image of a dense aggregate is given in (*5*)]. At somewhat lower concentrations (~10 μg/ml), a number of low-density patches form (Fig. 1B). The "popcorn" texture comes from the modulation due to the helix pitch (Fig. 1B is oriented so as to emphasize this). The helix pitch in most of the samples of random-sequence DNA that we have measured is 36 Å. The uncertainty in this number varies with the nature of the adsorbate being imaged. Densely packed aggregates with two-dimensional (crystal-like) order allow very accurate measurements to be made (particularly from the Fourier-transformed image) so that the uncertainty is ~0.1 Å. In loose aggregates, the uncertainty is far greater because of fluctuations in the helix direction (~0.5 Å). The helix is far less regular when the samples are dried. A larger range of pitches is seen in synthetic nucleic acids. For example, RNA (in what is probably A form) has a pitch of ~30 Å, whereas poly(dGC) · poly(dCG) (which may be Z form) has a pitch greater than 40 Å. Important exceptions to these results may occur near gross structural features (such as kinks). It becomes very difficult to define a pitch near regions of large structural fluctuation.

A close-up image showing three complete 146-bp fragments is shown in Fig. 1C (lower left to middle—the middle two fragments are in contact at their top end). Each shows structure compatible with 15 roughly full turns of the double helix along their length, but the helix meanders considerably. Since we have never seen such variation in images of dense aggregates of high molecular weight calf thymus DNA (*5*), we conclude that the structure is affected by the packing, a conclusion consistent with other studies (*10*).

The data in Fig. 1, A through C, were low pass–filtered to smooth out features smaller than about 15 Å. We have retained this fine structure in Fig. 1D (emphasizing it with a curvature-keyed gray scale and choice of perspective). It is almost a side-on view of a strand that crosses from the upper-left to lower-middle regions of the image (two other partially obscured strands are visible behind it). The regular striations that cross the molecule are approximately consistent with the 15 to 20 Å modulation expected for the minor to major groove variation in B-DNA (*3*). However, we do not consider the data reliable at this level of resolution because of the strong interaction between the tip and molecule, and we expect that the features are distorted in a complex way that depends on the angle of approach between tip and molecule, as well as the "local" deformability of the molecule (*5*).

Better control of the interaction between the tip and molecule is obtained with the atomic force microscope (AFM). Recent AFM experiments demonstrate what we believe to be the most important advantage of operation in water, which is the ability to monitor bimolecular reactions as they proceed (*11*). Finally, we note that DNA extracted from nucleosomes is probably not random sequence (*12*). We have observed recurring chain configurations that may in fact be sequence directed.

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8. Available from Angstrom Technology, 1815 West First Avenue, Mesa, AZ.
9. These tunnel currents are somewhat less than those used in (*5*). The contrast in the images presented here appears to be positive, but careful inspection of a trace over a DNA molecule shows both positive and negative contributions (the negative contribution appearing as the black shadow beside each "molecule," most obvious in Fig. 1C). The contrast arises from deformation of the tip, substrate and molecule, as well as from hysteretic effects associated with the servo response, as explained in (*5*). The apparent height (of about 30 Å) should not be interpreted literally.
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Mammal-Like Dentition in a Mesozoic Crocodylian

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Crocodylian teeth are generally conical with little differentiation in shape along the tooth row. The mandible is incapable of any fore-aft movement, and feeding typically involves little or no intraoral processing. Complex, multi-cusped, mammal-like teeth differentiated along the tooth row have been found in a Cretaceous crocodylian from Malawi. The morphology of the teeth and mandible indicates that food items were processed by back-to-front (proal) movement of the mandible, unlike living crocodylians but as in some mammals and *Sphenodon* (the tuatara).

