Journal of African Earth Sciences 163 (2020) 103738

Contents lists available at ScienceDirect

Journal of African Earth Sciences

journal homepage: www.elsevier.com/locate/jafrearsci

Sauropod dinosaur fossils from the Kem Kem and extended 'Continental Intercalaire' of North Africa: A review

Femke M. Holwerda[a,b,*]

[a] Faculty of Geosciences, Utrecht University, Princetonlaan 8a, Utrecht, 3584 CB, the Netherlands
[b] Fachgruppe Paläoumwelt, GeoZentrum Nordbayern, Friedrich-Alexander Universität Erlangen-Nürnberg, Loewenichstr. 28, Erlangen, 91054, Germany

ARTICLE INFO

Keywords:
Gondwana
Cretaceous
Sauropoda
Neosauropoda
Africa
Cenomanian

ABSTRACT

The Cretaceous (likely Aptian-Cenomanian) Kem Kem beds of Morocco are famous for their fossil-richness, including theropods, and several sauropod body fossils, such as *Rebbachisaurus garasbae*, as well as isolated sauropod teeth. Deposits from this particular age, however, stretch across Algeria and Tunisia, with possibly contemporaneous fossiliferous beds also being known from Egypt and Niger. Although the sediments of North Africa have yielded more complete sauropod specimens in recent years dated to either Cenomanian or Campanian-Maastrichtian, in general, these sites are not well-known. A recent study on isolated sauropod teeth from Morocco and Algeria revealed that a diverse sauropod fauna existed, and, moreover, evidence has been found of sauropod migration from Africa to Europe in the Cretaceous. In order to provide a better overview of the sauropod presence in the Albian-Cenomanian of North Africa, an overview of all sauropod material known from this time is necessary. Therefore, several previous reports on sauropod fossils and teeth from the Kem Kem and the 'Continental Intercalaire' of North Africa are here reviewed and summarized.

1. Introduction

The Cenomanian 'Continental Intercalaire' of Morocco (Kem Kem beds), Algeria, Tunisia, Libya, Niger, and Egypt are probably most famous for the presence of theropod dinosaurs such as *Spinosaurus*, *Carcharodontosaurus*, and crocodyliforms; however, historically, also sauropod body fossils (e.g. *Aegyptosaurus, Rebbachisaurus,* Stromer (1932); Lavocat (1954)), are noted. Moreover, in recent decades, several more sauropod remains have been (re)described (e.g. Ibrahim et al., 2014). The carnivorous vertebrate fauna seems to be over-represented, especially in the Kem Kem beds of Morocco (see Läng et al., 2013). Herbivorous fauna, however; is present as well. Studies of sauropod material from this region recognize rebbachisaurids (Lavocat, 1954; Lapparent, 1960; Russell, 1996; Fanti et al., 2013; Mannion and Barrett, 2013; Wilson and Allain, 2015; Holwerda et al., 2018) as well as several titanosauriform remains, and also a possible titanosaurian (Broin et al., 1971; Kellner and Mader, 1997; Mannion and Barrett, 2013; Lamanna and Hasegawa, 2014; Ibrahim et al., 2016). However, most evidence of large dinosaurs, especially sauropods, exists only as isolated fragments and teeth (Holwerda et al., 2018). Isolated elements do contribute to the overall picture of biodiversity, and can even show relative abundance of groups in a given region. Many isolated fragments have been reported ever since Lapparent (1960) and Gorce (1960) wrote a comprehensive study of the Continental Intercalaire. Therefore, this paper focuses on reviewing these sauropod elements in order to give an overview of the sauropod diversity in the region during the Aptian-Albian-Cenomanian.

1.1. Institutional abbreviations

LINHM; Long Island Natural History Museum, Long Island, NY, USA (defunct).

MNN; Musée National du Niger, Niamey, Republic of Niger.

NMC; National Museum of Canada, Ottawa, Ontario, Canada (now CMN; Canadian Museum of Nature).

UT-TEN; University Al Fateh, Tripoli, Libya.

Vb; Institut für Paläontologie, Free University Berlin, Berlin, Germany (now IPFUB).

1.2. Geological setting

This paper uses previous literature on the Kem Kem and 'Continental Intercalaire' sauropod fauna from the Albian-Cenomanian of North Africa.

The Kem Kem beds lie in the south-east of Morocco. They form an escarpment around the eastern end of the Anti-Atlas (Wellnhofer and

* Faculty of Geosciences, Utrecht University, Princetonlaan 8a, Utrecht, 3584 CB, the Netherlands.
E-mail address: f.m.holwerda@uu.nl.

https://doi.org/10.1016/j.jafrearsci.2019.103738
Received 19 February 2019; Received in revised form 27 November 2019; Accepted 12 December 2019
Available online 13 December 2019
1464-343X/

Buffetaut, 1999; Cavin and Forey, 2004) and along the east at the Algerian border, ending in the southeast of Morocco (Ibrahim et al., 2016). The Kem Kem is traditionally considered to be Cenomanian, as it has been found to match ammonites from the Lower Cenomanian of Bahariya, Egypt (Le Loeuff et al., 2012). However, the age probably spans over the Albian–Cenomanian (Underwood and Ward, 2018), which is closer to the age given to the Cretaceous 'Continental Intercalaire' of Algeria (Lefranc and Guiraud, 1990; Le Loeuff et al., 2012; Läng et al., 2013; Benyoucef et al., 2015; Meister et al., 2017) and to the fossil-rich Cretaceous 'Continental Intercalaire' beds of Tunisia (Fanti et al., 2016) as well as to the 'Continental Intercalaire' of Niger (Sereno and Wilson, 2005; Rauhut and López-Arbarello, 2009; Le Loeuff et al., 2012), and Libya (Le Loeuff et al., 2012). The unit named 'Continental Intercalaire', however, as mentioned, consists of several localities spread over the northern margins of the African craton, not all of which are easily dated (Le Loeuff et al., 2012), and is therefore somewhat problematic as a geological term; however, many authors still refer to it as a common name (similar to the Kem Kem being applied to the entire depositional range in southeastern Morocco, whereas the 'true' Kem Kem only applies to one specific area; Underwood and Ward (2018)). While more well-known beds such as the Kem Kem of Morocco and the Bahariya of Egypt can be dated by marine invertebrates and palynomorphs, other deposits not closely linked to the opening of the Central Atlantic Ocean are harder to pinpoint to an exact age (Rauhut and López-Arbarello, 2009; Le Loeuff et al., 2012). However, in the recent decade or so, more and more specific datings have been made, giving an age of (Aptian)-Cenomanian for the Kem Kem (Morocco and Algeria), Wadi Milk Formation (Sudan) and Bahariya (Egypt), a broadly Early Cretaceous age for fossil bearing deposits of Niger (but see Rauhut and López-Arbarello, 2009), Aptian for Tunisia, and Hauterivian-Barremian for the Libyan Cabao Formation (Le Loeuff et al., 2012).

