CROCODYLIAN SCATOLOGY – A LOOK INTO MORPHOLOGY, INTERNAL ARCHITECTURE, INTER- AND INTRASPECIFIC VARIATION AND PREY REMAINS IN EXTANT CROCODYLIAN FECES

JESPER MILÀN[1,2]

[1] GeomuseumFaxe/Østsjællands Museum, Østervej 2, DK-4640 Faxe, Denmark, e-mail: jesperm@oesm.dk;
[2] Department of Geography and Geology, University of Copenhagen, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark

Abstract—Seventeen specimens of fresh scats from 10 species of extant crocodylians from CrocodileZoo in Denmark are compared with regard to morphology, internal architecture, inter- and intraspecific variation and undigested prey remains. Crocodylian feces are typically cylindrical to tapering with rounded terminations, and longitudinal striations in the surface were observed in one specimen. They often have one or two bends of 120-150°. Internally, they consist of concentric layers of darker clay-like material and a lighter mass containing undigested prey remains. The prey remains (piglets, rats and chickens) comprise relatively well-preserved hair, and partly dissolved feathers with only the rachis left. Even when sieved to a mesh size of 0.122 mm, no remains of bones could be found. Scats from a gharial with a strictly piscivorous diet contained no remains of bones or scales. The diameter of the feces correlates well with the total body length of the animal. This enables a reasonable estimate of the producers' size from fossil coprolites. The intraspecific variation in morphology within crocodylian feces reflects the full spectrum of observed interspecific variations, making it impossible to distinguish scats of different species from each other.

INTRODUCTION

Coprolites are important paleobiological indicators that can provide important information about predator/prey interactions, and the diets of extinct animals in reconstructions of ancient ecosystems (e.g., Thulborn, 1991; Hunt et al. 1994; Northwood, 2005; Souto 2008; Eriksson et al., in press). However, the most challenging task when dealing with coprolites is to identify the exact producer of the coprolites, as feces from many animals can be very similar in appearance, and large variations can occur within the morphology of feces among a single group of animals, according to different diets, and mode of egestion (e.g., McAllister, 1985; Chin, 2002; Chame, 2003). This study describes the morphology of fresh fecal specimens from 10 species of crocodylians, with regard to external and internal morphology, and with regard to inter- and intraspecific variation. The study attempts to identify characters typical of crocodylian feces and also examines the amount and type of undigested prey remains in the feces.

MATERIALAND METHODS

Seventeen specimens of fresh feces from six species of extant crocodiles (*Osteolaemus tetraspis*, *Crocodylus cataphractus*, *C. moreletii*, *C. siamensis*, *C. mindorensis* and *C. rhombifer*) three alligatorids (*Paleosuchus palpebrosus*, *P. trigonatus* and *Melanosuchus niger*) and the gharial (*Gavialis gangeticus*) were collected at the facility of KrokodilleZoo, Denmark (Fig. 1). Each specimen was externally examined by measuring length and diameter (Table 1), and by recording distinct surface features. As the diet of the animals was well-documented, a number of the specimens were examined for undigested food remains by disaggregating and screen washing feces (mesh size of 0.122 mm). Regression analysis compared the length and diameter of the scat vs. the total length of the producer.

SPECIMENS

Paleosuchus palpebrosus, Dwarf Caiman

This specimen is from an adult animal with a total length of 140 cm. The animal had been fed a diet of rats and chickens. The scat specimen measures 10.6 cm in length, and has a greatest diameter of 3.4 cm at the middle where it bends 150°. Toward the ends the diameter decreases to 2.4 cm (Fig. 2A). The surface is covered by a smooth, light, clay-like layer, and where this layer is missing, internal contents of hair and feather rachis can be seen (Fig. 2B). In transverse section through the middle, the specimen shows several concentric, different colored layers, some of which contain hair, while others are homogeneous and clay-like (Fig. 2C).

Paleosuchus trigonatus, Smooth-fronted Caiman

This specimen is from a subadult animal with a total length of 100 cm, which was fed a diet of rats and chickens. The scat specimen is 10.5 cm long, generally circular in circumference, and with a largest diameter of 2.5 cm. Several constriction marks can be seen along its surface, and one end pinches off abruptly (Fig. 1P). Prey remains in the form of hair are visible in the surface layers.

Melanosuchus niger, Black Caiman

Originating from an adult animal with a total length of 220 cm, this scat specimen is 11.5 cm long with a greatest diameter of 2.7 cm. The animal was fed a diet of rats, chickens and piglets. The surface of the specimens is highly irregular, with several constriction marks along its length. The specimen is increasingly curved toward one end, terminating in an almost 90° bend. Hairs are abundant in the surface of the scat (Fig. 1O).

