

North China Plate (sometimes called the Sino-Korean Plate) and the South China Plate (or Yangtze Plate) about 130 million years ago, in Triassic times. But the dates of UHP metamorphism are far older than this. Radiometric dating gives the age of formation of the parent basaltic and granitic rocks as late Precambrian (1200 million years), an age of UHP metamorphism of about 260 million years (Carboniferous) and the time when the rocks returned to crustal levels as 180 million years (Permian). Thus UHP metamorphism occurred while the South China and North China Plates were widely separated on either side of the Palaeotethys Ocean. We can grasp the length of time involved by making a comparison with Britain. Imagine that Torridonian sandstones had been taken down to the mantle during the early stages of the Caledonian orogeny, returned to the base of the crust at the end of the Hercynian orogeny, and finally reached the surface during uplift of the New Red Sandstone continent. The comparison suggests that there was more than one cycle of ocean growth and subduction in China. This raises problems because only the final collision and its associated subduction have been documented. But it also suggests the intriguing possibility that the Dabie UHP rocks may have remained in the mantle for quite a long period of time, perhaps through a whole Wilson Cycle of ocean growth and decay.

The mechanism of uplift of the UHP metamorphic rocks is also a source of discussion. The UHP rocks occur in thrust sheets overlying a complex dome structure, centred on the town of Luotian (Fig. 1). During the last stages of uplift, the inner metamorphic core complex of gneiss was intruded by acid and basic magmas, which caused it to rise as a dome, and the overlying sheets of UHP and other metamorphic rocks slid off to the north-east and south-west (Fig. 2). In a recent (1998) review paper, You, Zilong, Zhang and Wei emphasize that these features indicate that uplift occurred during a period of extension, in contrast to the collision that is usually considered to have occurred at the time. They emphasize that the rocks display a complex sequence of different metamorphic events, and do not attempt an explanation of the uplift from mantle depths to the lower crust.

Thus the existence of UHP metamorphic rocks has revised ideas about the range of conditions of metamorphism. Their occurrence in extensive terrains such as the Dabie Mountains shows that their metamorphism at great depth and return to the surface are not freak local events but fundamental, widespread processes. It is likely that they have some relationship to continental collision, but exactly what is still unclear.

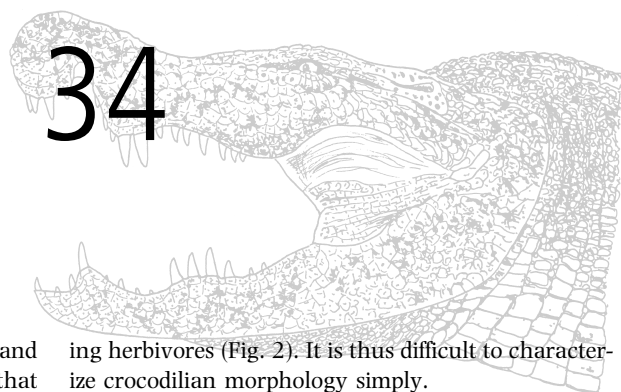
Fossils explained 34

Crocodylians

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Crocodylians – crocodiles, alligators, gharials and their fossil relatives – are quadrupedal reptiles that first appeared in the late Triassic. The extant species are amphibious predators, proficient at preying on most kinds of animals, large and small. They inhabit all continents except Europe and Antarctica and range from the dwarf caimans (*Paleosuchus*), which may be adult at 1.4 m, to the Saltwater crocodile (*Crocodylus porosus*), which may exceed 7 m and a tonne in weight (Fig. 1). While extant crocodylians are ecologically and morphologically diverse, they are conservative in body shape compared with the full variety of fossil crocodylians. The latter include marine forms with paddles and vertical tail fins, long-legged terrestrial forms with tall skulls and blade-like teeth, 'duck-billed' aquatic giants, and burrow-dwell-



ing herbivores (Fig. 2). It is thus difficult to characterize crocodylian morphology simply.

Their scaly skin, generally homodont (undifferentiated) dentition and poikilothermic ('cold blooded') physiology have traditionally meant that crocodylians have been classified alongside other extant reptiles in a group that excludes birds. However, numerous soft- and hard-tissue features show that crocodylians are more closely related to birds than to lizards, snakes and turtles, and, together with pterosaurs, dinosaurs and other groups, birds and crocodiles are part of the reptilian subgroup called the Archosauria. Some fossil crocodylians display the bony opening between the nostril and orbit, called the antorbital fenestra, that is unique to the Archosauria ('ruling reptiles'). Other unique archosaurian features, including the latero-

sphenoid bone in the braincase and the fourth trochanter, a prominent muscle attachment site on the posteromedial surface of the femur, are evident in crocodylians. Important soft-tissue features seen in crocodylians and birds, and by inference in fossil archosaurs as well, include a four-chambered heart and the absence of the Jacobson's organ.