The 'Continental Intercalaire' of Algeria, Tunisia, Libya and Niger is less studied than the Kem Kem beds of Morocco, and most occurrences of herbivores are restricted to isolated remains.

2. Results

2.1. Morocco and Algeria

Several sauropod remains have been described from Morocco. De Lapparent (1960) and Lavocat (1954) already mention sauropod bones from Morocco and Algeria. Russell (1996) described more sauropod bones from around Erfoud and Taouz, Morocco. Amongst these were remains ascribed to *Rebbachisaurus garasbae*, the latter taxon being formally (re)described by Wilson and Allain (2015). The holotype of *Rebbachisaurus* (Lavocat, 1954) contains dorsal and sacral centra and neural arches, as well as a right humerus, scapula and ischium. Associated material consists of a posterior dorsal centrum and a partial neural arch, described by Russell in 1996. Russell also added some isolated teeth to this taxon; however, this has been rejected by Wilson and Allain (2015), since these isolated teeth cannot be safely assigned to *Rebbachisaurus* due to their unclear provenance. Russell (1996) describes these two sets of teeth, one of which (two teeth) are assigned to *Rebbachisaurus*, these being described as being pencil-shaped, lingually curved, and having chisel-shaped, oblique wear facets, something indeed seen in rebbachisaurids such as *Nigersaurus* (Sereno et al., 2007). The other set of teeth described by Russell (1996) as Sauropoda indet., are described as having acutely tapering apices, and lacking oblique wear facets, and showing faint longitudinal grooves. The teeth are not figured in the paper, therefore assignment to any group can only be speculated upon; however, the titanosauriform morphotype of Holwerda et al. (2018), does match this morphological description.

Another tooth described by Kellner and Mader (1997, tooth LINHM 003) shows a similar SI and CI (see Table 1) to the teeth described as non-rebbachisaurid by Russell (1996). This tooth slightly curves to the lingual side, and shows sinusoidal, V-shaped striations at the base (Fig. 1). A similar peculiar enamel wrinkling pattern is seen in two teeth from the Kem Kem beds of Morocco and Algeria, described in Holwerda et al. (2018) as being possibly derived from rebbachisaurids. A brachiosaurid was also reported from Rouis El Djir, Algeria, by Lapparent (1960), and by Taquet (2010); however, this has more recently been found to be Jurassic, and the material belongs to a non-neosauropodan eusauropod, *Chebsaurus* (Läng and Mahammed, 2010; Mahammed et al., 2005). Rebbachisaurids, together with titanosauriforms, have been confirmed from postcranial elements as well by Mannion and Barrett (2013), who assigned a caudal vertebra to Rebbachisauridae, and diagnosed a partial dorsal vertebra as belonging to a somphospondylian titanosauriform. Furthermore, postcranial titanosauriform material from the Kem Kem beds of Morocco, consisting of an anterior dorsal vertebra and a right ischium was described by Lamanna and Hasegawa (2014) Finally, Ibrahim et al. (2016) found evidence for the presence of lithostrotian titanosaurs in Morocco from caudal vertebrae, which differed from the *Aegyptosaurus* caudal figured by Stromer (1932). Furthermore, the caudal vertebra showed characters uniting it to those of lithostrotian South African titanosaurs *Rukwatitan* and *Malawisaurus* (Jacobs et al., 1993; Gorscak et al., 2014), adding to the roster of sauropod presence in the 'Middle' Cretaceous of Morocco, rebbachisaurids, basal titanosauriforms, and more derived titanosauriform sauropods such as somphospondylians, and lithostrotian titanosaurs.

2.2. Tunisia

An isolated sauropod tooth has been described by Bouaziz et al. (1988, tooth unnumbered) from the Aptian Chenini Member of the Aïn el Guettar Formation, Tunisia. This tooth is broken, and is described as being cylindrical, but slightly compressed, and displaying irregular linear striations. The tooth does show a chisel-shape, which could place it within Rebbachisauridae (Fig. 1), which is also alluded to by Russell (1996). Rebbachisaurids are confirmed from Tunisia in recent publications by Fanti et al. (2013, 2015), who described the rebbachisaurid *Tataouinea hannibalis*, which displays extreme vertebral pneumatization. No other sauropod group is confirmed from Tunisia; however, another report by Fanti et al. (2012) showed a different type of isolated sauropod teeth from the Oum ed Diab Member of the Aïn el Guettar Formation, one of which shows a D-shaped cross section (Fig. 1). These teeth are described as having a convex labial and concave lingual surface, and subparallel mesial and distal ridges, which do not expand or taper towards the apex. The teeth show fine longitudinal wrinkling. Fanti et al. (2012) refer these teeth to Rebbachisauridae, however, D-shaped teeth from Morocco and Algeria have been assigned to Titanosauriformes indet. by Holwerda et al. (2018). Moreover, possible neosauropodan, or even titanosauriform, D-shaped teeth are known from the Jurassic of Argentina (Carballido et al., 2017), as well as in titanosaurs (García and Cerda, 2010a; 2010b; Mannion, 2011).