Osteolaemus tetraspis, Dwarf Crocodile

This specimen is produced by an adult dwarf crocodile (*Ostelaemus tetraspis*), with a total length of 160 cm, which was fed a diet composed of rats, chickens and fish. The scat specimen is 12.8 cm long, cylindrical, 3.8 cm in diameter, with rounded terminations. The outer surface is covered by a hard, smooth, clay-like crust. The specimens show bi-directional bending, one end bending at a 145° angle and the other end at 150° (Fig. 2D). A transverse section through the specimen shows the feces to be composed of concentric layers (Fig. 2E). The different layers contain different prey remains; the outer layers contain abundant undigested hair, while the inner layer contains feather rachis (Fig. 2F). The specimen was disaggregated and screen washed down to a mesh-size of

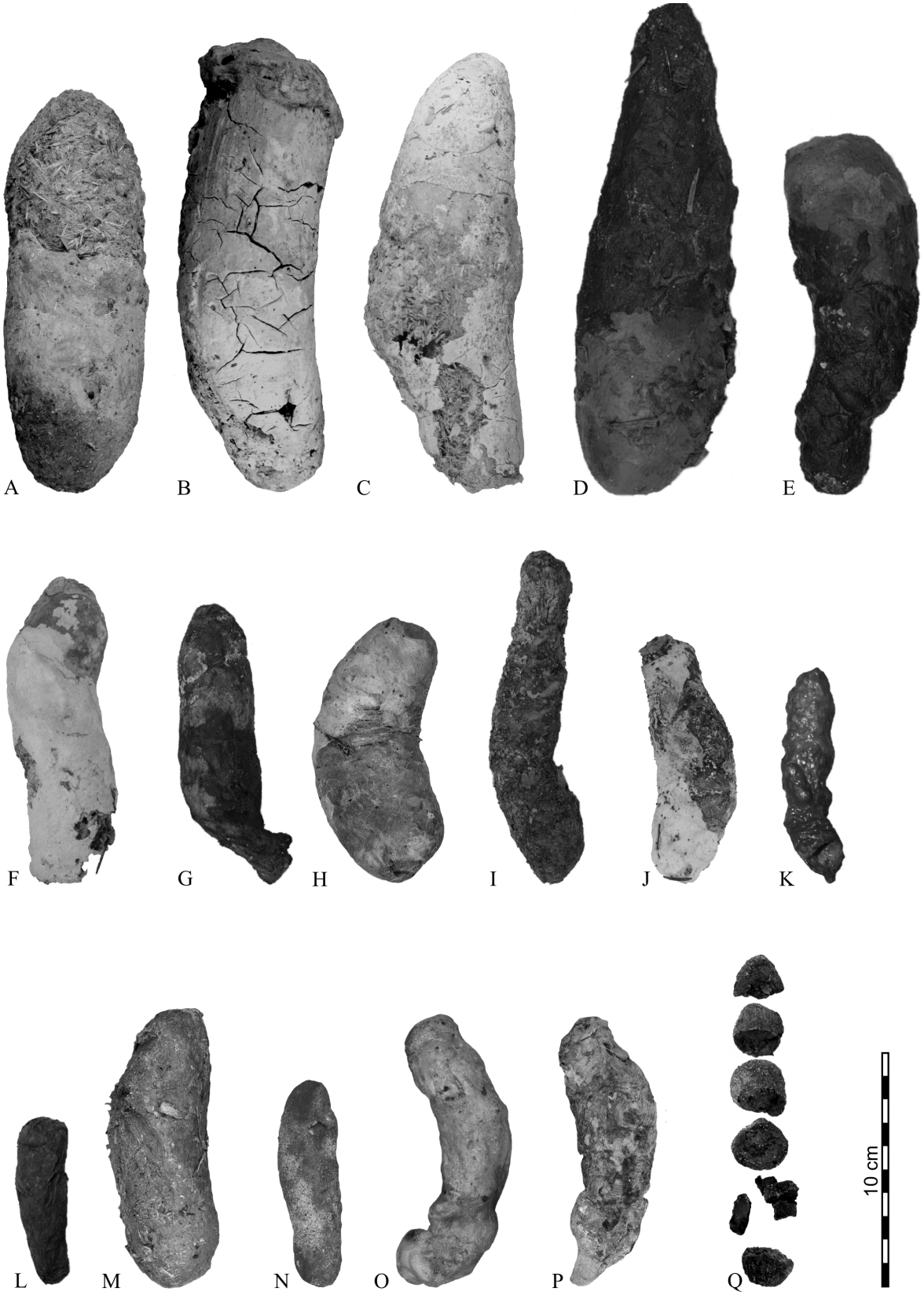


FIGURE 1. The 17 examined specimens of crocodylian scat reproduced to the same scale. **A-E**, Slender-snouted crocodile (*Crocodylus cataphractus*). **F-H**, Dwarf crocodile (*Osteolemus tetraspis*). **I**, Morelet's crocodile (*Crocodylus moreletii*). **J**, Dwarf caiman (*Paleosuchus palpebrosus*). **K**, Siamese crocodile (*Crocodylus siamensis*). **L**, Philippine crocodile (*Crocodylus mindorensis*). **M-N**, Cuban crocodile (*Crocodylus rhombifer*). **O**, Black caiman (*Melanosuchus niger*). **P**, Smooth-fronted caiman (*Paleosuchus trigonatus*). **Q**, Gharial (*Gavialis gangeticus*). Notice the bending in several of the specimens, and the different types of terminations. The intraspecific variation is pronounced in the specimen from *C. cataphractus* (**A-E**) and *O. tetraspis* (**F-H**).

TABLE 1. Measurements of length and diameter of the scats, and the total lengths of the animals that made them.