Crocodylians are not descendants of dinosaurs. While both groups do belong to the Archosauria, they are from fundamentally different lineages. Living crocodylians are not 'living fossils' that have remained unchanged since the Mesozoic. In fact, modern-type crocodylians are a relatively recent evolutionary phenomenon and it is incorrect to imply that crocodylian evolution has been static or lethargic. With between 22 and 28 extant species (ideas differ as to whether some populations should be recognized as distinct species) distributed in habitats nearly worldwide, crocodylians are more speciose than many other groups often regarded as the epitome of evolutionary success. They cannot be regarded as a group 'on the decline', nor as a sorry vestige of a past glory. However, many species are in critical danger imposed by habitat loss and hunting, and whether these will survive into the near future is doubtful.

What's in a name?

Textbooks traditionally use the name **Crocodylia** for the living crocodylians and their fossil relatives. The problem with this term is that its usage has not been consistent throughout history; it has at times been applied to archosaurs that are not closely related to modern crocodylians. Consequently, it is now restricted (with the new spelling **Crocodylia**) to what is known as the crown group: the common ancestor of the living species and all of its descendants. 'Crocodylia' in the traditional sense has been renamed **Crocodyliformes** and, allied with a group of 'proto-crocs' called the sphenosuchians, forms the **Crocodylomorpha** (Table 1). While the term crocodylian can be used for crown-group members of the **Crocodylomorpha**, the informal term crocodylian is still often used for the **Crocodylomorpha**.

Morphology

Living crocodylians are of a uniform body shape. Their skulls are rigid, strongly braced with extensive overlapping sutures, and have a bony secondary palate that separates the nasal chamber from the mouth. The external nostrils, located at the tip of the snout, and ears can be closed by muscular flaps and, together with the eyes, are located on the dorsal surface of the skull. Muscles are attached to the retroarticular process (a bony prong on the posterior part of the mandible), the inside of the mandible, the side of the braincase and to the transverse pterygoid flanges – large wing-like processes that grow downwards from the back of the palate and contact the inside surface of the mandibles by way of a sliding joint (Fig. 3). Crocodylians are thus provided with an impressive bite force; in alligators this has been measured at 13 300 newtons (N) and is the most powerful bite of any living animal (humans have a maximum bite force of around 750 N, lions a maximum of 4168 N). The teeth of living crocodylians are conical, set in sockets and without serrated keels. As demonstrated below, many fossil crocodylians depart radically from the morphologies discussed here.

Skulls with raised ridges have evolved several times among crocodylians and are seen in fossil forms that

Fig. 1. Living crocodylians can be dynamic, awesome predators. Here, an Australian Saltwater crocodile (*Crocodylus porosus*) lunges vertically to grab bait. *Crocodylus porosus* can reach 7 m in total length and includes most kinds of animals in its diet, including humans and their livestock. (Photo courtesy Steve Salisbury.)



Table 1 A taxonomic scheme for the **Crocodylomorpha**.

Some controversial or poorly known taxa, and many family level clades including only one or a few genera, are not included here. Monophyly of the Ziphosuchia is controversial. Some of the more important group names are shown in bold type.

