Crocodilian Nest in a Late Cretaceous Sauropod Hatchery from the Type Lameta Ghat Locality, Jabalpur, India

Rahul Srivastava1, Rajeev Patnaik2, U. K. Shukla3, Ashok Sahni2

1 361/II, Tikait Rai LDA Colony, Lucknow-226017, India, 2 Centre of Advanced Study in Geology, Panjab University, Chandigarh-160014, India, 3 Department of Geology, Banaras Hindu University, Varanasi-221006, India

Abstract

The well-known Late Cretaceous Lameta Ghat locality (Jabalpur, India) provides a window of opportunity to study a large stable, near shore sandy beach, which was widely used by sauropod dinosaurs as a hatchery. In this paper, we revisit the eggs and eggshell fragments previously assigned to lizards from this locality and reassign them to crocodylomorphs. Several features point to a crocodilian affinity, including a subspherical to ellipsoidal shape, smooth, uneven external surface, discrete trapezoid shaped shell units with wide top and narrow base, basal knobs and wedge shaped crystallites showing typical inverted triangular extinction under crossed nicols. The crocodylomorph eggshell material presented in this paper adds to the skeletal data of these most probably Cretaceous-Eocene dryosaurid crocodiles.

Introduction

The Late Cretaceous Lameta Formation of India is widespread and contains a great wealth of sauropod dinosaur egg nests. From this predominantly sauropod dinosaur hatchery, we report for the first time a crocodile egg nest. In a global context, the fossilized crocodile nests are very rare (around 20 reported till date) and our find implies that this sauropod hatchery of Lameta Formation was also occupied by other large reptiles like crocodiles also for laying eggs. This paper is a sequel to an earlier one wherein a purported lizard nest was described from the Maastrichtian Type Lameta Ghat section, near Jabalpur. Additional work now shows that attribution of the eggshells to a large lizard was incorrect. Instead, examination of ultrastructure of the eggshell indicates the nest belongs to a crocodile. The identification of eggs as those of a lizard in last communication, was primarily based on the size of these eggs and their amorphous (non-crystalline) structure as seen in radial and cross sections. However, more analysis and comparison with the recent and fossil crocodilian eggshells reveals that the eggshells belong to crocodylomorphs. These crocodiles most probably belong to a Cretaceous-Eocene group of dryosaurid crocodiles that were dominant in South Asia during that time range and survived the K-Pg boundary.
In the previous paper [2], an error was made while making the measurements. The size of the eggs that was given in the previous paper was apparent and we did not consider the tangential erosion and sectioning of the outcrop. Another error in identification was that we chose a highly silicified portion of an eggshell for our thin section study. Based on the revised comparisons, we conclude here that the eggshell belongs to crocodylomorphs, closest to that described from Crocodylia [3, 4]. The dominant crocodiles in the drifting Indian Plate in the Cretaceous and early Paleogene were the mesoeucrocodiles [5–11], therefore there is a possibility that the nest belongs to this group. However there is no direct physical evidence for this.

In a spatial context, the crocodylomorph nest lies within the range from where sauropod nests have been reported before [12] and herein (Fig 1A). The concentric layered arrangement of these sauropod eggshells (Fig 1C and 1D) and their shell microstructure confirms that the eggshells belong to those of Megaloolithus jabulpurensis [13].

In spite of the concerted efforts of several group of workers, the palaeo-depositional environments of the Lameta in the Type area of Jabalpur and in the surrounding outcrops, has been a matter of debate [2, 12–18]. Shukla and Srivastava [2] proposed the presence of an alkaline lagoon at the Lameta Ghat locality while others have argued for the calcareous limestone to be pedogenic in origin. Fossils found within the limestone have consistently shown a freshwater character [17, 19–22]. The only estuarine element recorded is the ray Igdabatis [23]. It is more than possible that during the deposition of the Lameta, the shoreline was at any one point of time not far away from the coastal fluvial complex that the sedimentation suggests. Keller et al. [24] have demonstrated the presence of a Trans Deccan Seaway traversing peninsular India during the Late Cretaceous—early Paleogene during the eruption of the Deccan volcanic.

