft, fused distal ischia, a right femur, a right proximal tibia, a right distal tibia with the tarsus, a left fibula, left metatarsals II-IV, metatarsal V, and several pedal phalanges.

In the study that described this taxon, Sereno *et al.* (1996) included a small phylogenetic analysis which placed *D. agilis* as a coelurosaur. Later, *D. agilis* was recovered as sister to Ornithomimosauria (Rauhut, 2000, 2003). Other studies placed this taxon in Ceratosauria (Carrano & Sampson, 2002; Sereno *et al.,* 2004; Carrano & Sampson, 2008; Pol & Rauhut, 2012). However, after a recent review of *E. bambergi,* together with other information, *D. agilis* was assigned to Noasauridae (Tortosa *et al.,* 2014; Rauhut & Carrano, 2016). Apesteguía *et al.* (2016), on the other hand, recovered *Deltradomeus* as a basal carcharodontosaur. Thus, the phylogenetic position of this taxon is still debated.

***Spinostropheus gautieri* (Lapparent, 1960) Sereno, Wilson & Conrad, 2004** – *S. gautieri* has a controversial history. Lapparent (1960) described two series of fossils from Tedreft, one a lot of probably unassociated (Carrano & Sampson, 2008) remains and the other an associated skeleton, as the new species *Elaphrosaurus gautieri.* As noted by Rauhut & Carrano (2016), these are all catalogued as syntypes under the number MNHN 1961-28. The incomplete description and illustration by Lapparent makes it difficult to know which elements belonged to the supposedly associated skeleton, and Carrano & Sampson further state some of the material cannot be located. Sereno *et al.* (2004) chose a mid-cervical from the unassociated lot (plate XI, fig. 5 in Lapparent) as the holotype, though Rauhut & Carrano noted this did not count as a formal lectotype designation under ICZN rules. Regardless, Sereno *et al.* proceeded to refer new specimen MNN TIG6 (an articulated axial column preserving the third cervical to the anterior sacrals with complete cervical and fragmentary dorsal ribs) to the species and made it the type of the new genus *Spinostropheus.* MNHN 1961-28 was found in Tedreft 250 km northwest of Agadez, while MNN TIG6 was found in Fako 100 km southwest of Agadez. Both specimens were found in to the Tiourarén Formation (Bathonian), which outcrops in Niger. A proximal metatarsal from the younger Continental Intercalaire was also assigned to the species by Lapparent; however, as this specimen is fragmentary and cannot clearly be assigned to *S. gautieri,* were do not consider it further.

Sereno *et al.* (2004) scored MNN TIG6 in their phylogenetic analysis and recovered it as a basal abelisauroid, while Carrano & Sampson (2008) scored the syntype material and MNN TIG6 and recovered it to be a basal ceratosaur. Most recently, Wang *et al.* (2017) included both specimens and recovered the OTU as a noasaurid. However, while Carrano & Sampson believed the mid cervical and at least one tibia are ceratosaur-like, Rauhut & Carrano (2016) stated it lacked synapomorphies of Ceratosauria and could belong to Tetanurae instead. They provided several differences from *Elaphrosaurus,* supporting the use of *Spinostropheus* for MNHN 1961-28, but stated it was quite different from MNN TIG6, so removed the latter specimen from the hypodigm.

Stratigraphic distribution and evolution of African Abelisauroidea

Based on the African records (Table 1), abelisauroids were a long-lived and successful group, with fossil representatives known from the Late Jurassic (Janensch, 1920, 1925) to the very end of the Cretaceous (Gemmellaro,

Table 1. Fossil records of Abelisauroidea in Africa.