2.3. Libya

Thus far, no postcranial sauropod material has been described from the 'Continental Intercalaire' of Libya. However, Le Loeuff et al. (2010, tooth UT-TEN 15) described a large spatulate isolated sauropod tooth from the Cabao Formation in Northwest Libya (Fig. 1). The tooth is described as being camarasaurid. The tooth shows low SI and CI (Table 1), finely reticulate to sinusoidal wrinkling, prominent lingual and labial grooves, possible pseudodenticles, and a prominent lingual buttress. The first two features are more indicative of a basal non-neosauropodan eusauropod or camarasaurid origin (Holwerda et al., 2015; Wiersma and Sander, 2016; Carballido et al., 2017); however, pseudodenticles and a lingual buttress are found in titanosauriforms, including african titanosauriform taxa *Giraffatitan* and *Malawisaurus* (Janensch, 1935; Gomani, 2005; Bonaparte et al., 2006; Barrett et al., 2016; Mannion et al., 2017; Holwerda et al., 2018). It is still possible,

Table 1
*Slenderness Index and **Compression Index (SI, and CI, *sensu* Díez Díaz et al., 2013; Upchurch, 1998) of isolated teeth elements.

Type	Nr	Max height	Max mesio-distal width	Max labio-lingual width	SI*	CI**	Country	Ref
Nigersaurus	MNN GDF 512	25	4	–	6,3	–	Niger	Sereno et al. (2007)
Nigersaurus	MNN GDF 512	20	3	–	6,7	–	Niger	Sereno et al. (2007)
Titanosauriformes indet.	LINHM 003	53	12	9	4,4	0,75	Morocco	Kellner and Mader (1997)
Rebbachisauridae indet.	Fig 2 J1-J2	25	14	11	1,8	0,7857	Tunisia	Bouaziz et al. (1988)
Rebbachisauridae indet.	Fig 14 N–S	39	11	8	3,5	0,7273	Tunisia	Fanti et al. (2012)
Rebbachisauridae indet.	NMC 41809	41	11	9	3,7	0,8182	Morocco	Russell (1996)
Rebbachisauridae indet.	NMC 41811	48	14	9	3,4	0,6429	Morocco	Russell (1996)
Rebbachisaurus	NMC 41810	35	13	9	2,7	0,6923	Morocco	Russell (1996)
Rebbachisaurus	NMC 41812	35	13	9	2,7	0,6923	Morocco	Russell (1996)
Titanosauria indet.	Vb-721	25,8	10	–	2,6	–	Sudan	Rauhut (1999)
Titanosauria indet.	Vb- 907	22,5	8,3	–	2,7	–	Sudan	Rauhut (1999)
Titanosauria indet.	Vb-901	21,7	7,5	–	2,9	–	Sudan	Rauhut (1999)
Titanosauriformes indet.	UT-TEN 15	74	34	21,5	2,2	0,6324	Libya	Le Loeuff et al. (2010)
Titanosauria indet.	Vb-911	9,2	2,4	–	3,8	–	Sudan	Rauhut (1999)
Titanosauria indet.	Vb-907/1	15,4	3,5	–	4,4	–	Sudan	Rauhut (1999)
Titanosauria indet.	Vb-605	17,2	7,7	5,8	2,2	0,7532	Sudan	Buffetaut et al. (1990)

therefore, that this tooth belongs to a titanosauriform sauropod. However, given the slightly older age (compared to the other 'Continental Intercalaire' deposits described in this paper) of Hauterivian-Barremian, it is also possible the tooth belonged to a more basal non-titanosauriform sauropod such as Camarasauromorpha or even a non-neosauropodan eusauropod.

2.4. Niger

The Early Cretaceous (Barremian-Aptian) Gadoufaoua beds, El Rhaz Formation, from Niger, have yielded the rebbachisaurid *Nigersaurus*, which is known from cranial and postcranial axial material (Taquet, 1976; Sereno et al., 2007; Le Loeuff et al., 2010, 2012; Wilson and

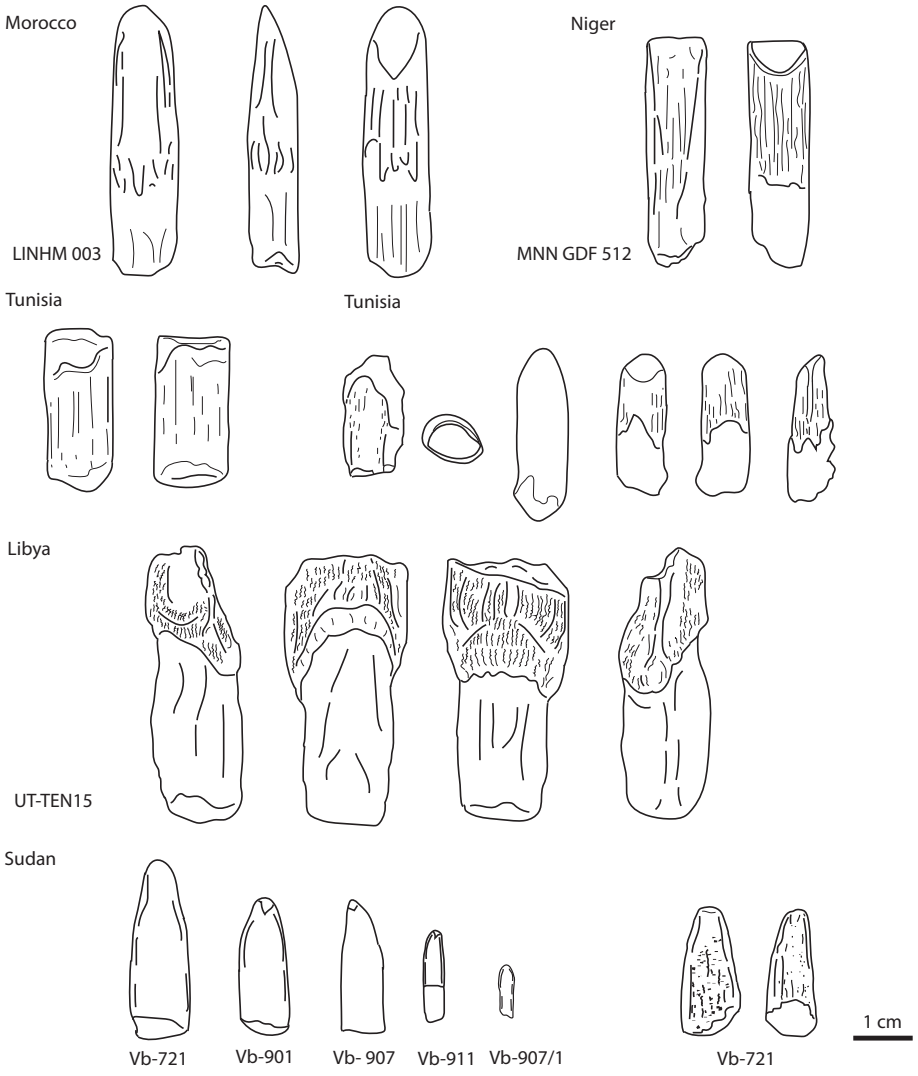

Fig. 1. Line drawings of isolated tooth specimens. Scalebar = 1 cm.