Material and Methods

Shukla and Srivastava [2] recovered a well-preserved nest with nine partial and two complete eggs from Lameta Ghat, (Fig 2). This eggshell material (catalogue no. LU/RS-01/9) described by Shukla and Srivastava as lizard eggshell [2] is catalogued in the Department of Geology, Lucknow University, Lucknow, India. Eggshells from their collection (VPL/CCE 3–5) were radially sectioned and polished and viewed under the light microscope Leica S8 APO and Leica SM 2500. These were then photographed under the crossed nicols using petrographic microscope Olympus CX31. The polished sections were then etched using 5% formic acid for 5 seconds and viewed under the scanning electron microscope (JEOL 6940). Eggshell (VPL/CCE- 1 & 2) outer, inner and freshly broken radial surfaces were also viewed under the SEM. The electron microscope and light microscope material used in this study is catalogued in the CAS in Geology, Panjab University Chandigarh, India.

Both the Universities (Panjab University and Lucknow University) have long and established museum repositories with full access of materials to all scientists and can be visited freely without permit at any time. There is a curator and staff dedicated to repository section.

Description

The eggs in the nest are in general sub spherical to ellipsoidal in shape with their size being ~ 68 x 44 mm (elongation index 1.54) (Figs 2 and 3). The thickness of the eggshell ranges between 0.43–0.47 mm [2]. The external surface is uneven (somewhat undulating) and smooth (does not show corrosion or contain nodes or tubercles) (Fig 4A) but the inner surface shows packing of basal knobs and pore canal openings (Fig 4B). The discrete shell units are trapezoidal in shape, the top is wider and the base becomes gradually narrower and bears the basal knobs (Figs 4D, 5A–5C and 6). These discrete units are attached to each other laterally and are
marked by straight pore canals that pass through the entire shell (Fig 5B and 5E). Under the crossed nicols inverted triangular extinction wedges are distinct (Figs 5A and 5B and 7B). Irregular extinction pattern, criss-cross calcite cleavages disrupting horizontal accretion patterns at places indicate recrystallization of the eggshells. The space between the basal knobs is less compared to those seen in extant crocodiles, for example in *Caiman latirostris*, *Gavialis gangeticus* and *Crocodylus porosus* [4, 1]. The innermost layer is characterized by radiating wedges originating at the basal knobs (Fig 5C & 5E). The horizontal accretion (growth) lines or the laminated tabular structure typical of crocodylomorph eggshell [4, 25, 26, 27] is visible throughout the shell thickness (Fig 5A). The middle and the outer portions of the eggshells show blocky texture with both discontinuous oblique and tabular cleavage pattern (Fig 5D). However, the three distinct layers found in extant crocodile eggshells are not observed in these eggshells.

Fig 1. Showing the study area, location of crocodile, dinosaur egg nests and a polished eggshell section. A. The study area (inset) and the location of crocodile (red star) and sauropod (red dots) nesting sites at Lameta Ghat (modified from Google Earth). B. Location of crocodile and dinosaur eggs, northern bank of Narmada River. C. Dinosaur nest of *Megaloolithus jabulpurensis* found in association with the crocodile nest at Lameta Ghat. D. Polished radial sections of *Megaloolithus* eggshell fragments in concentric arrangement (VPL/CCE - 5C).
Comparisons

The present eggshells are clearly distinct from those of the lizards in lacking the characteristic numerous, slender densely packed columnar shell units [28, 26, 29] (Fig 6). Bird eggshells would differ from the present eggshells in having the typical three layered (mammillary, prismatic and external) structure [28, 30]. Eggshell of turtles are distinct from the present eggshells in having the cylindrical shell units spherulite with spherical base made up of aragonite crystalites [28, 30]. Dinosaurs on the other hand have spheroliths as the shell-forming unit. Sauropod dinosaurs in particular show sweeping extinction pattern under crossed nics [28].