Crocodylomorpha Walker

Sphenosuchia Huene

Crocodyliformes Hay

Protosuchia Brown

Mesoeucrocodylia Whetstone and Whybrow

Ziphosuchia Ortega and colleagues

Sebecosuchia Simpson

Notosuchia Dollo

Thalattosuchia Fraas

Dyrosauridae de Stefano

Pholidosauridae Eastman

Bernissartiidae Dollo

Hsisosuchia Young and Chow

Neosuchia Clark

Atoposauridae Gervais

Goniopholididae Cope

Eusuchia Huxley

Hylaeochampsa Seeley

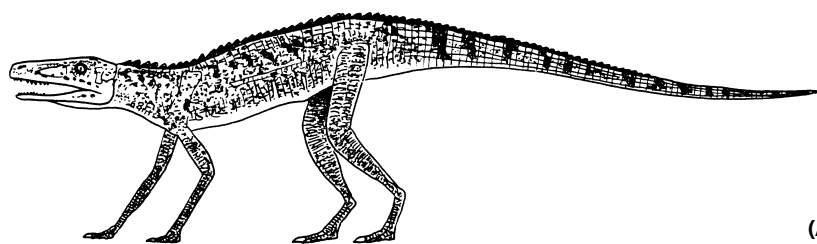
Stomatosuchidae Stromer

Crocodylia Gmelin

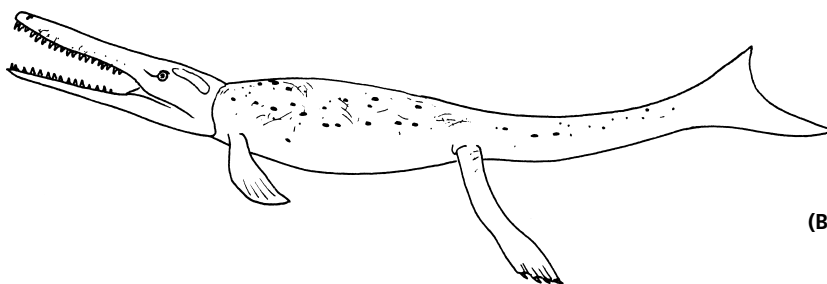
Gavialoidea Cuvier

Alligatoidea Gray

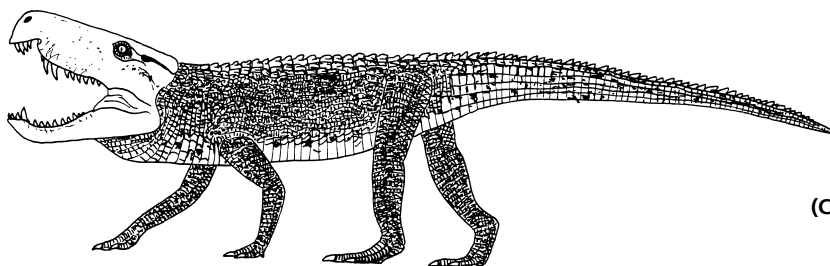
Crocodyloidea Cuvier



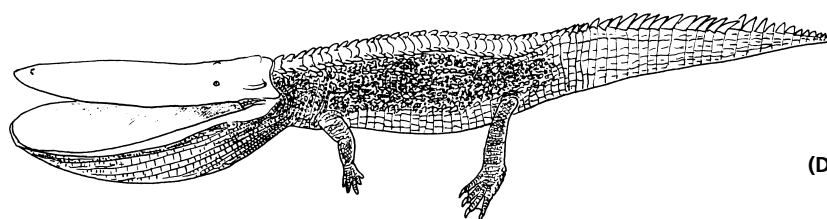
(A)



(B)



(C)



(D)



Fig. 2. Life restorations of a diversity of fossil crocodylians.

(A) Upper Triassic sphenosuchian *Barberenasuchus brasiliensis* from Brazil (total length 1 m). (B) Middle Jurassic thalattosuchian *Metriorhynchus* from Europe, South America and elsewhere (total length 4–6 m). (C) Upper Cretaceous sebecosuchian *Bretesuchus bonapartei* from Brazil (total length approximately 4 m). (D) Upper Cretaceous eusuchian? *Stomatosuchus inermis* from Egypt (total length 10 m). (This and other figures were produced by Trudie Bradbury and Stig Walsh.)

might have been terrestrial predators. These crocodylians, which include the Cretaceous to Miocene sebecosuchians of South America (Fig. 2C) and the Cenozoic pristichampsids of Europe and North America, have laterally compressed, serrated teeth. The common term ziphodonts ('sword-toothed') is often used for these crocodylians. The discovery of ziphodont teeth in the Palaeogene of Argentina originally led to the suggestion that theropod dinosaurs had survived into the Cenozoic.

Fish-eating crocodylians have elongate tubular snouts. Among living crocodylians, the Gharial (*Gavialis gangeticus*) represents an extreme in snout lengthening, but this appears modest compared to some fossil forms. *Atlantosuchus*, a dyrosaurid from the Palaeocene of Morocco, had jaws perhaps twice as elongate as those of *Gavialis*.

Bony scutes – osteoderms – cover the dorsal surface of the crocodylian body and may also be present on the ventral surface and the sides of the body as well. Because of their durability and abundance, scutes (together with isolated teeth) are the commonest crocodylian fossils. Crocodylian scutes have a distinctive pock-marked outer surface and can be rounded or rectangular (Fig. 5). In the most primitive crocodylians, as in other early archosaurs, the scutes are arranged in pairs along the dorsal midline. In later crocodylians, the scutes behind the head have been lost or reduced and the number of longitudinal scute rows was now as many as 10 at mid-body. While it is traditionally assumed that scutes evolved for self-defence, their proliferation in later crocodylians has been suggested to be for temperature regulation, providing a larger surface area for heat collection. However, studies of crocodylian musculature show that the scutes on the back provide attachment

Fig. 3. Gaping skull of a modern crocodyloid, a juvenile Nile crocodile (*Crocodylus niloticus*). Note the recess behind the eye socket for the external ear and the descending flange on the palate with its area of lower jaw contact. Although living crocodylians are traditionally regarded as homodont, note that the teeth do actually differ notably in size and shape.