Allain, 2015). The dentition of *Nigersaurus* is characterized by showing no apical tapering (Fig. 1), and showing one high angled and one low angled wear facet (Sereno et al., 2007, MNN GDF 512), a feature seen in other isolated teeth from Morocco and Algeria (Holwerda et al., 2018) and in the aforementioned isolated tooth described by Kellner and Mader (1997). Sereno et al. (2004) also mention undescribed rebbachisaurid and titanosaurian sauropod remains from Niger.

2.5. Sudan

The Aptian-Cenomanian Wadi Milk Formation of Sudan has yielded several postcranial elements, as well as isolated teeth. Rauhut (1999) described an anterior and middle caudal, as well as a distal end of a right tibia and the proximal end of a left fibula, as an indeterminate dicraeosaurid. However, Mannion and Barrett (2013) disputed this claim, and placed the material as a somphospondylan titanosaur. Rauhut (1999) also described a dorsal vertebra, as well as anterior, mid and posterior caudal vertebrae, together with isolated appendicular elements (distal end of fibula, proximal end of a radius, metacarpals), assigning them to Titanosauridae indet., which was later amended by Mannion and Barrett (2013) to also be somphospondylian titanosaurian. Finally, Rauhut described some isolated teeth, both from juvenile and adult titanosaurs, numbered Vb-901, 907, 911, 907/1, and Vb-721. These adult teeth (Fig. 1) indeed resemble the slight pear-shaped teeth from the Kem Kem of Morocco and Algeria, described by Holwerda et al. (2018), which are tentatively placed therein as either non-titanosaurian titanosauriforms or titanosaurs. The slight labial curvature, apical tapering and apical to slightly triangular mesial and distal wear facets are seen in the Tanzanian titanosaurian taxon *Mnyamawamtuka* (Gorscak and O'Connor, 2019). Furthermore, the mostly smooth enamel of the Sudan isolated tooth specimens matches that of the titanosaurians *Huabeisaurus, Alamosaurus* and *Atsinganosaurus* (Kues et al., 1980; D'Emic et al., 2013; Díez Díaz et al., 2013). The presence of apical carinae is similar to that of several teeth from the titanosauriform/titanosaurian morphotype from Holwerda et al. (2018), and to that of *Atsinganosaurus*. A very similar tooth to this type has also been described from Sudan by Buffetaut et al. (1990, tooth Vb-605), see Fig. 1.

The juvenile teeth from this isolated Sudan type are interestingly morphologically similar to the adult teeth; however, there is no information on the expression of enamel wrinkling on these.

2.6. Egypt

The Bahariya Formation of West Egypt corresponds largely to the Cenomanian Kem Kem beds of Morocco (Le Loeuff et al., 2012). Two sauropods from the Bahariya Fm are known thus far; *Aegyptosaurus baharijensis* and *Paralititan stromeri* (Stromer, 1932; Smith et al., 2001). The material of *Aegyptosaurus*, consisting of appendicular and axial elements, was largely destroyed in April 1944 when the palaeontological repository in Munich was bombed. *Paralititan* consists of caudal vertebrae, pectoral girdle and forelimb elements (Smith et al., 2001). Isolated teeth are mentioned, but not figured, for these sauropods.

3. Discussion

3.1. Diversity

The Early Cretaceous 'Continental Intercalaire' of North Africa has so far yielded sauropod remains indicating the presence of rebbachisaurids and several taxa of titanosauriforms, including basal forms, somphospondyloians and lithostrotian titanosaurs (Fig. 2). Moreover, one tooth from Libya hints at either a camarasauromorph or even a basal eusauropodan presence (Le Loeuff et al., 2010). Interestingly, one late surviving diplodocid is known from the Early Cretaceous of Neuquen, Argentina, South America (Gallina et al., 2014). It is possible a similar late surviving non-titanosauriform neosauropod lineage existed in Africa; however, more postcranial material would be needed to confirm this. Besides this one peculiar find, and despite mostly fragmentary sauropod body fossil elements being present, a relatively representative assemblage for the 'Middle' Cretaceous is found.

3.2. Palaeobiogeography

The Moroccan and Libyan rebbachisaurids are shown to be closely affiliated to European taxa, e.g. *Demandasaurus*, and *Histriasaurus* (Torcida Fernández-Baldor et al., 2011) and also to *Nigersaurus* from Niger. Moreover, rebbachisaurids have been found as far north as the UK (Mannion, 2009). It is therefore safe to assume this group displayed a mobility across the carbonate platforms in what is now the Mediterranean (Dalla Vecchia, 2002; Csiki-Sava et al., 2015), see Fig. 2. Moreover, rebbachisaurid remains from Argentina show affinities with the North African sample (Calvo and Salgado, 1995), hinting at an exchange of species before the break-up of the two continents.

Titanosauriform sauropods from Brazil and Argentina have been linked in previous studies to those from North Africa (Kellner et al., 2006; Zaher et al., 2011; França et al., 2016).

Titanosaur remains from Southern Europe (Spain and France) have been linked to those of Morocco and Algeria (Díez Díaz et al., 2012; 2013, 2014). Moreover, titanosaurian remains from Italy have been linked to North Africa (Dal Sasso et al., 2016). Finally, South American titanosaurs have been found to be similar to the North African ones (Bonaparte et al., 2006).