Compared to the present eggs and eggshells those of the dinosaur *Megaloolithus jabulpurensis* eggs are circular to sub-circular, much larger (~ 14 cm in diameter, Fig 1C) and thicker (~1.5 mm, Fig 7C), have a tuberculated external surface, an inner surface with mammillae showing resorption craters (Fig 8D), fan-shaped spheroliths showing arcuate accretion lines, radiating fracture patterns and sweeping extinction pattern under crossed nics (Fig 7C) [13]. Fossilized crocodilian eggshells from Pliocene sediments of Siwaliks [31] are very similar to the present material in having a smooth outer surface, prominent basal knobs, trapezoid shell units, horizontal accretion lines, and blocky extinction pattern under crossed nics (Fig 7A).
The egg size (~68 x ~44 mm), elongation index (IE) (~1.54) and thickness (~0.5 mm) fall closest to the size (66 x 46 mm and 60 x 40.9 mm), IE (1.43 and 1.54) of modern alligatorid Caiman latirostris [4, 1, 32]. Egg size, EI and shell thickness of modern gavialid Gavialis gangeticus is around 82 x 56 mm; 1.46; .30-.59 mm respectively and that of crocodylid Crocodylus porosus is ~77 x 52 mm; 1.48; .53 mm, respectively [3]. Caiman latirostris eggshells surface is corroded, whereas that of Crocodylus porosus is smooth with stepped concentric ring structure on the rim of the pore openings [4]. The outer surface of Gavialis gangeticus is generally smooth with funnel-like pores [4, 25]. Unlike the present eggshells all these extant crocodiles show wide interbasal knob space/cavity that reaches almost half the width of the eggshell [3]. Among the fossil crocodiles described so far the present eggs come closest in size and elongation index (size = 68 x 44 mm; EI = 1.55) to those from the Eocene Bridger Formation, USA reported by Hirsch and Kohring [33, 1]. However, the Eocene eggshells are thicker (0.75 mm) than the present eggshells. The fossil crocodilian eggshells reported from Late Cretaceous intertrappean beds, Bombay [34], differ from the present eggshells in being thinner (~.35 mm) showing distinct

Fig 3. A schematic diagram showing position of eggs in the nest. Incomplete eggs shown by dotted lines.

doi:10.1371/journal.pone.0144369.g003
mammillary layer and with diverging micro crystallites. The Pliocene Siwalik crocodile eggshells [31] are thinner, have smooth outer surface, discrete wedges, mammillary layer or inner layer with diverging crystallites and distinct continuous tabular accretion lines (Fig 7B). Another crocodilian egg from the Siwaliks of Pakistan [3] differs from the present egg and eggshells in being larger in size (84 x 64 x 54 mm) and having an ornamented outer surface.

### Discussion

The microstructure of fossil and extant crocodilian eggshells has long been debated. Ferguson [35] found five separate layers in the *Alligator mississippiensis* eggshell. However, Hirsch [25] considered the presence of a single calcified layer in fossil crocodiles, but found the basal plate groups, the mammillary layer of Ferguson [35] and the wedge-like crystals as separate entities. Hirsch [25] followed by Mikhailov [28, 26] consider the crocodyloid morphotype as single-
layered eggshell with ‘rough’ shell units. Kohring and Hirsch [36] following this approach established the Krokolithidae oofamily, which has been used by other authors [3, 37, 38]. However, recent studies [39, 40, 1] on both fossil and recent crocodiles have shown that crocodilian eggshell is composed of several structural layers attesting to the observation of Ferguson [35]. A typical feature of crocodilian eggshell thin section under crossed nicols is the presence of blocky extinction with an upside down triangular shape [1].

Fig 5. Crocodylomorph eggshell sections under petrographic and scanning electron microscopes. A. Crocodylomorph eggshell (VPL/CCE 3) section under crossed nicols showing floating quartz grain in calcareous matrix and horizontal accretion lines and the typical crocodilian inverted triangle extinction pattern. B. One portion of the eggshell (VPL/CCE 4) cut tangentially to show overlapping trapezoid shell units and irregular blocky extinction. C. Scanning Electron Micrograph of polished and etched eggshell section showing basal knob (BK) and smooth but uneven outer surface. D. The outer part of the same section enlarged showing herringbone pattern. E. Inner layer showing wedges diverging outwards from the basal knobs (BK) and the pore canal (PC).