	Total body length/cm	Feces length/cm	Feces diameter/cm
Paleosuchus palpebrosus	140	10.6	3.4
Paleosuchus trigonatus	100	10.5	2.5
Melanosuchus niger	220	11.5	2.7
Osteolaemus tetraspis 1	160	12.8	3.8
Osteolaemus tetraspis 2	160	12	3.5
Osteolaemus tetraspis 3	150	10.1	3.5
Gavialis gangeticus	225	8	2.4
Crocodylus cataphractus 1	450	19.4	6
Crocodylus cataphractus 2	450	20.5	7
Crocodylus cataphractus 3	450	18.5	7.5
Crocodylus cataphractus 4	450	21	8
Crocodylus cataphractus 5	450	14	5.6
Crocodylus moreleti	120	13	3
Crocodylus siamensis	140	9	3
Crocodylus mindorensis	98	7	2.3
Crocodylus rhombifer 1	120	8.4	1.8
Crocodylus rhombifer 2	250	11.3	3.9

0.122 mm, but no skeletal remains could be detected. A second specimen from the same animal, previously described by Milàn and Hedegaard (2010), is a thick, smooth-sided, cylindrical specimen 12 cm in length, with a greatest diameter of 3.5 cm. One end of the specimen is rounded, and the other end thins abruptly to about 1.5 cm in diameter at a 130° bend (Fig. 1G). A third specimen is from an adult animal with a total body length of 150 cm. The specimen is 10.1 cm long, curved, slightly tapering and with a largest diameter of 3.5 cm. Each end terminates in a small concavity, and small constriction marks are present on its surface (Fig. 1H).

Gavialis gangeticus, Gharial

The gharials are a subadult male and female with total lengths of 240 and 215 cm. They are fed exclusively on a diet of diverse fresh-water fish, 20-40 cm in length. Within their enclosure the gharials tend to defecate in the water, making it very difficult to discover and obtain any fecal mass. However, one specimen was discovered and retrieved in time before it broke apart in the water (Fig. 3). The specimen broke in several pieces during handling, but the estimated total length is 8 cm and the diameter is 2.4 cm. It is cylindrical in cross section, and when broken apart splits into short concavo-convex units. The fecal mass appears totally homogenous, almost clay-like. After external examination, the specimen was disaggregated in water and screen washed to a grid size of 0.122 mm. Even in this fraction, no skeletal remains could be identified.

Crocodylus cataphractus, Slender-Snouted Crocodile

A total of five specimens from a slender-snouted crocodile were investigated. The specimens came from an enclosure with two adults, a male and a female, both with an approximate total length of 4.5 meters and an estimated body mass of 200 kg. They are fed a diet consisting of piglets, fish and chickens. The first scat specimen is 19.4 cm long, with an average greatest diameter of 6 cm. It is slightly bent into a banana shape. One end is rounded, whereas the other is flattened and expanded from contact with the floor in the enclosure (Fig. 4A). The surface is smooth, with a pattern of approximately 1 mm thick polygonal desiccation cracks. Longitudinal striations are present in parts of the surface along the middle of the specimen. The striations are preserved in epirelief, and are less than 0.5 mm in height, and on average 1 mm wide, and separated by an average spacing of 3 mm (Fig. 4B).

A second specimen is 20.5 cm long with an average diameter of 7 cm. It is straight, with symmetrical rounded terminations (Fig. 4C). The surface is covered by a smooth layer, but where this layer is broken off, the interior shows abundant prey remains in the form of intermingled hair and feather rachis (Fig. 4D). A transverse section through the middle of both specimens showed a concentric zonation of darker and lighter areas. The dark areas had an almost claylike substance without any prey remains; while the coarser gray layers had abundant hairs and feathers. A third specimen is 18.5 cm long with a greatest diameter of 7.5 cm (Fig. 4E). The specimen shows its greatest diameter about 2/3 of its length from this end, expanding evenly from its narrower end to its greatest diameter. From its greatest diameter the specimen bends 135°, and thins abruptly toward its rounded opposite termination. Feather rachis is recognizable in several areas of the surface, where the smooth outer layer is cracked. In longitudinal section, the internal layering is clearly visible. The area to the right on Figure 4F consists of a hard, dark colored, clay-like mass, with few hairs present. This wraps around a lighter part, consisting of intermingled hairs and feather rachis, with little ground mass present.

Two specimens previously illustrated by Milàn and Hedegaard (2010) show quite different shapes. The first is a large, elongated drop-like specimen, measuring 21 cm in length and up to 8 cm in diameter, and is circular in circumference (Fig. 1D). The second specimen measures 14 cm in length. Although broader at one end, this form is more cylindrical in shape, without the drop-like terminations. This scat has two characteristic bends, each of approximately 145° (Fig. 1E).

Crocodylus moreletii, Morelets Crocodile

One scat specimen from a subadult Morelet's crocodile (*Crocodylus moreletii*), with a total length of 120 cm, measures 13 cm in length, and is cylindrical with its diameter slightly increasing from 2 to 3 cm towards one droplike terminal end. The specimen has a 142° bend in the thickest part (Fig. 1I). The animal had been fed on a diet comprising rats, chickens and fish.

Crocodylus siamensis, Siamese Crocodile

This scat specimen is from a subadult with a total body length of 140 cm. It is 9 cm long with a uniform diameter of about 2 cm. Several constriction marks are present along the surface. The specimen has a 138° bend towards one of its ends. One end of the specimen is droplike, and the other end terminates in a concavity (Fig. 1K). The animal had been fed a diet of chickens and fish.

Crocodylus mindorensis, Phillippine Crocodile

The small specimen is from a subadult animal with a total length of 98 cm. The specimen is 7 cm in length, and cylindrical to cone shaped, tapering towards one end. The terminations of the specimens are abrupt and slightly rounded (Fig. 1L). The animal had been fed on a diet of chickens.