Migratory routes during the 'Middle' Cretaceous between especially Africa and Europe are tentatively and indirectly suggested by the sauropod fauna of North Africa (Pereda Suberbiola et al., 2003; Gheerbrant and Rage, 2006; Upchurch, 2008; Canudo et al., 2009; Torcida Fernández-Baldor et al., 2011; Holwerda et al., 2018; Sallam et al., 2018; Mannion et al., 2019). Migration is further supported by several isolated sauropod elements from North Africa being similar to South African titanosaurs, as well as South African titanosaurs showing a north-south mobility for Early Cretaceous sauropods throughout Middle Gondwana and West Laurasia.

4. Conclusions

All published North African 'Middle' Cretaceous sauropod material is reviewed. The presence of rebbachisaurids, non-titanosaurian titanosauriforms, and titanosaurs in the 'Middle' Cretaceous of North Africa has been confirmed, based on a review of published sauropod material. A possible non-neosauropodan eusauropod or camarasauromorph presence is hinted at. Non-titanosaurian titanosauriform elements are comparable to South American taxa, whilst titanosaurian remains are linked to Southern European taxa. This further supports previously proposed migratory routes and mobility for the rich mid-Cretaceous sauropod assemblage from North Africa.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The author is indebted to reviewers José Ignacio Canudo, Nizar Ibrahim and Verónica Díez Díaz for their insightful corrections and recommendations, which improved this paper. Furthermore, editors Xabier Pereda Suberbiola, Carlos Cónsole and Mohamed Abdelsalam are thanked for providing the opportunity to feature this work in their special volume.

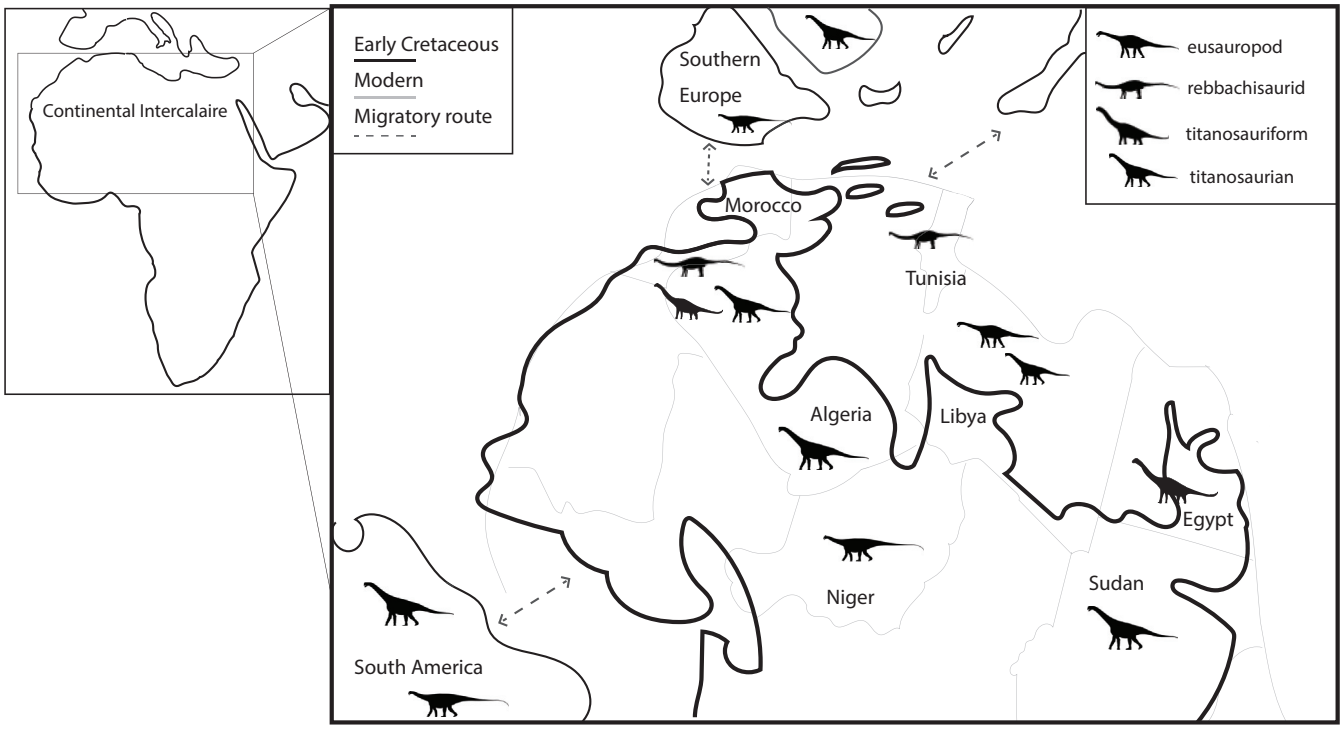

Fig. 2. Geographical distribution map of North African Early Cretaceous sauropods. Map based on Csiki-Sava et al. (2015) and Holwerda et al. (2018).

References

Barrett, P.M., Pouech, J., Mazin, J.-M., Jones, F.M., 2016. Teeth of embryonic or hatchling sauropods from the berriasian (early cretaceous) of cherves-de-cognac, France. Acta Palaeontol. Pol. 61, 591–596. https://doi.org/10.4202/app.00257.2016.

Benyoucef, M., Läng, E., Cavin, L., Mebarki, K., Adaci, M., Bensalah, M., 2015. Overabundance of piscivorous dinosaurs (theropoda: spinosauridae) in the mid-cretaceous of North Africa: the Algerian dilemma. Cretac. Res. 55, 44–55.

Bonaparte, J.F., González Riga, B.J., Apesteguía, S., 2006. *Ligabuesaurus leanzai* gen. et sp. nov. (Dinosauria, Sauropoda), a new titanosaur from the Lohan Cura Formation (Aptian, Lower Cretaceous) of Neuquén, Patagonia, Argentina. Cretac. Res. 27, 364–376.

Bouaziz, S., Buffetaut, E., Ghanmi, M., Jaeger, J.-J., Martin, M., Mazin, J.-M., Tong, H., 1988. Nouvelle decouvertes de vertebres fossiles dans l'Albien du Sud tunisien. Bull. Soc. Geol. Fr. 4, 335–339.