Taxa/specimen	Author	Stratigraphy	Age	Description
Tanzania				
Elaphrosaurus bambergi	Janensch, 1920	dd locality of the Middle Dinosaur Member of the Tendaguru Formation	Kimmeridgian	16 presacral vertebrae, 6 sacral vertebrae, 18 caudal vertebrae, a middle caudal chevron, the left humerus, both ilia, the proximal left pubis, both ischia, the left femur, the left tibia, the proximal left fibula, the left astragalus-calcaneum, the left metatarsals II and III, the proximal left metatarsal IV, left pedal phalanges II-1, IV-2 and IV-4, a left and a right scapulocoracoid, a right metacarpal II, and a left metacarpal IV.
Abelisauridae indet MB.R.3625	Janensch, 1925	Middle Dinosaur Member of the Tendaguru Formation Kimmeridgian Left tibia.		
Abelisauroidea indet MB.R.1750	Janensch, 1925	St locality of the Middle Dinosaur Member of the Tendaguru Formation	Kimmeridgian	Left tibia.
Abelisauridae indet MB.R.3621	Janensch, 1925	TL locality of the Upper Dinosaur Member (Tithonian) of the Tendaguru Formation.	Tithonian	Right femur.
Abelisauridae indet MB.R.3626	Janensch, 1925	TL locality of the Upper Dinosaur Member Tendaguru Formation.	Tithonian	Right tibia.
Abelisauroidea indet MB.R.1751	Janensch, 1925	H locality from the Upper Dinosaur Member Tendaguru Formation	Tithonian/Berriasian	Left tibia.
Niger				
Kryptops palaios MNN GAD1	Sereno & Brusatte, 2008	Elrhaz Formation	Aptian-Albian	Left maxilla.
Rugops primus MNN IGU1	Sereno, Wilson & Conrad, 2004	Echkar Formation	Cenomanian	Partial skull, partially complete cranium, missing the posterior sides of the skull roof, the palate, the jugal, quadratojugal, quadrate, postorbital and squamosal.
Afromimus tenerensis MNBH GAD112	Sereno, 2017	Elrhaz Formation	Cenomanian	Dorsal rib fragment, seven partial mid and distal caudal vertebrae, two partial chevrons, right tibia and incomplete fibula partially coossified with the astragalocalcaneum, right pedal phalanx II-2, right pedal ungual II, right pedal phalanx III-1.
Undescribed abelisaur	Sereno, Wilson & Conrad, 2004	Elrhaz Formation	Cenomanian	Almost complete articulated skeleton.
Spinostropheus gautieri MNHN 1961-28 (syntypes) (Problematic taxon)	Lapparent, 1960	Tiouraren Formation	Bathonian	(many individuals) mid cervical vertebra, two anterior dorsal vertebrae, posterior dorsal vertebra, four dorsal fragments, three sacral fragments, three caudal vertebrae, two caudal fragments, partial left humerus, ulna, distal right pubis, distal femur, incomplete right tibia, incomplete fibula, proximal metatarsal, four metatarsal fragments, partial pedal phalanx (single individual) cervical neural arch, two fused cervical centra, two dorsal vertebrae, partial caudal vertebra, three manual unguals, tibiae, distal fibula, proximal metatarsal, four pedal phalangeal fragments.
MNN TIG6 (Problematic taxon)	Sereno, Wilson & Conrad, 2004	Tiouraren Formation	Bathonian	posterior third cervical vertebra, fourth through tenth cervical vertebra, cervical rib, first through eighth dorsal vertebra, partial ninth through thirteenth dorsal vertebra, fragmentary dorsal ribs, first through third sacral neural arches, ossified tendons.
Tunisia				
Abelisauridae indet MGGC 21889	Fanti *et al.,* 2014	Oum ed Diab Member of Ain el Guettar Formation	Aptian-Albian	Fragment of a left dentary.
Abelisauridae indet ONM TM 02	Fanti *et al.,* 2014	Oum ed Diab Member of Ain el Guettar Formation	Aptian-Albian	Small fragment of a left dentary.
Abelisauridae indet	Fanti *et al.,* 2014	Oum ed Diab Member of Ain el Guettar Formation	Aptian-Albian	Morphotype 1 (2 teeth), Morphotype 2 (13 teeth), Morphotype 6 (9 teeth), Morphotype 7 (2 teeth), Morphotype 8 (4 teeth).
Libya				
Abelisauroidea indet PRC.NF.1.21	Smith *et al.,* 2010	Cabao Formation	Aptian	2 incomplete dorsal vertebrae, a centrum of a caudal vertebra, part of a caudal neural arch, the distal part of a right femur, and right tibia.
Abelisauridae indet MPCM 13693	Smith & Della Vecchia, 2006	Cabao Formation	Aptian-Albian	2 crowns.
Morocco				
Berberosaurus liassicus (Problematic taxon) MHNM Pt (x)	Allain, Tykoski, Aquesbi, Jalil & Monbaron, 2007	Continental series of Toundoute	Pliensbachian-Toarcian	cervical vertebra (Pt9), anterior part of a sacrum (Pt23), II left metacarpal (Pt22), right femur (Pt19), left tibia (Pt21), the distal end of a right tibia (Pt16), left fibula (Pt20).