Crocodylus rhombifer, Cuban Crocodile

The last specimens come from a subadult and an adult Cuban crocodile; both fed a diet of fish, chickens and piglets. The adult animal has a total length of 250 cm; its scat is 11.3 cm long, cylindrical, with one rounded termination and one tapering end. Abundant hair is visible on the surface. The greatest diameter is 3.9 cm (Fig. 1M). The subadult individual has a total length of 120 cm, and its scat is 8.4 cm long, cylindrical, and with rounded terminations. No prey remains are visible on the surface (Fig. 1N).

DISCUSSION

External Morphology

Crocodylian scats have a varied morphology, but are generally

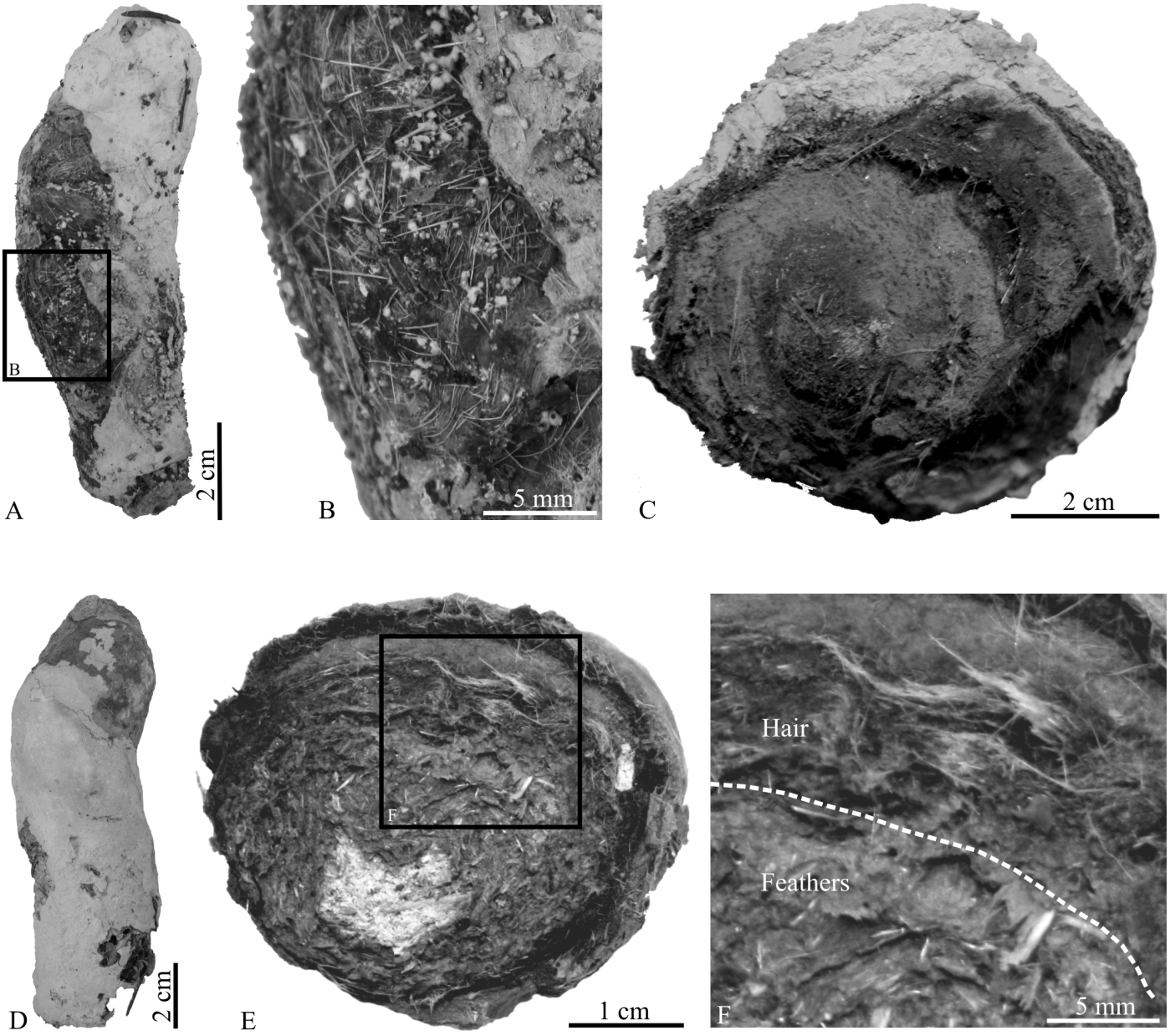


FIGURE 2. **A**, Scat from an adult dwarf caiman, *Paleosuchus palpebrosus*. **B**, Enlarged section of the portion of the specimen bracketed in panel A, showing abundant hair from the prey animal. **C**, Cross-section through the greatest diameter of the scat. Notice the internal layering in dark dense layers and lighter layers with prey remains. **D**, Scat from an adult dwarf crocodile, *Osteolamus tetraspis*. Notice the bi-directional bending of the specimen. **E**, In cross section the specimen is seen to contain different prey remains in different layers. **F**, Enlarged section of **E**, showing an inner layer with feather remains and an outer layer containing hairs.

FIGURE 3. Scat from a gharial, *Gavialis gangesticus*. The specimen broke into several concavo-convex units during examination.