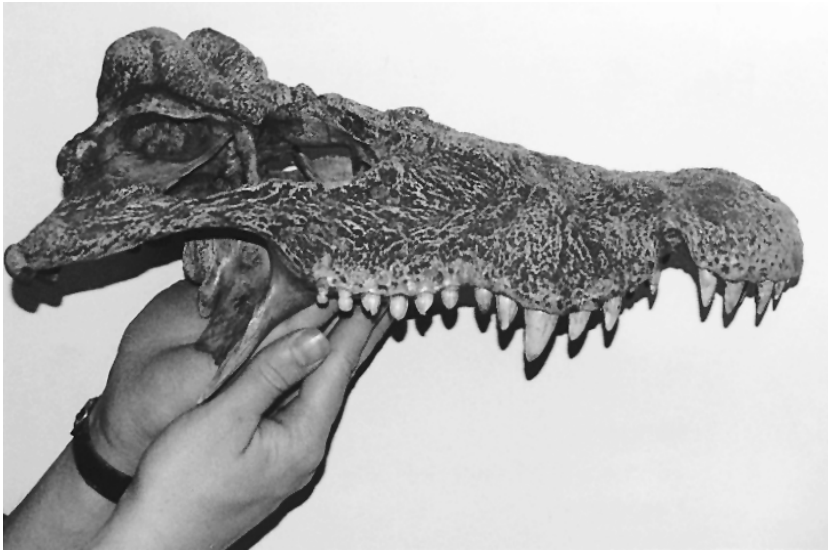


Fig. 4. Skull of a recently extinct crocodyloid crocodilian, the large and robust '*Crocodylus*' *robustus* from the Holocene of Madagascar. Recent studies show that this is not a species of *Crocodylus*, but instead a close relative of *Osteolaemus*, the living dwarf crocodile. Note the prominent caudodorsal 'horns'.

sites for musculature that runs along the length of the vertebral column and form what is referred to as a built-in I-beam. This helps stiffen the body during locomotion and, using this system, living crocodiles can move with a distinctive high walk where the limbs are held semi-erect and the body is well off the ground. Some living species can run with a bounding gallop, and they can also walk with a sprawling gait.

The earliest crocodilians, the sphenosuchians and protosuchians, were long-legged predators (Fig. 2A). Their skulls were altirostral, their tails were not laterally compressed, and their leg, foot and toe bones were slender, suggesting fast-running abilities. It therefore appears that crocodilians were originally nimble terrestrial predators that only later took to the amphibious lifestyle we are familiar with today. This primitive lifestyle may explain the elongate proximal foot bones seen in these animals and all later crocodilians.

Most crocodilians have unusual pelvic bones where the pubis does not participate in the acetabulum (the socket for the head of the femur) as it does in virtually all other reptiles. Instead, the pubis has a mobile joint with either one or both of the other hip bones and is a mediolaterally broad bone that serves as the attachment site for muscles that help to expand the skin of the belly ventrally, aiding inflation of the lungs. This method of ventilating the lungs is called pubic aspiration. It has recently been suggested that amphibious crocodilians may use this mechanism to deflate their lungs and decrease their buoyancy in water, thus allowing descent. These bony pelvic fea-

tures were not present in sphenosuchians and protosuchians – they have narrow, immobile pubic bones – and appear to have first evolved in the mesoeucrocodylian clade, the group that includes all modern-type crocodilians.

Crocodylian diversity

Sphenosuchians were slender-limbed crocodilians from the Triassic and early Jurassic, and are among the most basal members of the Crocodylomorpha. Features seen in the ear regions of these animals led to suggestions in the 1970s that they were the closest relatives of birds, an idea that has since been discounted. *Phyllodontosuchus*, a sphenosuchian from the Lower Jurassic of China, has leaf-shaped teeth and could have been herbivorous.