doi:10.1371/journal.pone.0144369.g005
Crocodylomorphs are characterized by the presence of ellipsoidal or elongated eggs, mostly ornamented egg surface with circular, step-like concentric erosion pore openings [1]. The subspherical to ellipsoidal shape and size (~68 x 44 mm) of the present eggs fall within the range of those of the extant and extinct crocodylomorphs. More importantly, the present eggshells show discrete wedge-like shell units, the typical crocodylomorph blocky inverted triangle extinctions and non-branching pore canals. Though, the present egg shells do not show the three layers of extant crocodiles, the horizontal tabular accretion feature characteristic of all the crocodylomorphs is present.

The identity of the producer of fossil eggs is best corroborated by finds of embryos within the eggs or by associated hatchlings. Such is not the case here and therefore there is no physical evidence to assign the crocodilian nest to a specific crocodylomorph group. However, crocodile elements mainly isolated teeth and vertebrae including a few fragmentary jaws are known from several sedimentary horizons associated with the Deccan Volcanics. In such a case it is necessary to evaluate the possible identity of the producer by an analysis of the crocodiles that inhabited the Indian Plate during the Late Cretaceous. There is only one taxon, *Pabweshi pakistanensis*, from the Late Cretaceous Pab Sandstone of Pakistan, that has been definitely assigned to the Mesoeucrocodilia [5]. The authors suggest that the Pakistani genus is a baurusuchid related closely to forms earlier described from Brazil and Argentina. Stratigraphically the Pab Sandstone represents a marginal facies of the Indian Plate suggesting a delta complex with basinwards, shelf and slope deposits. The Pab Sandstone is sourced from sediments derived from the Deccan Volcanics and coeval rocks. From a phylogeny point of view, Buscalioni et al [41] presented a global distribution of Late Cretaceous crocodylomorphs, but he could not place the isolated fragmentary crocodylomorph data from the Late Cretaceous of India in his distribution map, primarily because the data is represented mainly by the isolated teeth [11, 42, 43]. The mesoeucrocodilians found on the Indian Plate (Pakistan and Indian localities) may be of intermediate nature and indicate close affinities with those found in Madagascar, South America [44, 45, 46] and Africa [47, 48, 49, 50].

The depositional palaeoenvironments of the dinosaur nest-bearing Lameta facies have been discussed at length by several workers [12, 14–16] including the specific locality mentioned in this paper [2, 24]. There is a general consensus that the nest-bearing levels are pedogenic in nature. In the present instance, the find of a crocodilian nest along with the nests of large sauropod dinosaurs specifically suggests a more nearshore, lagoonal facies within a stable sandy beach depositional setup [2]. In this environment as well, pedogenesis occurs suggesting stability of the supratidal deposits and provides some clues to the egg-laying behavior of titanosaurid
This further adds to our knowledge of hatchery strategies of early crocodylomorphs belonging most probably to the South Asian dryosaurids, that go on to survive the Cretaceous-Pg extinction event.

Conclusions

Crocodile eggshells have been reported from several localities throughout the world and are well known from India as well from the K/Pg transition beds of the Mumbai Intertrappeans to Siwalik occurrences [3, 34, 31]. There are excellent studies of the shell ultrastructure of several taxa of modern crocodiles including the Caiman, Alligator and the more common Crocodylus. Additional work on the Lameta crocodile nest confirms that it does not belong to the varanoid lizards as previously indicated. Detailed ultrastructure of the eggshell and the tabular crystal structure of the mammillae, the thickness and radial structure suggest crocodilian affinities. Presence of ellipsoidal eggs, trapezoid shaped wedge like discrete shell units with blocky
extinction pattern places the present eggs and eggshells in Crocodylomorpha. The dominant crocodilian in the Cretaceous and early Paleogene of India belong to the mesoeucrocodiles, family Dryosauridae.

