to the four strongest lines of delta-ferric oxide[2-5], as well as to some of the stronger lines of alpha-ferric oxide (haematite). Further study, however, tended to rule out the presence of delta-ferric oxide. A fifth band at 1·98 Å may have been due to an oxide of aluminium[6]. Differential thermal analysis (DTA) of the lichen-covered crust in an atmosphere of nitrogen gave a single large exotherm at 300° C caused by recrystallization to haematite, as shown by X-ray diffraction. Similar DTA patterns are given by beta (but not delta) FeOOH and by certain naturally occurring, as well as synthetic, ferric oxide gels[7,8]. Mössbauer spectroscopy suggested the presence of the beta-polymorph. Magnetic susceptibility revealed no evidence of ferromagnetism, suggesting that delta-ferric oxide was not present. A dehydration curve constructed with the aid of infrared spectrophotometry showed no break within the range of temperature in which the DTA curve indicated expulsion of water; therefore, the unknown mineral must be a polymorph of Fe_2O_3, not FeOOH.

The ferric oxide associated with the lichen may contain a poorly crystallized form of alpha-Fe_2O_3, although the data suggest certain similarities to beta-ferric oxide; the presence of delta-ferric oxide can probably be ruled out. The substance might be colloidal beta-ferric oxide which on ageing and dehydrating has partially re-crystallized to alpha-Fe_2O_3, but further work is needed to establish its identity. Because the ferric oxide is biogenic, as shown by its exclusive association with the lichen, consideration should be given to the possibility that the formation of the mineral is an epitaxial phenomenon involving an organic template—possibly the "lichen acid" of *S. vulcani*—excreted by the lichen or by its associated microflora (compare refs. 8 and 9).

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Evolutionary and Systematic Significance of Crocodilian Nesting Habits

DIFFERENT species of crocodilians build one of two kinds of nest. For example, the Nile crocodile (*Crocodylus niloticus*) lays its eggs in a simple hole in the earth, usually sand or loose gravel, which is then covered over with the excavated material to the level of the surrounding ground[1-6], whereas the American alligator (*Alligator mississippiensis*) constructs a mound of vegetation, cleared from the surrounding area, in which it lays its eggs[7-13]. Schmidt[14] suggested that nesting habits might be indicative of relationship, but his idea failed to gain acceptance. One reason for this might be the belief, most recently expressed in an authoritative monograph in 1953[15], that the differences in nesting habits are not sharp but instead show all possible intermediate stages. In pursuing Schmidt's idea, however, I have reviewed nearly all the literature on crocodilian nesting habits (summarized in Table 1) and conclude that there are absolute differences in these nesting habits and, as I hope to show, these differences are also closely correlated with the evolution and systematics of the group.

Table 1. FOUR ASPECTS OF THE NESTING HABITS OF CROCODILIANS

Species *gangeticus*	Nest type	♀ stays in vicinity of nest	Young vocal in egg	♀ aids young in escaping nest
Gavialidae				
Gavialinae				
Gavialis				
gangeticus	Hole[17]			
Crocodylidae				
Crocodylinae				
Crocodylus				
acutus	Hole[14,18-21]	+		
intermedius	Hole[22]	+		
johnsoni	Hole[23]	+		
niloticus	Hole[1-6]	+	+	+
palustris	Hole[24-26]	+	+	+
rhombifer	Hole[27]			
siamensis	Hole[25]			
cataphractus	Mound[28-30]			
novaeguineae	Mound[31]			
porosus	Mound[23,25,26,32-34]	+	+	
moreleti				
Osteolaemus				
tetraspis	Mound[28,29]	+		
Alligatorinae				
Alligator				
mississippiensis	Mound[7-13]	+	+	+
sinensis				
Caiman				
crocodilus	Mound[35,36]	+	+	
latirostris	Mound[37]			
Melanosuchus				
niger	Mound[38-41]	+		
Paleosuchus				
palpebrosus	Mound[42,43]	+		
trigonatus				
Tomistominae				
Tomistoma				
schlegeli	Mound[44]			

The "nest type" column indicates whether the female lays her eggs in a hole in the ground or in a mound of vegetation. A check in any of the following three columns indicates that there is evidence in the literature for, respectively, (1) the female's remaining in the vicinity of the nest during incubation, (2) vocalization of the young in the egg before hatching, and (3) the female's aiding the young to escape the nest after hatching.

Living crocodilians are divided into four major taxa: the family Gavialidae, and the subfamilies Crocodylinae, Alligatorinae and Tomistominae in the family Crocodylidae (Table 1). The Gavialidae and the Crocodylinae are thought to have arisen from a common ancestor, while the Alligatorinae and Tomistominae seem to have arisen independently from the Crocodylinae in the Cretaceous[16]. If the nesting habits of these groups are superimposed on their evolutionary history, we have a plausible history for the evolution of the habits (Fig. 1). The common eusuchian ancestor of the gavialids and crocodylines, and therefore all living crocodilians, was probably a hole nester. This primitive habit was retained by the gavialids and some crocodylines, but in one group of crocodylines mound building habits evolved, and it was this group that gave rise to the alligatorines and tomistomines.