Like sphenosuchians, protosuchians were small, slender terrestrial predators. Though they are well known from the Triassic and Lower Jurassic, recent finds show that protosuchians survived into the Cretaceous. Protosuchians appear more closely related to other crocodilians than sphenosuchians, sharing with them a groove for the ear flap, pit and groove sculpturing on the skull bones and other features, and together protosuchians and 'higher crocodilians' (the mesoeucrocodylians) form the Crocodyliformes. Mesoeucrocodylians are united by their

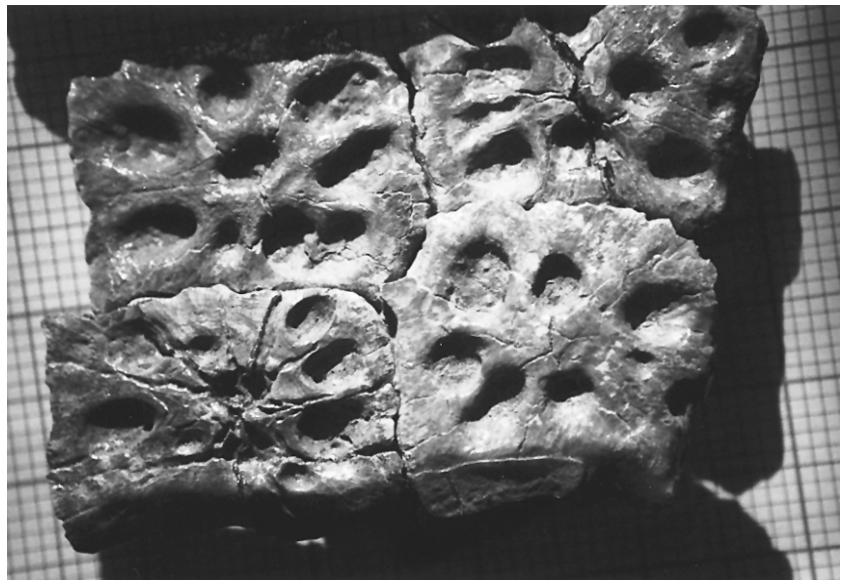


Fig. 5. Crocodylian scutes, such as these from a Middle Jurassic teleosauroid thalattosuchian, are often rectangular in shape and with a pock-marked upper surface.