Broin, F., Grenot, C., Vernet, R., 1971. Sur la découverte d'un nouveau gisement de Vertébrés dans le 'Continental Intercalaire' saharien: la Gara Samani (Algérie). Comptes Rendus de l'Académie des Sciences de Paris 272, 1219–1221.

Buffetaut, E., Bussert, R., Brinkmann, W., 1990. A new nonmarine vertebrate fauna in the Upper Cretaceous of northern Sudan. Berliner Geowissenschaftlische Abhandlungen 120, 183–202.

Calvo, J.O., Salgado, L., 1995. *Rebbachisaurus tessonei* sp. nov. a new Sauropoda from the Albian–Cenomanian of Argentina; new evidence on the origin of the Diplodocidae. Gaia 11, 13–33.

Canudo, J.I., Barco, J.L., Pereda-Suberbiola, X., Ruiz-Omeñaca, J.I., Salgado, L., Fernández-Baldor, F.T., Gasulla, J.M., 2009. What Iberian dinosaurs reveal about the bridge said to exist between Gondwana and Laurasia in the Early Cretaceous. Bull. Soc. Geol. Fr. 180, 5–11. https://doi.org/10.2113/gssgfbull.180.1.5.

Carballido, J.L., Holwerda, F.M., Pol, D., Rauhut, O.W., 2017. An early jurassic sauropod tooth from patagonia (cañadón asfalto formation): implications for sauropod diversity. Publicación Electrónica de la Asociación Paleontológica Argentina 17, 50–57.

Cavin, L., Forey, P.L., 2004. New mawsoniid coelacanth (sarcopterygii: actinistia) remains from the cretaceous of the Kem Kem beds, southern Morocco. Mesoz. Fish. 3, 493–506.

Csiki-Sava, Z., Buffetaut, E., Ősi, A., Pereda-Suberbiola, X., Brusatte, S.L., 2015. Island life in the Cretaceous - faunal composition, biogeography, evolution, and extinction of land-living vertebrates on the Late Cretaceous European archipelago. ZooKeys 469https://doi.org/10.3897/zookeys.469.8439. 1–161.

Dal Sasso, C., Pierangelini, G., Famiani, F., Cau, A., Nicosia, U., 2016. First sauropod bones from Italy offer new insights on the radiation of Titanosauria between Africa and Europe. Cretac. Res. 64, 88–109.

Dalla Vecchia, F.M., 2002. Cretaceous dinosaurs in the Adriatic–Dinaric carbonate platform (Italy and Croatia): paleoenvironmental implications and paleogeographical hypotheses. Mem. Soc. Geol. Ital. 57, 89–100.

D'Emic, M.D., Mannion, P.D., Upchurch, P., Benson, R.B.J., Pang, Q., Zhengwu, C., 2013. Osteology of *Huabeisaurus allocotus* (Sauropoda: Titanosauriformes) from the upper cretaceous of China. PLoS One 8, e69375. https://doi.org/10.1371/journal.pone.0069375.

Díez Díaz, V.D., Garcia, G., Knoll, F., Suberbiola, X.P., Valentin, X., 2012. New cranial remains of titanosaurian sauropod dinosaurs from the Late Cretaceous of Fox-Amphoux-Métisson (Var, SE France). PGA (Proc. Geol. Assoc.) 123, 626–637.

Díez Díaz, V.D., Ortega, F., Sanz, J.L., 2014. Titanosaurian teeth from the upper cretaceous of "lo hueco"(cuenca, Spain). Cretac. Res. 51, 285–291.

Díez Díaz, V.D., Tortosa, T., Le Loeuff, J., 2013. Sauropod diversity in the Late Cretaceous of southwestern Europe: the lessons of odontology. In: Annales de Paléontologie. Elsevier, pp. 119–129.

Fanti, F., Cau, A., Cantelli, L., Hassine, M., Auditore, M., 2015. New information on *Tataouinea hannibalis* from the Early Cretaceous of Tunisia and implications for the tempo and mode of rebbachisaurid sauropod evolution. PLoS One 10, e0123475. https://doi.org/10.1371/journal.pone.0123475.

Fanti, F., Cau, A., Hassine, M., Contessi, M., 2013. A new sauropod dinosaur from the Early Cretaceous of Tunisia with extreme avian-like pneumatization. Nat. Commun. 4. https://doi.org/10.1038/ncomms3080.

Fanti, F., Cau, A., Panzarin, L., Cantelli, L., 2016. Evidence of iguanodontian dinosaurs from the lower cretaceous of Tunisia. Cretac. Res. 60, 267–274.

Fanti, F., Contessi, M., Franchi, F., 2012. The "Continental Intercalaire" of southern Tunisia: stratigraphy, paleontology, and paleoecology. J. Afr. Earth Sci. 73, 1–23.

França, M.A., Júlio, C. de A., Riff, D., Hsiou, A.S., Langer, M.C., 2016. New lower jaw and teeth referred to *Maxakalisaurus topai* (Titanosauria: aeolosaurini) and their implications for the phylogeny of titanosaurid sauropods. PeerJ 4, e2054.

Gallina, P.A., Apesteguía, S., Haluza, A., Canale, J.I., 2014. A diplodocid sauropod survivor from the Early Cretaceous of South America. PLoS One 9, e97128. https://doi.org/10.1371/journal.pone.0097128.

García, R.A., Cerda, I.A., 2010a. Dentition and histology in titanosaurian dinosaur embryos from Upper Cretaceous of Patagonia, Argentina. Palaeontology 53, 335–346.

García, R.A., Cerda, I.A., 2010b. Dentición de titanosaurios (Dinosauria, Sauropoda) del Cretácico Superior de la provincia de Río Negro, Argentina: morfología, inserción y reemplazo. Ameghiniana 47, 45–60.

Gheerbrant, E., Rage, J.-C., 2006. Paleobiogeography of Africa: how distinct from Gondwana and Laurasia? Palaeogeogr. Palaeoclimatol. Palaeoecol. 241, 224–246.

Gomani, E.M., 2005. Sauropod dinosaurs from the early cretaceous of Malawi, Africa. Palaeontol. Electron. 8, 27A–37p.