Buscalioni et al. [41] in a fairly comprehensive review have tried to trace the evolutionary phylogeny of the crocodylomorphs spatially as well as temporally. Relevant here is the fact that they consider the crocodylomorphs to be monophyletic. The basal group comprises the mesoeucrocrodilians which are well represented in the Indian plate even though the absence of skulls and other distinguishing elements, make it difficult at this stage to precisely designate the taxa involved or their affinities because of the isolated material. With a few exceptions, e.g. Pabwehsli from the Late Cretaceous Pab Sandstone of Pakistan [5], the Indian material consists either of isolated teeth [42,43] or of isolated vertebrae [11]. Lower jaws have also been described from Dindori, but these are fragmentary and cannot be assigned to a specific taxon [5]. Crocodilian teeth found at Naskal are distinctly serrated and suggest affinities to the basal Ziphosuchia.

**Acknowledgments**

One of us (UKS) is thankful to Dr. Omnath Saha for his help and assistance in field. We would like to thank the reviewers for their valuable suggestions in improving the manuscript.
Author Contributions
Conceived and designed the experiments: RS RP UKS AS. Performed the experiments: RS RP UKS AS. Analyzed the data: RS RP UKS AS. Contributed reagents/materials/analysis tools: RS RP UKS AS. Wrote the paper: RP AS RS UKS. Took thin sections and SEM photographs: RP.

References
1. Marzola M, Joa’o R, Octa’vio M. Identification and comparison of modern and fossil crocodilian eggs and eggshell structures. Hist. Biol. 2015; 27 (1): 115–133.
2. Shukla UK, Srivastava R, Lizard eggs from Upper Cretaceous Lameta Formation of Jabalpur, central India, with interpretation of depositional environments of the nest-bearing horizon. Cret Res. 2008; 29: 674–686.
3. Panade’s I Blas X, Patnaik R. A complete crocodylian egg from the Upper Miocene (Chinji Beds) of Pakistan and its palaeobiographical implications. PalArch’s J Vertebr Paleontol. 2009; 6(1): 1–8.
4. Schleich HH, Kaestle W. Reptile Eggshells: SEM Atlas. Gust Fisch Verl. 1988.
5. Wilson JA, Malkani MS, Gingerich PD. New crocodyliiform (Reptilia: Mesoecrocodylia) from the Upper Cretaceous Pab Formation of Vitakri, Balochistan (Pakistan). Contr Mus of Paleont. The Univ of Michigan. 2001; 30: 321–336.
6. Khosla A, Joseph JW, Sertich JJW, Prasad GVR Verma O. Dyrosaurid Remains from the Intertrappean Beds of India and the Late Cretaceous Distribution of Dyrosauridae. J Verteb Paleontol. 2009; 29(4): 1321–1326.
7. Storrs GW. A dyrosaurid crocodile (Crocodylia: Mesosuchia) from the Paleocene of Pakistan. Postil. 1986; 197: 1–16.
8. Buffetaut É. Données nouvelles sur les crocodiéliens paléognés du Pakistan et de Birmanie. Compt Rendu de l’Acadé des Sci de Paris. 1977; 285: 869–872.
9. Buffetaut É. Crocoddilian remains from the Eocene of Pakistan. Neu Jahr für Geol und Paläont Abhand.1978; 156: 262–283.
10. Buffetaut É. A dyrosaurid (Crocodylia, Mesosuchia) from the Upper Eocene of Burma. Neu Jahr für Geol und Paläont Monatshe.1978b; 5: 273–281.
11. Rana RS. Dyrosaurid crocodile (Mesosuchia) from the infratrappean beds of Vikarabad, Hyderabad District, Andhra-Pradesh. Curr Sci.1987; 56: 532–534.
12. Sahni A, Tandon SK, Jolly A, Bajpai S, Sood A, Srinivasan S. Upper Cretaceous dinosaur eggs and nesting sites from the Deccan volcano-sedimentary province of peninsular India. In: Carpenter K, Hirsch K, Homer J., editors. Dinosaur Eggs and Babies, Cambridge University Press, New York; 1994. pp 204–226.
13. Fernández MS, Khosla A. Parataxonomic review of the Upper Cretaceous dinosaur eggshells belonging to the oofamily Megaloolithidae from India and Argentina. Historical Biology: An Inter Jour of Paleobo. 2015; 27 (2): 158–180.
14. Brookfield ME, Sahni A. Palaeoenvironments of the Lameta Beds, Late Cretaceous at Jabalpur, Madhya Pradesh, India: soil and biotas of a semi-arid alluvial plain. Cret Res. 1987; 8: 1–14.
15. Tandon SK, Sood A, Andrews JE, Dennis PF. Palaeoenvironment of Dinosaur-bearing Lameta Beds (Maastrichtian), Narmada valley, Central India. Palaeogeo Palaeoclimat Palaeoecol. 1995; 117: 153–184.
16. Tandon SK, Andrews JE. Lithofacies association and stable isotopes of palustrine and calcareous carbonates: example from an Indian Maastrichtian regolith. Sedimentol. 2001; 48: 339–355.
17. Khosia SC, Rathore AS, Nagori ML, Jakhar SR. Non-Marine Ostracoda from the Lameta Formation (Maastrichtian) of Jabalpur (Madhya Pradesh) and Nand-Dongargaon Basin (Maharashtra), India: Their correlation, age and taxonomy. Revist Español de Micropaleontol. 2011; 43 (3): 209–260.
18. Saha O, Shukla UK, Rani R. Trace Fossils from the Late Cretaceous Lameta Formation, Jabalpur Area, Madhya Pradesh: Paleoenvironmental Implications, J. Geol. Soc. Ind. 2010; 76: 607–620.
19. Khosia A. Upper Cretaceous (Maastrichtian) charophyte gyrogonites from the Lameta Formation of Jabalpur, Central India: palaeobiogeographic and palaeoecological implications. Act Geol Poloni. 2014; 64 (3): 311–323.
20. Khosia A, Sahni A. Biodiversity during the Deccan volcanic eruptive episode. J Asian Earth Sci. 2003; 21: 895–908.
21. Mohabey DM. Depositional environments of Lameta Formation (Late Cretaceous) of Nand-Dongargaon Inland Basin, Maharashtra: the fossil and lithological evidences. Mem Geol Soc Ind. 1996; 37: 363–386.