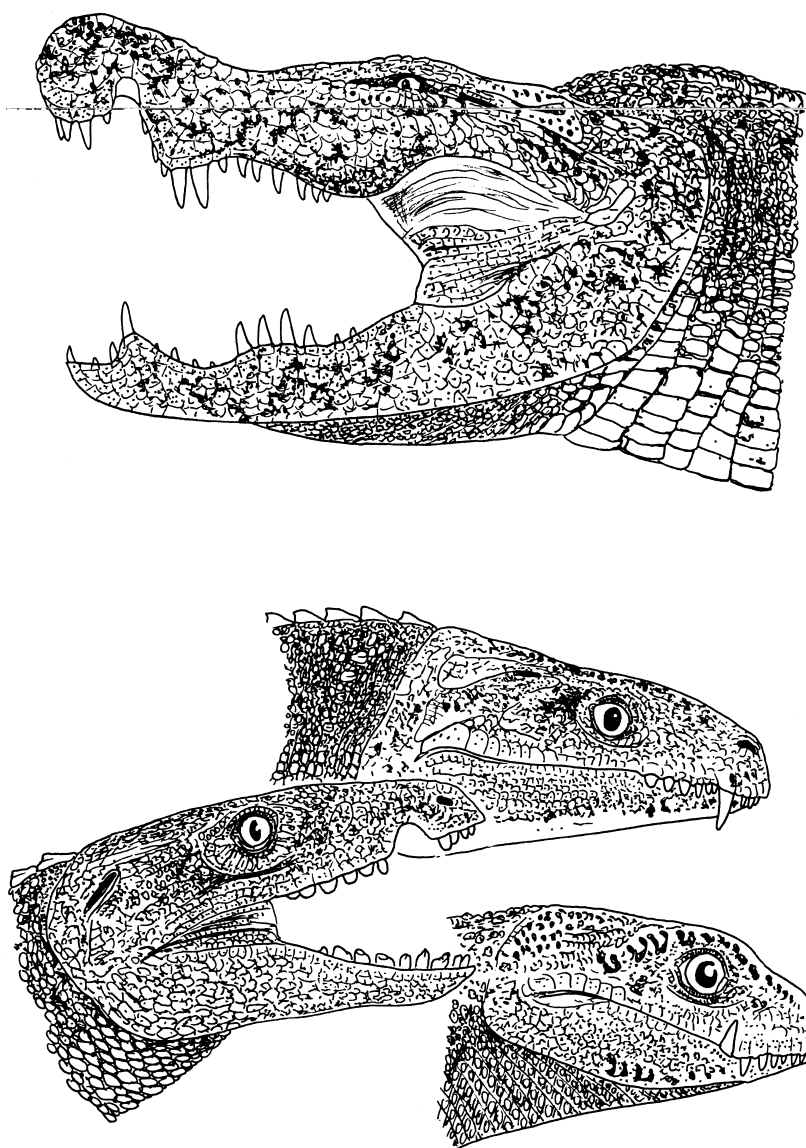


Fig. 6. Restored heads of a diversity of fossil crocodylians. At the top, the mekosuchine crocodyloid *Baru darrowi* (Miocene of Australia); middle, the notosuchian *Notosuchus terrestris* (Upper Cretaceous of Argentina); bottom left, an as-yet-unnamed protosuchian (Upper Triassic of North America); bottom right, the notosuchian *Comahuesuchus brachybuccalis* (Upper Cretaceous of Argentina). Not drawn to same scale throughout.

elongate rostrum. Elongate snouts evolved many times among crocodylians, so the presence of a clade supposedly united by this feature is suspicious. Several groups of this long-snouted clade took to life in the sea and one Mesozoic group, the thalattosuchians, became specialized mariners. Teleosaurid thalattosuchians, best known from the Lower Jurassic of Europe, were superficially like living gharials. Metriorhynchids, which may have evolved from teleosaurids in the Middle Jurassic, had vertical tail flukes, paddle-like limbs and no osteoderms (Fig. 2B). It is inferred that metriorhynchids needed to return to land in order to lay eggs. This would have placed a constraint on their upper size limit, in contrast to live-bearing marine reptiles like ichthyosaurs but, even so, thalattosuchians grew to lengths of 5 m and more. Stomach contents show that metriorhynchids ate fish and cephalopods, but some species have robust skulls and could have tackled large vertebrate prey. A metriorhynchid tooth is preserved stuck in the healed frontal bone of the gigantic Oxford Clay fish *Leedsichthys*, suggesting an aggressive encounter between the two. One long-snouted mesoeucrocodylian group, the Dyrosauridae, survived across the Cretaceous/Tertiary boundary and became important nearshore predators in the Palaeogene.

Among the strangest crocodiles were the notosuchians, a mostly southern hemisphere group of

complete secondary bony palates and mobile pubic bones. Their rather clumsy name reflects the fact that they include both 'mesosuchians' (a paraphyletic assemblage of mostly Mesozoic forms) and eusuchians. They appear to encompass three primary radiations, though differing views exist as to the validity of some of these groupings.

Particularly problematic is a group composed of mesoeucrocodylians that all exhibit the same kind of

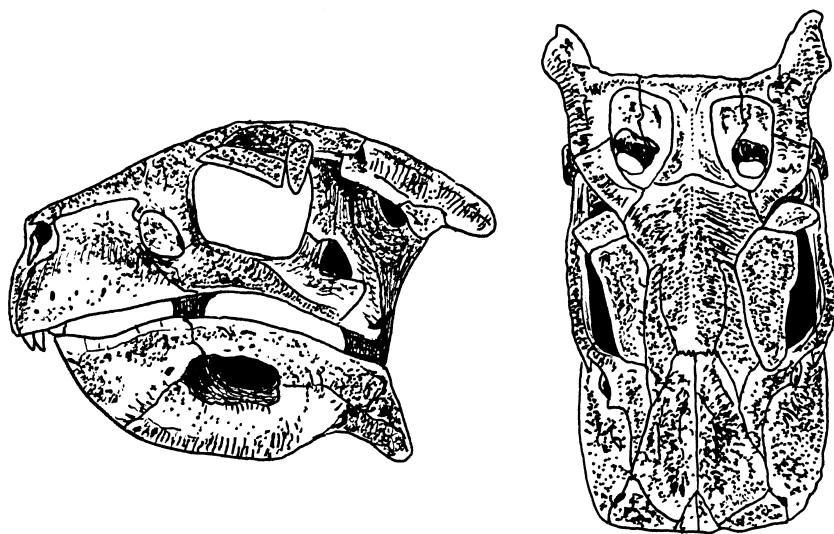


Fig. 7. Skull of one of the strangest crocodylians, the notosuchian *Simosuchus clarki* from the Upper Cretaceous of Madagascar. The skull is approximately 150 mm long (after Buckley and colleagues; see Suggestions for further reading).

small, short-skulled mesoeucrocodylians with heterodont teeth and (in some forms) the ability to move the lower jaws backwards and forwards (Figs 6 and 7). Some notosuchians have molariform teeth and have been dubbed 'mammal-toothed crocodiles'. *Simosuchus* (Fig. 7), from the late Cretaceous of Madagascar, has perhaps the most peculiar teeth of any crocodylian – they have expanded, laterally compressed crowns that sport large, subtriangular cusps. Perhaps notosuchians were herbivores, although they may have eaten small animals. Some notosuchian fossils are preserved inside burrows and have features indicative of an ability to burrow with their heads.