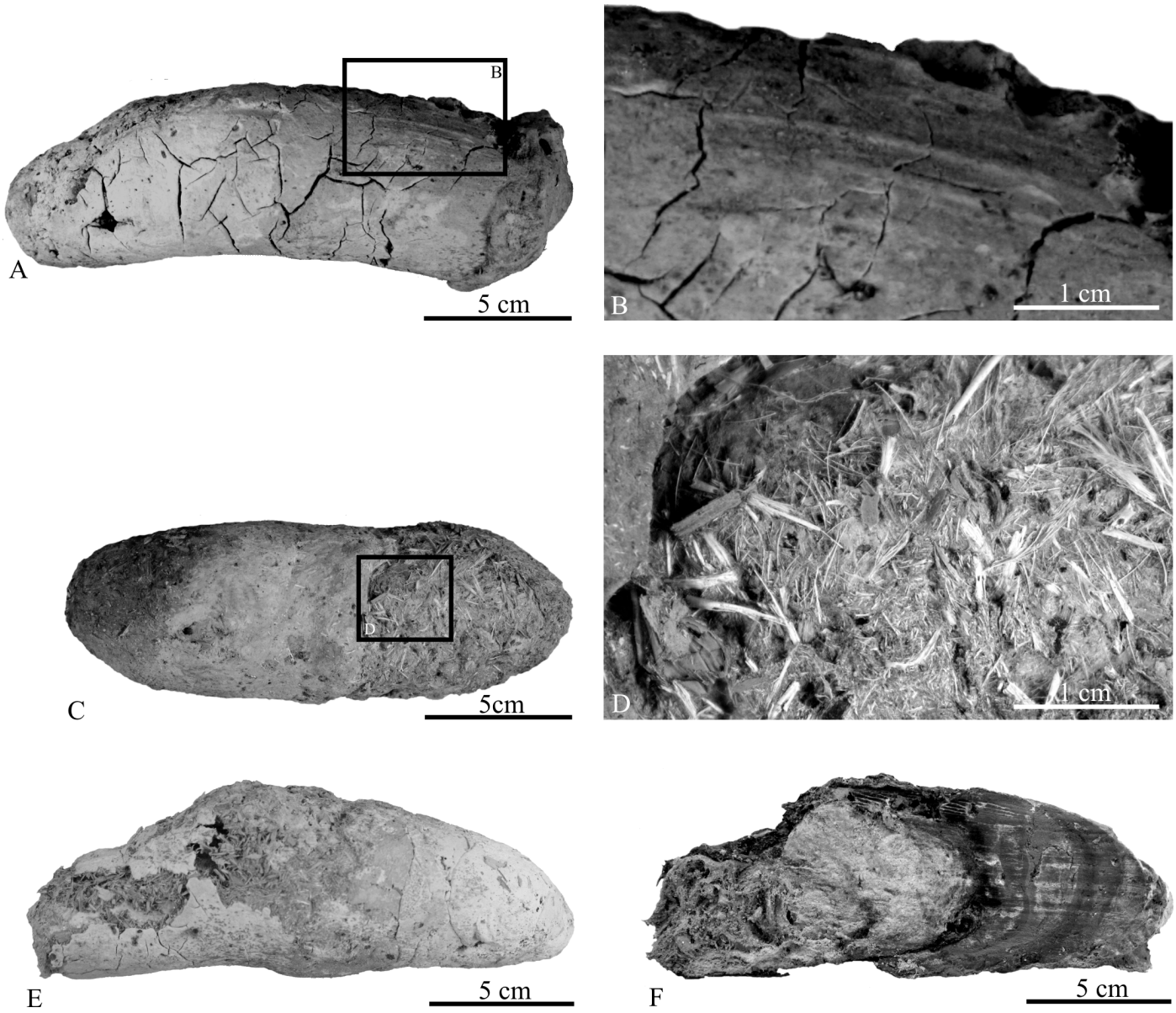


FIGURE 4. Scat from adult slender-snouted crocodile, *Crocodylus cataphractus*. **A**, The surface is smooth, with areas of polygonal desiccation cracks and longitudinal striations. **B**, Close up of the part of the scat bracketed in panel A, showing longitudinal striations. The striations are preserved in epirelief, and are on average 1 mm wide, less than 0.5 mm in height, and separated by a spacing of 3 mm. **C**, Ellipsoid scat from adult slender-snouted crocodile, *C. cataphractus*. The surface is rough, and where the surface layer is broken off, abundant feather rachis can be seen. **D**, Close up of the part of the scat bracketed in panel C, showing the tightly packed, partly digested feather rachis, intermixed with the fecal groundmass. **E**, Irregularly-shaped scat from adult slender-snouted crocodile, *C. cataphractus*. **F**, In longitudinal section, the internal structure is that of a central (lighter) rounded mass, with several darker concavo-convex units accreted against it.

elongate, cylindrical to tapering in shape, and with rounded terminations. They often show a uni- or bi-directional bending of 130-150°. Both the uni- and bi-directional bending are observed in fossil crocodylian coprolites from the Cretaceous of Brazil (Souto, 2010), where two of the illustrated coprolites show a bend of 125° and 145°, respectively, and one specimen (Souto, 2010, Fig. 1A) shows bidirectional bending of 150°. Two-hundred-and-five Paleocene crocodylian coprolites from the Wannagan Creek Quarry (Sawyer, 1981) show a wide range of morphologies, ranging from dome to cylindrical and teardrop-shaped, with several specimens bent or even slightly coiled in appearance.

The scats from the specimens in this study were all collected from dry surfaces within the animals' enclosures, except for the gharial scats, which were retrieved from their pond. The bending of the specimens could thus be related to the vertical distance between the cloacae and the ground during defecation, with the specimens bending when they came into contact with the ground before being fully egested, a topic for further exploration.