22. Mohabey DM, Samant B. Lacustrine facies association of a Maastrichtian lake (Lameta Formation) from Deccan volcanic terrain central India: implications to depositional history, sediment cyclicity and climates. Gond Geol Mag. 2005; 8: 37–52.

23. Courtillot V, Besse J, Vandamme D, Montigny R, Jaeger JJ, Cappetta H. Deccan flood basalts at the Cretaceous/Tertiary boundary? Earth Planet Sci. Lett. 1986; 80: 361–374.

24. Keller G, Adatte T, Bajpai S, Mohabey DM, Widdowson M, Khosla A, et al., K–T transition in Deccan Traps of central India marks major marine Seaway across India. Earth and Planet Sci Lett. 2009; 282: 10–23

25. Hirsch KF. Fossil crocodylian eggs from the Eocene of Colorado.—J Palaeont. 1985; 59: 531–542.

26. Mikhailov KE. Fossil and recent eggshell in amniotic vertebrates; fine structure, comparative morphology and classification. Spec Pap Palaeontol. 1997; 56:80.

27. Jackson FD, Varricchio DJ. Fossil eggs and eggshell from the Lowermost Two Medicine formation of western Montana, Sevenmile Hill locality. J Vertebr Paleontol. 2010; 30: 1142–1156.

28. Mikhailov KE. Classification of fossil eggshells of Amniotic vertebrates. Acta Palaeontol Pol. 1991; 36: 193–238.

29. Hirsch KF. Parataxonomic classification of fossil chelonian and gecko eggs. J Vertebr Paleontol. 1996; 16(4): 752–762.

30. Mikhailov KE, Bray ES, Hirsch KF. Parataxonomy of fossil egg remains (Veterovata): basic principles and applications. J Vertebr Paleontol, 1996; 16(4): 763–769

31. Patnaik R, Schleich HH. Fossil crocodile from the Upper Siwaliks of India. Mitteilungen der Bayerisch Staatsam fur Palaeont und Hist Geol.1993; 33: 91–117.