Neosuchians include the living crocodylians and their close relatives. A Jurassic to early Cretaceous neosuchian group, the atoposaurids, well known from the Purbeck of Dorset, are small (less than a metre long), short-skulled and with conical, leaf-shaped and button-shaped teeth. Atoposaurids are usually regarded as predators of small animals, but their leaf-shaped teeth suggest to some that they might have eaten plant material. The late Jurassic to Cretaceous goniopholidids were the first crocodylians superficially to resemble living forms and, like them, appear to have been amphibious predators.

The eusuchians

The three groups of crocodylians that survive today together form part of the Eusuchia, a clade characterized by procoelous (anteriorly concave) vertebrae. *Hylaeochampsa*, the earliest known eusuchian, is from the Wealden of the Isle of Wight and was blunt-snouted with enlarged posterior crushing teeth. Later eusuchians, the three lineages Gavialoidea, Alligatoroidea and Crocodyloidea, all have living representatives and form the crocodylomorph crown-group, the Crocodylia.

Gavialoids have only a single living species, the Gharial of tropical southern Asia, while crocodyloids and alligatoroids are diverse. However, fossil gavialoids are known from Africa and South America. An apparently endemic radiation of crocodyloids, the mekosuchines, inhabited Australia and New Caledonia from the Eocene until the Holocene (Fig. 6). Like many of Australasia's mammals and birds, they were convergent in morphology to taxa from elsewhere. In historical terms, we have just missed out on seeing an extant representative of this group: *Mekosuchus* was still living on New Caledonia as recently as 1600 years ago. Extant crocodyloid species, both in Africa and Australia, began to appear in the Pliocene.

Alligatoroids include the largest of all known crocodylians, *Deinosuchus*, from the Upper Cretaceous of North America. Until recently regarded as a crocodyloid, *Deinosuchus* may have preyed on dinosaurs and large turtles (as evidenced by tooth-marked

bones). Histological studies suggest that it reached its great size (10 m and up to 5 tonnes) by living longer than related species, and by maintaining juvenile-style growth for a few decades, as opposed to 5–10 years. *Purussaurus*, a caiman from the Miocene of the Amazon, reached a similar size.

A bizarre group of South American fossil alligatoroids, the nettosuchids, had elongate blunt skulls and have been called 'duck-billed' alligators. What nettosuchids ate is a mystery – it has even been suggested that they scooped up floating plants. An unrelated, but morphologically similar crocodylian, *Stomatosuchus* from the Upper Cretaceous of Egypt, was gigantic (perhaps 10 m long) with lower jaws that suggest the presence of a pelican-like throat pouch (Fig. 2D). The teeth in the upper jaw were conical and small, while the lower jaws may have been toothless. It has been speculated that *Stomatosuchus* was a plankton feeder, similar to baleen whales. Procoelous vertebrae suggest that it was a eusuchian. Unfortunately, the only known specimen was destroyed during World War II.

Crocodylian lifestyle and behaviour

Living crocodylians exhibit diverse kinds of ecology, lifestyle and behaviour, and allow us to speculate about the lifestyles of extinct forms. As babies, living crocodylians prey on arthropods and frogs. With increasing size, large vertebrate prey become important, but small prey still form part of the diet. Most crocodylians grasp large prey with forward lunges or rapid lateral head movements, and may propel themselves out of the water to grab prey (Fig. 1). Most living species can lunge for a distance equal to their body length and some species can leap vertically. Crocodylians handle prey using inertia and rely largely on gravity to get food into the gullet.

Crocodylian social behaviour is complex and involves a repertoire of vocal and visual signals including bellowing, gaping, nasal geysering, tail wagging, head slapping, inflating the body and lifting the snout. These displays are used in asserting aggressive intentions, dominance, submission and conciliation. Notably, most of these signals are performed in the water, a medium that the animals use to acoustic and visual advantage. Were similar signals used by extinct terrestrial crocodylians?