Gorce, F., 1960. Etude de quelques vertébrés du Muschelkalk du Djebel Rehach (Sud-tunisien). Mém. S.G.F. T. 39, 34 Mém 88B.

Gorscak, E., O'Connor, P.M., 2019. A new african titanosaurian sauropod dinosaur from the middle cretaceous galula formation (mtuka member), rukwa rift basin,

southwestern Tanzania. PLoS One 14, e0211412.
Gorscak, E., O'Connor, P.M., Stevens, N.J., Roberts, E.M., 2014. The basal titanosaurian *Rukwatitan bisepultus* (dinosauria, Sauropoda) from the middle cretaceous galula formation, rukwa rift basin, southwestern Tanzania. J. Vertebr. Paleontol. 34, 1133–1154.
Holwerda, F.M., Díaz, V.D., Blanco, A., Montie, R., Reumer, J.W.F., 2018. Late Cretaceous sauropod tooth morphotypes may provide supporting evidence for faunal connections between North Africa and Southern Europe. PeerJ 6, e5925. https://doi.org/10.7717/peerj.5925.
Holwerda, F.M., Pol, D., Rauhut, O.W.M., 2015. Using dental enamel wrinkling to define sauropod tooth morphotypes from the Cañadón Asfalto Formation, Patagonia, Argentina. PLoS One 10, e0118100. https://doi.org/10.1371/journal.pone.0118100.
Ibrahim, N., Dal Sasso, C., Maganuco, S., Fabbri, M., Martill, D.M., Gorscak, E., Lamanna, M., 2016. Evidence of a derived titanosaurian (dinosauria, Sauropoda) in the "Kem Kem beds" of Morocco, with comments on sauropod paleoecology in the cretaceous of Africa. N. M. Mus. Nat. Hist. Sci. Bull. Cretac. Period: Biot. Diver. Biogeogr. 149–159.
Ibrahim, N., Sereno, P.C., Sasso, C.D., Maganuco, S., Fabbri, M., Martill, D.M., Zouhri, S., Myhrvold, N., Iurino, D.A., 2014. Semiaquatic adaptations in a giant predatory dinosaur. Science 345, 1613–1616. https://doi.org/10.1126/science.1258750.
Jacobs, L., Winkler, D.A., Downs, W.R., Gomani, E.M., 1993. New material of an Early Cretaceous titanosaurid saurepod dinosaur from Malawi. Palaeontology 36 523–523.
Janensch, W., 1935. Die Schädel der Sauropoden *Brachiosaurus, Barosaurus* und *Dicraeosaurus* aus den Tendaguruschichten Deutsch-Ostafrikas. Palaeontographica Suppl. 7 145–298.
Kellner, A.W., Mader, B.J., 1997. Archosaur teeth from the cretaceous of Morocco. J. Paleontol. 71, 525–527.
Kellner, A., Campos, D., Azevedo, S., Trotta, M., Henriques, D., Craik, M., Silva, H., 2006. On a new titanosaur sauropod from the bauru group, late cretaceous of Brazil. Boletim do Museu Nacional 74, 1–31.
Kues, B.S., Lehman, T., Rigby, J.K., 1980. The teeth of Alamosaurus sanjuanensis, a Late Cretaceous sauropod. J. Paleontol. 54, 864–869.
Lamanna, M.C., Hasegawa, Y., 2014. New titanosauriform sauropod dinosaur material from the Cenomanian of Morocco: implications for paleoecology and sauropod diversity in the Late Cretaceous of north Africa. Bull. Gunma Mus. Nat. Hist. 18, 1–9.
Läng, E., Boudad, L., Maio, L., Samankassou, E., Tabouelle, J., Tong, H., Cavin, L., 2013. Unbalanced food web in a Late Cretaceous dinosaur assemblage. Palaeogeogr. Palaeoclimatol. Palaeoecol. 381–382, 26–32. https://doi.org/10.1016/j.palaeo.2013.04.011.
Läng, E., Mahammed, F., 2010. New anatomical data and phylogenetic relationships of *Chebsaurus algeriensis* (dinosauria, Sauropoda) from the middle jurassic of Algeria. Hist. Biol. 22, 142–164. https://doi.org/10.1080/08912960903515570.
Lapparent, A.F., 1960. Les dinosauriens du "Continental Intercalaire" du Sahara Central. Mémoire de la Société Géologique de France 39, 1–57.
Lavocat, R., 1954. Reconnaissance géologique dans les Hammadas des confins algéro-marocains du Sud. Notes et Mémoires du Service Géologique du Maroc 116 1–147.
Le Loeuff, J., Läng, E., Cavin, L., Buffetaut, E., 2012. Between tendaguru and Bahariya: on the age of the early cretaceous dinosaur sites from the 'continental Intercalaire' and other african formations. J. Stratigr. 36, e502.
Le Loeuff, J., Métais, E., Dutheil, D.B., Rubino, J.L., Buffetaut, E., Lafont, F., Cavin, L., Moreau, F., Tong, H., Blanpied, C., 2010. An early cretaceous vertebrate assemblage from the Cabao Formation of NW Libya. Geol. Mag. 147, 750–759.
Lefranc, J.P., Guiraud, R., 1990. The 'Continental Intercalaire' of northwestern Sahara and its equivalents in the neighbouring regions. J. Afr. Earth Sci. 10, 27–77.
Mahammed, F., Läng, É., Mami, L., Mekahli, L., Benhamou, M., Bouterfa, B., Kacemi, A., Chérief, S.-A., Chaouati, H., Taquet, P., 2005. The 'giant of ksour', a middle jurassic sauropod dinosaur from Algeria. Comptes Rendus Palevol 4, 707–714.
Mannion, P.D., 2009. A rebbachisaurid sauropod from the lower cretaceous of the isle of wight, england. Cretac. Res. 30, 521–526.
Mannion, P.D., 2011. A reassessment of *Mongolosaurus haplodon* Gilmore, 1933, a titanosaurian sauropod dinosaur from the Early Cretaceous of Inner Mongolia, People's Republic of China. J. Syst. Palaeontol. 9, 355–378. https://doi.org/10.1080/14772019.2010.527379.