ALTHOUGH LIVING CROCODYLIANS display a variety of skull shapes ranging from the long, tubular snout of the Indian gharial to the broad, flat snout of the alligator, there is little diversity in dental morphology. Indeed, nearly all dental diversity so far observed within the Crocodylia, both fossil and living, involves lateral compression or the degree of bluntness or slenderness of teeth (*1*). Mandibular movement during feeding is also quite uniform among living crocodylians, consisting mainly of prolonged closure of the mouth on the prey (*2*). Unlike that of most other diapsid amniotes (for example, lizards and birds), the crocodylian skull is akinetic, and the mandible does not move backward or forward when it is adducted. The discovery of a fossil crocodylian with an extremely heterodont dentition including multi-cusped teeth and a mandible that moved fore and aft is therefore worthy of note.

The specimens of this new crocodylian were collected in 1984 and 1987 in northern Malawi, southeast Central Africa, from beds mapped as Lower Cretaceous (*3*). They include five partial skulls with lower jaws and several isolated teeth (*4*). All the skulls

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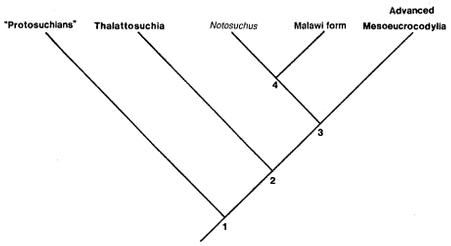

Fig. 1. Cladogram showing the hypothesized relationships of the new form to other crocodylians. Derived characters at the following nodes only include those present on specimens of the new form: node 1, quadrate firmly sutured to the braincase and contacts laterosphenoid, parietal unpaired, squamosal broadly overhangs ear region, basipterygoid joint closed, exoccipitals meet broadly above foramen magnum, postfrontal absent, splenial extensively involved in symphysis; node 2, cranioquadrate passage closed laterally by squamosal, exoccipital, and quadrate, frontal unpaired, palatine secondary palate present; node 3, basisphenoid exposure on ventral surface of braincase less than the length of the basioccipital, foramen vagi closer to foramen magnum than to cranioquadrate passage, ventrolateral process of exoccipital absent; and node 4, articulation surface for quadrate on articular much longer than broad, supratemporal fenestrae elongate and narrow, premaxilla-maxilla contact vertically oriented and lacking any indentation.

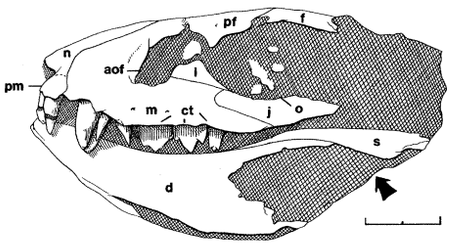

Fig. 3. Left lateral view of CD-1-2, a skull with articulated mandible, with an outline interpretation. Abbreviations: aof, antorbital fenestra; ct, "cheek" teeth; d, dentary; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nares; o, orbit; pf, prefrontal; pm, premaxilla; s, surangular. The arrow indicates the direction of movement inferred for the action of the M. pterygoideus muscles. Scale bar, 1 cm.

are small, with a midline skull length of approximately 5 to 8 cm. By analogy with living crocodylians they appear to be subadults, as indicated by the lack of sculpturing on skull bones and the lack of interalveolar septa between teeth.

The affinities of this taxon are indicated by derived features (Fig. 1), placing it within the mesosuchian grade group (*5, 6*). Three characters ally the new form with *Notosuchus* from the Late Cretaceous of Argentina (*7*). Thus, we refer the Malawi crocodylian to the Notosuchidae (*7, 8*).

The most distinctive of the three notosuchid features is that the surface on the articular bone forming the joint between the skull and mandible is elongate (Fig. 2) (*9*). This surface is twice as long as in comparably sized living crocodylians. The functional consequence of this elongation is that, unlike in living crocodylians, the mandible was capable of fore-aft movement at its articulation with the quadrate. The articular of CD-6-1-1 indicates that the approximately 8-cm long mandible had 3.5 mm of latitude in fore-aft movement.