Taxa/specimen	Author	Stratigraphy	Age	Description
Deltadromeus agilis (Problematic taxon) SGM Din-2	Sereno, Dutheil, Larochene, Larsson, Lyon, Magwene, Sidor, Varricchio & Wilson, 1996	Kem Kem beds	Cenomanian	Cervical rib, anterior dorsal neural arches, two dorsal ribs, two gastralia, four anterior caudal neural spines, eighteen middle to posterior caudal vertebrae, five chevrons, partial scapulocoracoid, humerus, proximal radius, proximal ulna, an impression of part of a left iliac lamina, ischial shaft, fused distal ischia, a right femur, a right proximal tibia, a right distal tibia with the tarsus, a left fibula, left metatarsals II-IV, metatarsal V, and several pedal phalanges.
Abelisauridae indet NMC 4186	Russell, 1996	Kem Kem beds	Cenomanian	Fragment of right dentary.
Abelisauridae indet NMC 41859	Russell, 1996	Kem Kem beds	Cenomanian	Fragment of a right dentary.
Abelisauridae CMN 50811	Russell, 1996	Kem Kem beds	Cenomanian	Centrum of a cervical vertebra.
Abelisauridae indet UCPC-10	Mahler, 2005	Kem Kem beds	Cenomanian	Fragment of a right maxilla.
Abelisauridae indet MPUR NS153-1, MPUR NS153-2	Porchetti *et al.,* 2011	Kem Kem beds	Cenomanian	Two incomplete main bodies of left maxilla.
Abelisauridae indet OLPH 025	Chiarenza & Cau, 2016	Kem Kem beds	Cenomanian	Proximal portion of a right fêmur.
Abelisauridae indet NMB-1672-R, GZG.V.19996, and GZG.V.19999	Richter *et al.,* 2013	Kem Kem beds	Cenomanian	Three teeth.
Abelisauridae indet. MHNM KK04	Kem Kem beds	Cenomanian	Partial right ilium.	
Noasauridae indet ROM 64666	Evans *et al.,* 2015	Kem Kem beds	Cenomanian	Left fêmur.
Abelisauroidea indet MPCM 13573	Novas *et al.,* 2005	Kem Kem beds	Cenomanian	Ungual phalanx, from the digit IV of the left foot.
Chenanisaurus barbaricus OCP DEK-GE 772* OCP DEK-GE 457** OCP DEK-GE 458***	Longrich, Pereda-Suberbiola, Jalil, Khaldoune & Jourani, 2017	Couche III of the Ouled Abdoun Basin	Maastrichtian	Fragment of the left dentary*, teeth**, teeth***.
Egypt				
Abelisauridae indet (Missing)	Stromer & Weiler, 1930	Nubian Sandstone	Campanian	A proximal portion of a tíbia.
Abelisauridae indet MGUP MEGA002	Gemmellaro, 1921	Duwi Formation	Maastrichtian	Crown.
Kenya				
Undescribed Abelisauridae Possible giant abelisaurid* Possible mid size abelisaurid**	Sertich *et al.,* 2013; Sertich *et al.,* 2006	Turkana Grits sandstones	Maastrichtian	Part of a skull, and axial and appendicular skeleton elements*, dental and axial materials**.
Zimbabwe				
Undescribed Abelisauroidea	Woolley *et al.,* 2015	Gokwe Formation	Cretaceous	Teeth and vertebra.

1921; Longrich *et al.,* 2017). This is a span of over 90 million years. African specimens give important insight into the origins of abelisauroids and their eventual extinction.

Fossil remains from Tanzania described by Janensch (1920, 1925), which include the holotype of *E. bambergi* and the isolated specimens (MB R 1750, MB R 3625) recently assigned to Abelisauroidea (Rauhut, 2005, 2011; Rauhut & Carrano, 2016), are the oldest known unequivocal abelisauroid records from continental Africa, dating from the Kimmeridgian, Upper Jurassic.