Mannion, P.D., Allain, R., Moine, O., 2017. The earliest known titanosauriform sauropod dinosaur and the evolution of Brachiosauridae. PeerJ 5, e3217.
Mannion, P.D., Barrett, P.M., 2013. Additions to the sauropod dinosaur fauna of the Cenomanian (early Late Cretaceous) Kem Kem beds of Morocco: Palaeobiogeographical implications of the mid-Cretaceous African sauropod fossil record. Cretac. Res. 45, 49–59. https://doi.org/10.1016/j.cretres.2013.07.007.
Mannion, P.D., Upchurch, P., Schwarz, D., Wings, O., 2019. Taxonomic affinities of the putative titanosaurs from the Late Jurassic Tendaguru Formation of Tanzania: phylogenetic and biogeographic implications for eusauropod dinosaur evolution. Zool. J. Linn. Soc. 185, 784–909. https://doi.org/10.1093/zoolinnean/zly068.
Meister, C., Piuz, A., Cavin, L., Boudad, L., Bacchia, F., Ettachfini, E.M., Benyoucef, M., 2017. Late Cretaceous (Cenomanian-Turonian) ammonites from southern Morocco and south western Algeria. Arab. J. Geosci. 10, 1.
Pereda Suberbiola, X., Torcida, F., Izquierdo, L.A., Huerta, P., Montero, D., Pérez, G., 2003. First rebbachisaurid dinosaur (Sauropoda, Diplodocoidea) from the early Cretaceous of Spain: paleobiogeographical implications. Bull. Soc. Geol. Fr. 174, 471–479. https://doi.org/10.2113/174.5.471.
Rauhut, O.W., 1999. A dinosaur fauna from the Late Cretaceous (Cenomanian) of northern Sudan. Palaeontologica africana 35, 61–84.
Rauhut, O.W.M., López-Arbarello, A., 2009. Considerations on the age of the tiouaren formation (iullemmeden basin, Niger, Africa): implications for gondwanan mesozoic terrestrial vertebrate faunas. Palaeogeogr. Palaeoclimatol. Palaeoecol. 271, 259–267.
Russell, D.A., 1996. Isolated dinosaur bones from the middle cretaceous of the tafilalt, Morocco. Bull. Mus. Natl. Hist. Nat. 4, 349–402.
Sallam, H.M., Gorscak, E., O'Connor, P.M., El-Dawoudi, I.A., El-Sayed, S., Saber, S., Kora, M.A., Sertich, J.J.W., Seiffert, E.R., Lamanna, M.C., 2018. New Egyptian sauropod reveals late cretaceous dinosaur dispersal between Europe and Africa. Nat. Ecol. Evol. 2, 445–451. https://doi.org/10.1038/s41559-017-0455-5.
Sereno, P.C., Wilson, J.A., 2005. Structure and evolution of a sauropod tooth battery. In: Curry Rogers, K., Wilson, J.A. (Eds.), The Sauropods: Evolution and Paleobiology. University of California Press, Berkeley, CA, pp. 157–177.
Sereno, P.C., Wilson, J.A., Conrad, J.L., 2004. New dinosaurs link southern landmasses in the Mid–Cretaceous. Proc. R. Soc. Lond. B 271, 1325–1330. https://doi.org/10.1098/rspb.2004.2692.
Sereno, P.C., Wilson, J.A., Witmer, L.M., Whitlock, J.A., Maga, A., Ide, O., Rowe, T.A., 2007. Structural extremes in a Cretaceous dinosaur. PLoS One 2, e1230. https://doi.org/10.1371/journal.pone.0001230.
Smith, J.B., Lamanna, M.C., Lacovara, K.J., Dodson, P., Smith, J.R., Poole, J.C., Giegengack, R., Attia, Y., 2001. A giant sauropod dinosaur from an Upper Cretaceous mangrove deposit in Egypt. Science 292, 1704–1706.
Stromer, E., 1932. Ergebnisse der Forschungsreisen prof. E. Stromers in den wüsten agyptens. II. Wirbeltier-reste der Baharıje-stufe (unterstes cenoman). 11. Sauropoda. Abhandlungen der Bayerischen akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Abteilung 10.
Taquet, P., 1976. Géologie et paléontologie du gisement de Gadoufoua (Aptien du Niger). Cahiers de Paléontologie. Centre National de la Recherche Scientifique (CNRS, Paris.
Torcida Fernández-Baldor, F., Canudo, J.I., Huerta, P., Montero, D., Pereda Suberbiola, X., 2011. *Demandasaurus darwini*, a new rebbachisaurid sauropod from the early cretaceous of the iberian peninsula. Acta Palaeontol. Pol. 56, 535–552. https://doi.org/10.4202/app.2010.0003.
Underwood, C.J., Ward, D.J., 2018. Site-specific limitations on the use of palaeontological resources. Geol. Curator 10, 617–631.
Upchurch, P., 1998. The phylogenetic relationships of sauropod dinosaurs. Zool. J. Linn. Soc. 124, 43–103.
Upchurch, P., 2008. Gondwanan break-up: legacies of a lost world? Trends Ecol. Evol. 23, 229–236.
Wellnhofer, P., Buffetaut, E., 1999. Pterosaur remains from the cretaceous of Morocco. Paläontol. Z. 73, 133–142. https://doi.org/10.1007/BF02987987.
Wiersma, K., Sander, P.M., 2016. The Dentition of a Well-Preserved Specimen of *Camarasaurus* sp.: Implications for Function, Tooth Replacement, Soft Part Reconstruction, and Food Intakepp. 1–17. https://doi.org/10.1007/s12542-016-0332-6.
Wilson, J.A., Allain, R., 2015. Osteology of Rebbachisaurus garasbae Lavocat, 1954, a diplodocoid (dinosauria, Sauropoda) from the early late cretaceous–aged Kem Kem beds of southeastern Morocco. J. Vertebr. Paleontol. 35, e1000701.
Zaher, H., Pol, D., Carvalho, A.B., Nascimento, P.M., Riccomini, C., Larson, P., Juarez-Valieri, R., Pires-Domingues, R., da Silva, N.J., de Almeida, C.D., 2011. A complete skull of an Early Cretaceous sauropod and the evolution of advanced titanosaurians. PLoS One 6, e16663.