The upper dentition comprises anterior caniniform teeth and closely appressed posterior "molariform" teeth (Fig. 3). The caniniform teeth include at least two premaxillary teeth and the three anterior maxillary teeth. The three posterior molariform teeth (Fig. 4) have an ovoid occlusal outline with a tall central cusp and cuspidate cingulum. A sharp, straight ridge extends from the apex of the central cusp along its posterior surface to the base. Cingula are developed around the posterior border of teeth. In lateral view the main cusp appears slightly asymmetrical, leaning posteriorly. There is a single open root with thecodont implantation, but a broad, vertical, shallow groove is occasionally present on the lingual surface.

The lower dentition is similar to the upper dentition except that caniniforms are not present. Teeth appear to be absent from the anterior end of the symphysis. The anteriormost tooth has only a weak cingulum, but posterior teeth are molariform. The lower

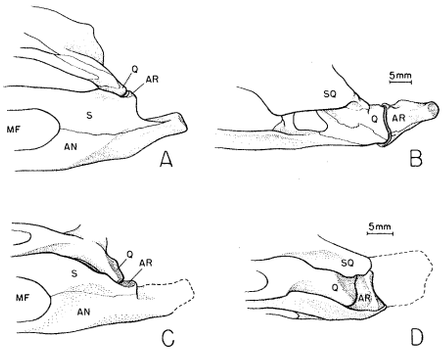

Fig. 2. Left lateral and dorsal views of the quadrate-articular joint in *Alligator mississippiensis* (**A** and **B**) and the Malawi crocodylian (CD-6-1-1) (**C** and **D**). Note the elongate mandibular articulation surface in the Malawi crocodylian in contrast with the posterior buttress of the articular that prevents anterior movement of the mandible in *Alligator* and other living crocodylians. Abbreviations: AN, angular; AR, articular; MF, lateral mandibular fenestra; Q, quadrate; S, surangular; and SQ, squamosal.

molariform teeth mirror the uppers; the sharp ridge is on the anterior, rather than posterior, surface, and the central cusp leans anteriorly. Cingula are on the anterior, buccal, and posterior borders.

The lower tooth row lies medial to the upper when the jaws are adducted. Both converge anteriorly, so that anterior movement of the jaw would bring the tooth rows closer together. The two are sufficiently separated to allow the degree of fore-aft movement indicated by the articular.

Wear on molariform teeth occurs as abrasion (*10*) at the apex of the central cusp, extending along the crest of the ridge, and on the apex of cingular cusps. There is no indication of thegosis or of direct dental occlusion, as in many mammals. Thus, the ridge on the central cusps of lower and upper molariform teeth did not consistently occlude with that of the opposite tooth to form a precise shear.

The posterior orientation of the central cusp on the upper molariform teeth and the presence of the sharp ridge on its posterior surface, coupled with an opposite and complementary configuration in lower molariform teeth, suggest that jaw movement during adduction was back-to-front (*11*). Proal movement would have brought the ridges and cingular cusps on antagonistic teeth toward one another and against food items lying between them.

This inference of proal movement is strongly supported by the architecture of the mandibular adductor muscles of living crocodylians. In crocodylians, unlike in other living tetrapods, the primary muscles responsible for jaw adduction are the M. pterygoideus anterior and posterior (*2, 12*). These muscles originate on the dorsal surface of the palatine and pterygoid bones and from tendons attaching to the pterygoid, and they insert on the adductor tendon and the angular and articular bones in the posterior part of the mandible. Thus, these muscles contract in an anterodorsal direction, so that in addition to their primarily upward direction, the resultant force vector also has a large anterior component (Fig. 2) (*2*). This anterior component is prevented from acting on the mandible in living crocodylians by the morphology of the joint surface on the articular, which has a posterior buttress preventing anterior movement of the mandible. The skull morphology of the Malawi crocodylian indicates that its adductor musculature was closely comparable to that of living crocodylians, with perhaps more emphasis upon the M. pterygoideus (*13*).