The prominent longitudinal striations present in one of the *C. cataphractus* feces (Fig. 4) are a feature that has been associated with scat and coprolites from archosauromorphs (Young, 1964; Sawyer, 1981; Rodriguez-de la Rosa et al., 1998; Northwood, 2005; Milàn, 2010; Souto, 2008, 2010). Indeed, the striations observed in the scat from *C. cataphractus* are very similar to those observed in Early Triassic coprolites from Australia (Northwood, 2005), Cretaceous coprolites from Brazil (Souto 2008, 2010), and coprolites from the Danian of Denmark (Milàn, 2010). That they only appear in one of the studied specimens could be related to the consistency of the feces at the time of excretion.

Intra- and Interspecific Variation

The five specimens collected from the slender-snouted crocodile, *C. cataphractus* (Fig. 1A-E), were collected from an enclosure with an adult male and female, each around 4.5 meters in total length. A common trait for all five specimens is the convex rounded shape of scat terminations, but apart from that, the shape varies from almost ellipsoid (Fig. 1A), through uniformly cylindrical (Fig. 1B), to more drop-like (Fig. 1D), to more irregular and bent (Fig. 1C,E). Scat length varies from 14-20.5 cm, and the diameter from 5.6-8 cm. The surface texture ranges from smooth with longitudinal striations (Figs. 1B, 4,) to more rough and irregular (Fig. 1E). Comparing the external morphology of *C. cataphractus* scats with those of the scats of the other species, the diversity in external appearances among scats from *C. cataphractus* does not distinguish it from the morphologies observed in scats from other species. Cylindrical shape with constant diameter is found in the scats from *C. cataphractus*, *O. tetraspis* and *G. gangesticus*, and tapering to drop-like shapes is found in *C. cataphractus*, *C. moreletii*, and *C. mindorensis*. Irregularly bent specimens are observed in *C. cataphractus* and *P. palpebrosus*, and sharp bends accompanied by a concave ending are seen in scats from *O. tetraspis* and *C. mindorensis*. The three specimens of scat from *O. tetraspis* (Fig. 1F-H) all show different morphologies: cylindrical, with irregular bends, to straight, cylindrical forms terminating in sharp bends, and pinched-off concave terminations, to curved shapes with tapering circumferences. Based on the available material it is not possible to distinguish scats from different crocodylian species based on the external morphology of their scats, because intraspecific variation is comparable to the interspecific variation.

Internal Morphology

When viewed in cross section, scats are seen to be composed of concentric layers of alternating lighter and darker material. The dark layers are very dense and almost clay-like in appearance, while the lighter layers are less dense, containing undigested prey remains, when present (Fig. 2). This internal layering is common in many types of feces and is not restricted to crocodylians, and indicates the original pattern of deposition from the intestine walls. Furthermore, it can commonly be recognized in fossil coprolites, either by studying them in polished cross sections or by CT-scanning (Farlow et al., 2010; Milàn et al, this volume). In longitudinal sections, the layering can be seen to originate from a rounded mass at one end, and then to be gradually accreted in concave-convexs units (Fig. 4F). The concave termination seen in the scats from *C. siamensis* and *O. tetraspis* (Fig .1), and crocodylian coprolites from the Cretaceous of Brazil (Souto, 2008, 2010) and the Lower Paleocene of Denmark (Milàn, 2010), is interpreted as the result of muscular contraction, dividing the fecal mass along the internal layering.

Prey Remains

The diets of the captive crocodylians in this study are well-documented, so it was possible to search for specific prey remains in the specimens. After the fecal masses were disaggregated, they were closely examined for any prey remains. Hair was relatively well-preserved and easily recognizable in all the examined specimens from animals that had been fed hairy mammals.

Late Neogene coprolites from the Pipe Creek Sinkhole of Indiana show internal, elongated, thin voids, which are interpreted as molds of hairs. This shows that hairs have the potential to be recognized in coprolites (Farlow et al., 2010). The feather remains from the crocodilian scat were partly digested so that only the rachis was left, and no remains of bones were found in any of the examined specimens. This lack of bone tissue is typical for crocodylians, because they have a very effective digestive system, with a hydrochloric acid concentration that exceeds mammalian carnivores by a factor of 50 (Coulson et al., 1989). This decalcifies and dissolves all bone tissue completely before excretion (Fischer, 1981; Coulson et al., 1989; Trutnau and Sommerlad, 2006). The gharial scats examined in this study were from animals with a strictly piscivorous diet of fresh-water fishes of relatively large size (20-40 cm), with large and hard scale; nevertheless, no remains of either bones or scales could be detected. This shows that a lack of skeletal remains is an important character when interpreting fossil coprolites as crocodylian, as many coprolites, which look superficially crocodylian-like, contain visible bone pieces (see Milàn et al., this volume).

Relation Between Total Length and Diameter and Length of Scat

The length and diameter of the scat are inequally related to the body size of the producer. When the lengths of the studied specimens are plotted against the total lengths of their producers, the result shows only a very loose correlation (Fig. 5). This can also be seen from the five specimens from *C. cataphractus*, which range in length from 14-20.5 cm. From the regression analysis, the length of the scat (LS) relates to the total length of the producer (TL) with LS = 0.03(TL) + 4.88, with a Pearson correlation coefficient of 0.861. Farlow et al. (2010) noted that the diameter of scat is a more reliable indicator of scat-maker size than its length, because feces tend to be pinched off during egestion. When the diameters of the specimens studied here are plotted against the total length of the animals, the diameters of the scat (DS) relate to the total length (TL) with the function DS = 0.012(TL) + 1.10, with a Pearson correlation coefficient of 0.915. Based on the graphs, the diameter of the scat shows a tight fit, and is in fact good enough to enable a reasonable estimate of the body length of the producer. This is very useful when coprolites are included in paleoecological studies, as they then can provide quick estimates of the body sizes of the crocodylians.