The phylogenetic position of the problematic taxon *B. liassicus* is still debated among researchers (Allain *et al.,* 2007; Carrano & Sampson, 2008; Ezcurra *et al.,* 2010; Rauhut & Carrano, 2016). Supposing that this theropod is a basal member of Abelisauroidea or a ceratosaur with abelisauroid affinities, this would be the oldest record of this lineage in Africa, dating back to the Early Jurassic (Allain *et al.,* 2007).

Once the phylogenetic affinities of *Elaphrosaurus* and *Berberosaurus* and their relationships with Abelisauroidea are better understood, these taxa will provide key information regarding the origin of the group. In particular, they have bearing on the hypothesis that Abelisauroidea began to diversify early in the Jurassic and split into Abelisauridae and Noasauridae during the Middle Jurassic (Allain *et al.,* 2007; Pol & Rauhut, 2012; Rauhut & Carrano, 2016). An earlier diversification of Abelisauroidea is also indicated by the appendicular specimens of Tanzania, the tibia MB R 3626 and the femur MB R 3621, both described by Janensch (1925) and assigned to Abelisauridae by Rauhut (2011). The material dates to the end of the Jurassic (Tithonian) and is the oldest Abelisauridae record from Africa. Together with *E. bambergi,* MB R 3626 and MB R 3621 also support the hypothesis that an African Abelisauroidea fauna formed by two families (Abelisauridae and Noasauridae) was established before the end of the Jurassic.

The fossil record of continental African Abelisauroidea has a great hiatus, spanning from the end of the Late Jurassic (Tithonian) to the end of the Early Cretaceous (Fig. 2). This most likely represents poor sampling, not genuine absence, seeing as we know that abelisauroids persisted until the end of the Cretaceous. After the hiatus, abelisauroids reappear in the Aptian-Albian fossil record of Africa. *Kryptops palaios* is a basal member of Abelisauridae (Sereno & Brusatte, 2008; Rauhut & Carrano, 2016; Longrich *et al.,* 2017). However, *Kryptops* is not the only abelisauroid record from the Aptian-Albian. In the same unit where *Kryptops* was found, in the Elrhaz Formation, Niger, another abelisauroid theropod was also discovered. The specimen has not yet been described, but it is possibly the most complete noasaurid known to date (Sereno *et al.,* 2004; Sereno & Brusatte, 2008; Sereno, 2010; Keillor, 2010). In addition to the material

from Niger, there are fossils of Aptian-Albian abelisauroids from many other parts of north Africa, which indicates that the group was diverse and occupied a large area at the time. These include specimens from Libya (MPCM 13693 and PRC.NF.1.2) and Tunisia (MGGC 21889, ONM TM 02, and several teeth with Abelisauroidea affinities described by Fanti *et al.* (2014).

During the Aptian-Albian of Africa, the Abelisauroidea was firmly established as one of the three main groups of medium to large-sized theropods. Along with abelisauroids, this so-called triumvirate of large carnivores also included carcharodontosaurids and spinosaurids (Brusatte & Sereno, 2008). This paleoecological grouping possibly had an earlier origin, but the first quality records of all three groups appearing together occur in the Aptian-Albian. This triumvirate of large theropods remained in Africa until at least the Campanian, and were also present together in other parts of Gondwana during the Mid-Late Cretaceous, particularly South America.

An abundance of abelisauroid fossils is also observed in the Cenomanian of Africa, as demonstrated by the abelisaurid *Rugops primus* from the Echkar Formation and the potential noasaurids *Afromimus* and *Deltadromeus agilis*. These taxa exemplify the evolutionary success of Abelisauroidea during the beginning of the Late Cretaceous. The Kem Kem Formation in Morocco also has yielded many other Cenomanian records: abelisaurid specimens NMC 4186 (*Majungasaurus* sp. in Russell, 1996), NMC 41859, UCPC – 10, MPUR NS153-1, MPUR NS153-2, and OLPH 025, the noasaurid ROM 64666, the abelisaurs CMN 50811, MHNM KK04 and MPCM 13573, and the three teeth with abelisaurid affinities described by Richter *et al.* (2013).