Female crocodylians construct nests from soil and vegetation and guard them during incubation. Babies call to their mothers for assistance or protection and mothers carry their babies from the nest to the water after hatching, guarding them for weeks or months. Female crocodylians respond to the distress calls of babies. Some crocodylians are highly tolerant of their kind and are only territorial during the breeding season; Nile crocodiles (*Crocodylus niloticus*) even co-operate in hunting and feeding. Conversely, other spe-

cies (particularly the Saltwater crocodile) are highly pugnacious and regularly fight with their own species.

Suggestions for further reading

- Brochu, C.A. 1999. Phylogenetics, taxonomy and historical biogeography of Alligatoroidea, *Journal of Vertebrate Paleontology*, v.19, Mem.6, pp.9–100.
- Buckley, G.A., Brochu, C.A., Krause, D.W. & Pol, D. 2000. A pug-nosed crocodyliform from the late Cretaceous of Madagascar, *Nature*, v.405, pp.941–944.
- Langston, W. 1965. Fossil Crocodylians from Colombia

and the Cenozoic History of the Crocodylia in South America, *University of California Publications in Geological Sciences*, v.52, pp.1–157.

- Ross, C.A. 1989. *Crocodiles and Alligators*. Merehurst Press, London.
- Russell, A.P. & Wu, X.-C. 1997. The Crocodylomorpha at and between geological boundaries: the Baden-Powell approach to change?, *Zoology*, v.100, pp.164–182.

Minerals explained 32

The tetrahedrite group

R. J. King

The tetrahedrite group is a member of a family not yet examined in *Geology Today*, the sulphosalts. The term 'sulphosalt' is used to indicate a certain type of unoxidized sulphur mineral that is structurally distinct from a sulphide. The family is diverse and quite large, with over a hundred species. Its members differ from sulphides, sulpharsenides and arsenides, as the semi-metals As, Sb and Bi in the formula act rather like metals in the structure. They may be thought of as double sulphides.

The members of the tetrahedrite group form a prominent group of non-stoichiometric compounds within the sulphosalt family, with variable ratios of metals, semi-metals and sulphur. In the group there are essentially seven sites or end-members with, however, at least 48 other possible sites and with the exotic possibility far beyond that number. For example, there are said to be 27 end-members of the group in the complex ore of the Sark Hope mine in the English Channel Islands. As a result there are many synonyms. Space here demands that we should be realistic, but also that we should look at the nomenclature in conjunction with the formulae.

The group is often described under the title 'the Fahlores', a useful field name taken from the part spelling of the old German word *fahlerz* for grey-coloured and ore. This is a useful term if only for the fact that members of the group are almost impossible to differentiate visually, being so similar crystallographically and physically. From observation it is

likely that the arsenical end-members are rarer than the antimonial end-members.

The fahlores are geographically universal and occur in many geological environments, but relatively few occur in well-developed crystals.

The chemistry of the fahlores

The group is notable for the wide variety of elements which are stable in its structure. The formula may be written as $A_{12}B_4X_{13}$, where $A = \text{Ag, Cu, Fe, Hg, Zn}$; $B = \text{As, Sb, Te}$; $X = \text{S, Se, Te}$. The Sb–As elemental components form a complete series from tetrahedrite to tennantite, with ratios being essentially $\text{Sb} : \text{As} = 1 : 1$. Species designators are at present based on the elements which constitute the plurality of occupation in the combined sites of A, B and X. Thus species formulae may be erected:

- tetrahedrite, $(\text{Cu, Fe, Ag, Zn})_{12}\text{Sb}_4\text{S}_{13}$;
 tennantite, $(\text{Cu, Ag, Fe, Zn})_{12}\text{As}_4\text{S}_{13}$;
 argentotennantite, $(\text{Ag, Cu})_{10}(\text{Zn, Fe})_2(\text{As, Sb})_4\text{S}_{13}$;
 freibergite, $(\text{Ag, Cu, Fe})_{12}(\text{Sb, As})_4\text{S}_{13}$;
 giraudite, $(\text{Cu, Zn, Ag})_{12}(\text{As, Sb})_4(\text{Se, S})_{13}$;
 goldfieldite, $\text{Cu}_{12}(\text{Te, Sb, As})_4\text{S}_{13}$;
 hakite, $(\text{Cu, Hg})_{12}\text{Sb}_4(\text{Se, S})_{13}$.

Tetrahedrite, $(\text{Cu, Fe, Ag, Zn})_{12}\text{Sb}_4\text{S}_{13}$, was so named by Haidinger in 1845 in allusion to its tetrahedral morphology. The synonyms panabase, clinodrite, fahlite, nepaulite, struderite, falkenhaynite and stlytopite are discredited. The last named has been shown to be a mixture. It was named from the Greek