Implicit in this hypothesis of the evolution of nesting habits in crocodilians is the notion that hole nesting is a primitive and mound nesting a more advanced habit. This theory is supported by the fact that the nesting habits of the other three surviving orders of reptiles are more similar to the habits of the hole nesting crocodilians than to the habits of the mound nesters. Turtles and the only living rhynchocephalian, the tuatara, simply dig a hole in the earth, lay their eggs and then cover them. Among Squamata, some lizards also bury their eggs, but most lizards and practically all snakes simply deposit their eggs in a hidden "nook" in the environment. This latter

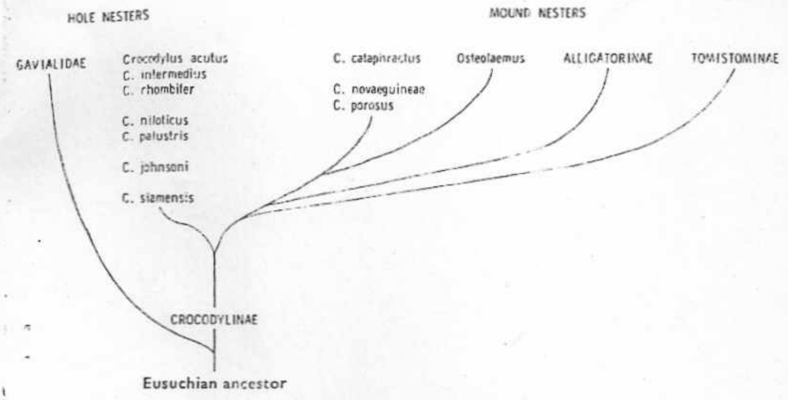

Fig. 1. The nesting habits of crocodilians interpreted phylogenetically.

form of "nesting" involves no acquisition of nesting material and in this regard it is more similar to the hole nesting of crocodilians, turtles, the tuatara and some lizards than to mound building. The three orders have been distinct from each other and from crocodilians since the Triassic, and it is therefore probable that primitive reptiles actively buried their eggs or simply left them hidden. In any case, it was probably very unlike the mound building of crocodilians.

The genus *Crocodylus* comprises both hole nesters and mound nesters and thus offers the possibility of an even finer check of the correlation between nesting habits and relationships. Unfortunately relationships within the genus are not clear, but there seem to be three pairs of closely related species[15]: in the *novaeguineae-porosus* species pair both species are mound nesters; in the *niloticus-palustris* species pair both are hole nesters; in the *moreleti-rhombifer* species pair, information on nesting habits is available only for *rhombifer*, a hole nester, but it is very likely that *moreleti* is also one.

If nesting habits are a good indication of relationship, it can be presumed that the alligatorines, for which we lack information on nest building, should be mound nesters as are the other species in their subfamily. Nesting habits may also provide a valuable guide for future analyses of relationships within this group, particularly for those species of *Crocodylus* whose relationships are totally unknown. *C. cataphractus*, for example, should prove to be most closely related to the only other known mound nesters in the genus, *novaeguineae* and *porosus*, whereas the closest relatives of *johnsoni* and *siamensis* are probably to be found among the other hole nesters rather than with the three mound nesters. Similarly, the monotypic crocodyline genus *Osteolaemus* is likely to be most closely related to the mound nesting species of *Crocodylus*, and it is within this whole mound nesting line of the crocodylines that the closest living relatives of the alligatorines and tomistomines are likely to be discovered.

There is as yet no clear explanation for the evolution of the two types of crocodilian nests. There seems to be no clear correlation between nest type and the general ecology of the species, but this is not too surprising given the probable great age of their evolution. If mound building habits are indicative of relationship, as suggested here, then the two nest types probably existed in the crocodyline stock that gave rise to the mound building alligatorines and tomistomines in the Late Cretaceous—a period very close to the origin of all crocodylids as indicated by the fossil record. The nesting types are therefore probably almost as old as crocodylids themselves, and the original ecological setting of the two nest types may have become obscure in 95 m.y. of subsequent evolution.

From a behavioural point of view the differences between the two nest types are qualitatively important but quantitatively unimpressive in comparison with the overall similarity in other aspects of crocodilian nesting behaviour. In both kinds of crocodilians, the female digs a hole in the substrate, lays her eggs and then covers them over again with the excavated material. There is also evidence that in both kinds of crocodilians the female may remain in the vicinity of the nest during incubation and, on hearing the croaking of the newly hatched young, respond by scraping away the overlying nesting material, thereby helping the hatchlings to escape the nest (Table 1). Because the entire sequence from excavation before egg laying to excavation after hatching is common to both kinds of crocodilians, it may be a primitive pattern for all crocodilians. What is new to this primitive sequence is the prior acquisition and structuring of nesting materials by the mound nesting crocodilians.

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