The differentiation of the teeth into caniniforms and molariforms indicates different functions for each. Comparison with living crocodylians and mammals suggests that the caniniform teeth were involved in prey capture and holding, and the molariform teeth in processing of the food. There is no indication that processing was as extensive as in most herbivorous mammals (*14*), but it may have been comparable in extent to the relatively brief processing found in carnivorans such as felids.

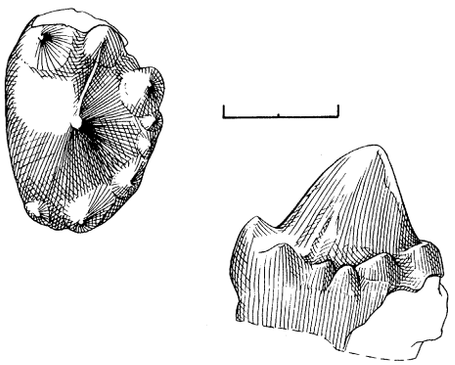

Fig. 4. Occlusal (left) and labial (right) views of the posteriormost right mandibular "cheek" tooth of CD-1-1. Anterior is to the top in the left figure, to the right in the right figure. Scale bar, 2 mm.

Young Nile crocodiles have a diet consisting mainly of insects, and as they grow larger they eat proportionately more vertebrates and fewer insects (*15*). If the Malawi crocodylian had a comparable life history, then the small, subadult fossil specimens were primarily insectivorous. However, the pronounced differences between the feeding mechanisms of the Malawi crocodylian and living crocodylians suggest a different or more specialized diet for the fossil form.

Several amniote groups have independently evolved the capacity for fore-aft movement of the mandible during adduction (*16*). Tortoises, and to a lesser extent some other turtles, retract their mandible in a palinal (front-to-back) motion (*17*), and extinct dicynodont (*18*) and tritylodontid (*19*) therapsids and multituberculate mammals (*11*) are inferred to have had palinal movement. Proal movement is, to our knowledge, only found in some mammals, especially rodents (*20*), and in sphenodontid rhynchocephalians (*21*), including the sole living member, *Sphenodon punctatus* (the tuatara). Anterior movement of the mandible in *Sphenodon* is accomplished by the M. pterygoideus, supporting our interpretation that this muscle was responsible for the same action in the Malawi crocodylian.

All of the amniotes with fore-aft mandibular movement lack other forms of cranial kinesis. This suggests that there is a functional relation between the evolution of fore-aft mandibular movement and having an akinetic skull. The evolution of a mechanism for intraoral food processing in the Malawi crocodylian may also have been related to its possession of a secondary palate, which could have allowed for the maintenance of breathing during food processing, as in living mammals.

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Transfer of a Protein Encoded by a Single Nucleus to Nearby Nuclei in Multinucleated Myotubes

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Specialized regions of muscle fibers may result from differential gene expression within a single fiber. In order to investigate the range of action of individual nuclei in multinucleated myotubes, C2 myoblasts were transfected to obtain stable cell lines that express a reporter protein that is targeted to the nucleus. Hybrid myotubes were then formed containing one or a few transfected nuclei as well as a large number of nuclei from the parental strain. In order to determine how far the products of a single nucleus extend, transfected nuclei were labeled with [^{3}H]thymidine before fusion and the myotubes were stained to identify the reporter protein. In such myotubes the fusion protein was not confined to its nucleus of origin, but was restricted to nearby nuclei.

IN ORDER TO CONSTRUCT AND MAINTAIN specialized subcellular domains, large extended cells like neurons and muscle fibers must be able to distribute proteins differentially within the cell. Muscle fibers are multinucleated; an adult muscle fiber may contain hundreds of nuclei evenly distributed throughout its length, each capable of producing mRNA and protein. Muscle fibers, nevertheless, produce proteins that have a restricted distribution within the fiber. A classic example is the acetylcholine receptor (AChR), which is concentrated at the neuromuscular junction (*1*). Another example is the demonstration by Salviati *et al.* (*2*) that a fast foreign nerve induces the production of fast myosin in dually innervated slow muscle fibers, but only in the region of the ectopic, fast end plate.

Restricted protein distribution in muscle

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