32. Fernández MS, Simoncini MS, Dyke G. Irregularly calcified eggs and eggshells of Caiman latirostris (Alligatoridae: Crocodylia). Naturwissenschaften. 2013; 100: 451–457. doi: 10.1007/s00114-013- 1044-3 PMID: 23604383

33. Hirsch KF, Kohring R. Crocodylian eggs from the middle Eocene Bridger Formation. Wyoming. J Vertebr Paleontol: 1992; 12: 59–65.

34. Singh SD, Sahni A, Gaffney ES, Schleich HH. Reptilia from the Intertrappean Beds of Bombay (India). Vero” ff Fuhlrott-Mus. 1998; 4: 307–320.

35. Ferguson MWJ. The structure and composition of the eggshell and embryonic membranes of Alligator mississippiensis. Trans Zool Soc Lond.1982; 36: 99–152.

36. Kohring R, Hirsch KF. Crocodylian and avian eggshells from the Middle Eocene of the Geiseltal, Eastern Germany. J Vertebr Paleontol. 1996; 16: 67–80.

37. Garcia G. Diversite des coquilles ‘Mince’ d’oeufs fossiles du Cretace superieur du Sud de la France. Geobios 2000; 33: 114–126.

38. Grellet-Tinner G, Makovich P. A possible egg of the dromaeosaur Deinonychus antirrhopus: phylogenetic and biological implications. Can J Earth Sci. 2006; 43: 705–719.

39. Jin X, Jackson FD, Varricchio DJ, Azuma Y, He T. The first Dictyoolithus egg clutches from the Lishui Basin, Zhejiang Province, China. J Vertebr Paleontol. 2010; 30: 188–196.

40. Moreno-Azanza M, Bauluz B, Canudo JI, Pue´rto-Mus. Pascual E, Selle’s AG. A re-evaluation of aff. Megaloolithidae eggshell fragments from the uppermost Cretaceous of the Pyrenees and implications for crocodylomorph eggshell structure. Hist Biol. 2013; 26(2): 195–205.

41. Buscalioni AD, P´erez- Moreno BP Sanz Jos´e Luis. Pattern of biotic replacement in modern crocodiles during the Late Cretaceous Colquios de Paleontologia. 2003; 1: 77–93.

42. Prasad GVR, Lapparent F. Late Cretaceous crocodile remains from Naskal (India): comparisons and biogeographic affinities. Annales de Paléontologie 2002; 88: 19–71.

43. Rana RS, Sati KK. Late Cretaceous-Palaeocene crocodiles remains from Naskal (India): comparisons and biogeographic affinities. Annales de Paléontologie 2002; 88: 19–71.

44. Barbosa JA, Kellner AWA, Viana MRS. New dyrosaurid crocodylomorph and evidences for faunal turnover at the K-P transition in Brazil. Proc Royal Soc B. 2008; 275: 1385–1391.

45. Schwarz D, Frey E, Martin T. The postcranial skeleton of the Hyposaurinae (Dyrosauridae; Crocodyliformes). J Palaeontol. 2006; 49: 695–718.

46. Hastings A, Bloch J. New short-snouted dyrosaurid (crocodylomorph) from the Paleocene of northern Colombia. J Vertebr Paleontol. 2007; 27(3, Supplement): 87A–88A.
47. Brochu CA, Bouaré ML, Sissoko F, Roberts EM, O'Leary MA. A dyrosaurid crocodyliform braincase from Mali. J Paleont. 2002; 76: 1060–1071.

48. Jouve S, Bouya B, Amaghzaz M. A short-snouted dyrosaurid (Crocodyliformes, Mesoeucrocodylia) from the Palaeocene of Morocco. J Palaeont. 2005; 48: 359–369.

49. Jouve S, Iarochene M, Bouya B, Amaghzaz M. A new species of Dyrosaurus (Crocodylomorpha, Dyrosauridae) from the early Eocene of Morocco: phylogenetic implications. Zoological J Linnean Soc. 2006; 148: 603–656.

50. Jouve S, Bouya B, Amaghzaz M. A long-snouted dyrosaurid (Crocodyliformes, Mesoeucrocodylia) from the Paleocene of Morocco: phylogenetic and paleobiogeographic implications. J Palaeont. 2008; 51: 281–294.