CONCLUSION

Crocodylian feces are typically elongate, cylindrical to tapering, and can have one or two bends of 120-150°. The surface texture varies from rough to smooth, with occasional longitudinal striations. Their internal structure is composed of concentric, lighter and darker layers, with the dark layers almost clay-like in structure and the lighter layers containing undigested prey remains. Hair and partly dissolved feather

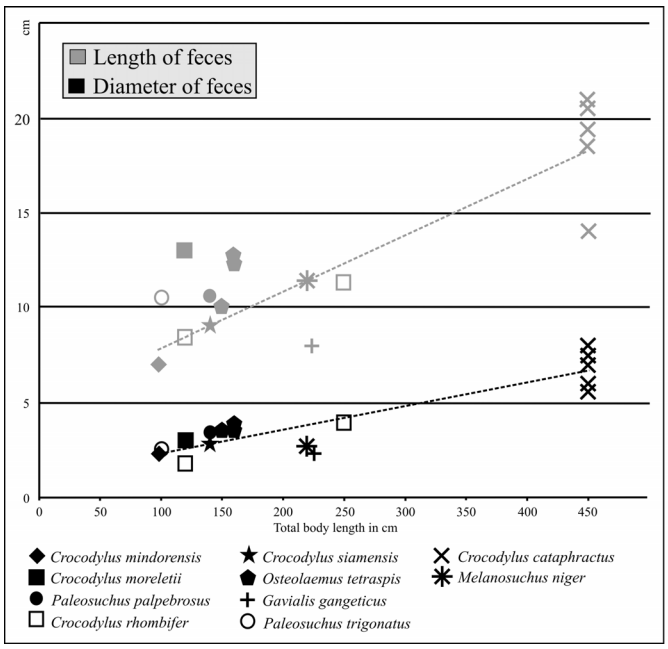


FIGURE 5. The length and diameter of the feces plotted against the total length of the producers. Scat length of the feces (gray symbols) does not give a very good correlation, while scat diameter (black symbols) gives a good correlation, enabling reasonable estimates of the total length of the producer from fresh scat or fossil coprolites.

rachis were found in the studied specimens, but there were no traces of skeletal material. The gharials, *Gavialis gangeticus*, which had been fed on a strictly piscivorous diet, had the most homogeneous scats, consisting of only clay-like masses without any traces of scales or bones. The intraspecific variation in morphology among crocodylian feces reflects the full range of observed interspecific variations, making it impossible to distinguish scats of different species from each other. The diameter of the feces is seen to correlate well with the total length of the animal. This enables a reasonable estimate of the producers' size from feces and fossil coprolites.

ACKNOWLEDGMENTS

This research is supported by the Danish Natural Science Research Council. I am grateful to Rene Hedegaard and all the staff at the Danish CrocodileZoo, especially Viktor Vest who helped to collect and secure the specimens from within the animal's enclosures. James O. Farlow kindly provided good advice and comments on an early version of the manuscript, and David R. Schwimmer and Paulo R. F. Souto provided constructive reviews of the manuscript.

REFERENCES

Chame, M., 2003, Terrestrial mammal feces: A morphometric summary and description: Memoirs Instituto Oswaldo Cruz, Rio de Janeiro, v. 98 (Supplement I), p. 71-94.

Chin, K., 2002, Analyses of coprolites produced by carnivorous vertebrates: Paleontological Society Papers, v. 8, p. 43-50.

Coulson, R.A., Herbert, J.D. and Coulson, T.D., 1989, Biochemistry and physiology of alligator metabolism in vivo: American Zoologist, v. 29, p. 921-934.

Eriksson, M.E., Lindgren, J., Chin, K. and Månsby, U., in press, Coprolite morphotypes from the Upper Cretaceous of Sweden: Novel views on an ancient ecosystem and its implications for coprolite taphonomy: Lethaia.

Farlow, J.O., Chin, K., Argast, A. and Poppy, S., 2010, Coprolites from the Pipe Creek sinkhole (late Neogene, Grant County, Indiana, U.S.A.): Journal of Vertebrate Paleontology, v. 30, p. 959-969.

Fisher, D.F., 1981, Crocodilian scatology, microvertebrate concentrations, and enamel-less teeth: Paleobiology, v. 7, p. 262-275.

Hunt, A.P., Chin, K. and Lockley, M.G., 1994, The paleobiology of vertebrate coprolites; *in* Donovan, S., ed., The Palaeobiology of Trace Fossils: John Wiley and Sons, London, p. 221-240.

McAllister, J.A., 1985, Reevaluation of the formation of spiral coprolites: University of Kansas, Paleontological Contributions, v. 144, p. 1-12.

Milàn, J., 2010, Coprolites from the Danian limestone (Lower Paleocene) of Faxe Quarry, Denmark: New Mexico Museum of Natural History and Science, Bulletin 51, p. 215-218.

Milàn, J. and Hedegaard, R., 2010, Interspecific variations in tracks and trackways of extant crocodiles: New Mexico Museum of Natural History and Science, Bulletin 51, p. 15-29.