A decline in the fossil richness of abelisaurids is observed towards the end of the Late Cretaceous, although this also may be an artifact of sampling rather than a genuine taxonomic signal. Indeed, until recently, little was known about the Abelisauroidea from this age, as latest Cretaceous dinosaur-bearing rocks are rare in Africa. There is only one record from the Campanian, a fragment of a tibia (possibly from an abelisauroidoid) that was collected in the Nubian Sandstone of Egypt. This fossil was described by Stromer & Weiler (1930) but was destroyed. Until a few years ago, there was little information about abelisauroids from the Maastrichtian of Africa. The fossil record was limited to a single tooth from the phosphates of the Ouled Abdoun Formation, Morocco (Buffetaut *et al.,* 2005). This material was recently redescribed by Longrich *et al.* (2017) and assigned to their new taxon *Chenanisaurus barbaricus,* and is the first abelisaurid named and comprehensively described from the Maastrichtian of Africa. It is possible that two other records from the end of the Cretaceous of Africa may also belong to abelisauroids. These specimens were collected in the Turkana Grits Formation, Kenya, but have not yet been described. The fossils could belong to two taxa: one gigantic abelisaurid and another large-size taxon (Sertich *et al.,* 2006; Sertich *et al.,* 2013).

Abelisaurids have also been reported from the Maastrichtian of South America, along with potentially carcharodontosaurids (Candeiro *et al.,* 2004, 2006, 2012; Azevedo *et al.,* 2013; Delcourt & Grillo, 2018). Carcharodontosaurids may have also been present in the Maastrichtian of Africa, but are currently unsampled because there are few places to find fossils of this age in Africa. But, based on the current fossil record, we can hypothesize that the Abelisauridae were the last group of large theropods to inhabit Africa. This would mean that abelisauroids were the longest surviving lineage of large-bodied theropods in Africa (Fig. 11). It is also noteworthy that abelisauroids may have evolved giant size at the very end of the Cretaceous in Africa, at the same time that colossal tyrannosaurids like *Tyrannosaurus* and *Tarbosaurus* had ascended to the apex predator role in North America and Asia. Abelisauroids also occupied the large-bodied predator role into the Maastrichtian in South America (Novas, 2013), although it may be that the African taxa were even larger-bodied, if the records from Kenya are verified.

CONCLUSION

Abelisauroidea were a major group of small-to-large-bodied theropods that lived on Africa during at least the last half of the Mesozoic, from the Late Jurassic until the end of the Cretaceous. Although the African abelisauroid fossils are not as abundant as those from South America, and although the first unequivocal records of abelisauroids on Africa were recognized only in the early 2000s, we can now recognize Africa as not just an important region for abelisauroid fossils, but the region with the second most diverse record of these theropods, after South America. The African fossil record includes two families (Abelisauridae and Noasauridae), into which are assigned five genera (*Afromimus, Chenanisaurus, Rugops, Kryptops,* and *Elaphrosaurus*) that are currently considered valid. Further research may elucidate the affinities of the problematic taxa *Deltadromeus agilis* and *Berberosaurus liassicus* and future formal descriptions of the materials from Kenya and Niger may increase the number of Abelisauroidea fossils in Africa.

The abelisauroids from Africa were part of the great dispersal and evolution of this group, which began at the end of the Jurassic and ended at the end of the Cretaceous. The oldest abelisauroid fossils from Africa were discovered in Tanzania and date from the end of the Jurassic (Kimmeridgian). If we consider the records from Tanzania with the specimens of *Ozraptor* (a possible Australian abelisauroid from the Middle Jurassic), *Eoabelisaurus* (a possible abelisauroid from the Middle Jurassic of South America), CCG 20011 (a noasaurid originally referred to *Chuandongocoelurus* from the Middle Jurassic of China) and *Limusaurus* (a noasaurid recorded in the Upper Jurassic of China), it is clear that – regardless of their center of origin – abelisauroids began to evolve and disperse very early. The first appearance of Abelisauroidea possibly occurred during the Early Jurassic, because fossils indicate that abelisauroids already inhabited different regions of Gondwana in the Middle Jurassic. Furthermore,

we argue that the Abelisauria fossil record from Africa supports the hypothesis of the incredible evolutionary and ecological success of the clade over its evolutionary history, given how many abelisauroid fossils, belonging to each of the two component subfamilies, are known from across the continent.

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