Milàn, J., Rasmussen, B.W. and Lynnerup, N., 2012, A coprolite in the MDCT scanner – internal architecture and bone contents revealed: New Mexico Museum of Natural History and Science Bulletin, this volume.

Northwood, C., 2005, Early Triassic coprolites from Australia and their palaeobiological significance: Palaeontology, v. 48, p. 49-68.

Rodríguez-de la Rosa, R.A., Cevallos-Ferriz, S. R.S. and Silva-Pineda, A., 1998, Paleobiological implications of Campanian coprolites: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 142, p. 231-254.

Sawyer, G.T., 1981, A study of crocodilian coprolites from Wannagan Creek Quarry Minnesota: Scientific Publications of The Science Museum of Minnesota, v. 5, p. 1-29.

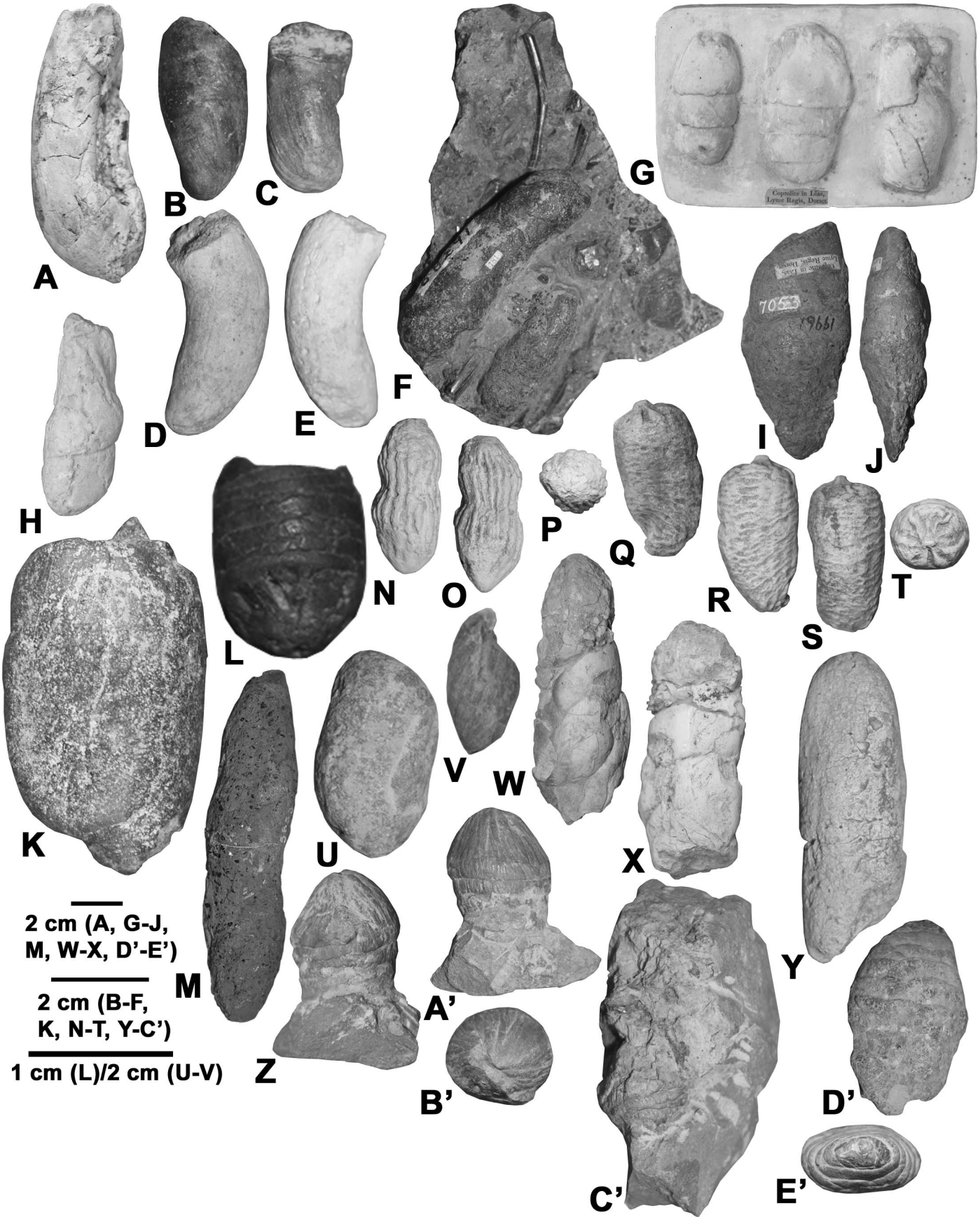
Souto, P.R.F., 2008, Coprólitos do Brazil – Principais occorências e studio: Rio de Janeiro, Publit, 93 p.

Souto, P.R.F., 2010, The crocodylomorph coprolites from Bauru Basin, Upper Cretaceous, Brazil: New Mexico Museum of Natural History and Science, Bulletin 51, p. 201-208.

Thulborn, R.A., 1991, Morphology, preservation and palaeobiological significance of dinosaur coprolites: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 83, p. 341-366.

Trutnau, L. and Sommerlad, R., 2006, Crocodilians. Their natural history and captive husbandry: Frankfurt am Main, Edition Chimaira, 646 pp.

Young, C.C., 1964, New fossil crocodiles from China: Vertebrate Palasiatica, v. 8, p. 190-208.



Selected coprolites in the collection of the National Museum of Natural History, Smithsonian Institution.