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INTRODUCTION TO *ALLIGATOR: DIGITAL ATLAS OF THE SKULL*

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INTRODUCTION

A CD-ROM (Compact Disc—Read Only Memory) included with this memoir presents a serial-section study of the skull of the modern American alligator, *Alligator mississippiensis*. The CD-ROM contains a three-dimensional (3-D) dataset of high-resolution X-ray Computed Tomographic (CT) 'slices' through the entire skull of a young specimen. The dataset includes 1391 separate digital CT images, each of which displays an approximately 250 μm (0.25mm) thick slice through the specimen. The images are arrayed on the CD-ROM into stacks and animations of consecutive slices designed to provide smooth navigation through the skull along the three orthogonal axes (viz., sagittal, coronal, and transverse). Also included are detailed anatomical labels for every 5th slice, a simple measuring tool for use with individual slices, animated 3-D visualizations of the entire skull, and several text files that offer technical information about *Alligator* and this technology.

Alligator: Digital Atlas of the Skull is designed to operate on most popular Macintosh and PC Windows desktop computers. All the software necessary to operate this CD-ROM is provided on the disc, including an interface that enables navigation through the many CT images, visualizations, and text files, using only a mouse or some other pointing device. Table 1 describes the system requirements and basic operation of the CD-ROM. Our Web site, *The Digital Morphology Group*, and other helpful sites are listed in Table 2. These sites provide on-line access to further information related to the technologies and taxa described below.

Our aim in presenting this *Digital Atlas* is twofold. First, *Alligator* figures prominently in a diversity of scientific enterprises, and our CT study is intended as a basic reference for researchers and educators. The dataset included on the CD-ROM shows *Alligator* cranial structure in intricate detail. Through software manipulations of the dataset, we generated a number of novel visualizations of 3-D morphology which convey information that was largely inaccessible to pre-digital morphologists. We believe that these visualizations will prove useful to anyone with a general interest in the morphology of the crocodylian skull. They may prove especially helpful with respect to interpreting tooth replacement sequences (Edmund, 1962), and the anatomy of the extensive pneumatic cavities of the snout and braincase (Witmer, 1995, 1997). Elsewhere in this volume, Brochu presents a phylogenetic analysis of *Alligator* and its extinct relatives that sets a historical context for understanding *Alligator* cranial anatomy. The *Digital Atlas* was developed partly in support of that effort (Brochu 1997a, b, c).

Our second aim with this CD-ROM is to introduce and test a merger among digital technologies that seems potentially useful to a wide segment of the audience for this journal. The core technology is industrial-grade high-resolution X-ray CT, which is emerging as a powerful new tool for morphologists (e.g., Rowe, 1996a, b; Rowe et al., 1993, 1995, 1997; Cifelli et al., 1996; Cifelli and de Muizon, 1998a, b; Rougier et al., 1998), as for Earth scientists in general (e.g., Carlson et al., 1995; Carlson and Denison 1992; Denison and Carlson, 1997; Ryan and Kappelman, 1997; Rowe et al., 1997). A second technology is the multimedia 'authoring' software that was used to build an interface to manipulate, assimilate, synthesize, and navigate through the large data volumes (several hundred to several thousand megabytes) typically comprising a complete 3-D set of high-resolution digital serial sections. A third technology is CD-ROM, which offers a feasible medium for the widespread and inexpensive distribution of large volumes of specialized digital information.

The *Digital Atlas* is the first large-scale field test of an alliance of these technologies. It follows two more-limited CD-ROM releases of our first prototype high-resolution X-ray CT study on the extinct cynodont *Thrinaxodon liorhinus*, a distant (Early Triassic) cousin of modern mammals. Our *Thrinaxodon* CD-ROM was released first for the MS-DOS computer platform (Rowe et al., 1993), and later with a completely new interface for PC Windows (Rowe et al., 1995). *Alligator: Digital Atlas of the Skull* is thus intended as a second prototype, and one that acknowledges growing interest among vertebrate paleontologists in generating, studying, and publishing superb CT datasets for special specimens. In the last two years, more than 100 significant fossil and modern vertebrate specimens have been scanned in the University of Texas High-Resolution X-ray CT Facility (Table 2) alone, including several in the smallest order of vertebrate size magnitudes. Over the last decade colleagues elsewhere have generated many valuable datasets using medical and commercial scanning facilities. In many cases, the exceptional quality of the imagery and significance of the particular specimens scanned make the data potentially interesting to a wide audience of researchers and educators. What now primarily prevents access by that audience is a proven pathway for publishing the large data volumes, and protocols to conveniently view and manipulate them on inexpensive computers. Whereas several seemingly feasible means of distributing large-volume digital datasets are now available, they are as yet largely untested on an international audience such as the one for this journal. We hope the publication of this CD-ROM will engender a useful discussion on a first generation of interface design, data management protocols, and standards for digital publication that might accelerate access to these unprecedented datasets by this journal's entire audience.

TABLE 1. System requirements.

The disc is formatted for use on Macintosh and PC (486 or higher) computers, with a minimum of 16 megabytes of RAM, a CD-ROM drive, a color monitor, and a pointing device. On PC computers, the CD will operate under the Windows 95, 98, and NT.

HOW TO OPERATE THE CD-ROM

PC platform:

1) put the disc in CD-ROM drive
2) log onto CD-ROM drive
3) using Windows Explorer, double click on *Pcgator* icon in the *Pcgator* folder.
4) The opening screen for *Alligator: Digital Atlas of the Skull* will appear
5) Click on the START button.
6) The *Slice by Slice* program will begin; other programs are available in the FILE pull down menu.

Macintosh platform:

1) put the disc in CD-ROM drive
2) log onto CD-ROM drive
3) Double-click on *Macgator* icon in the *Macgator* folder.
4) The opening screen for *Alligator: Digital Atlas of the Skull* will appear
5) Click on the START button.
6) The *Slice by Slice* program will begin; other programs are available in the FILE pull down menu.

TABLE 2. Relevant Internet Sites (URLs)

High Resolution X-ray CT Facility	http://www.ctlab.geo.utexas.edu/
Digital Morphology Group	http://www.ctlab.geo.utexas.edu/dmg/index.html
Department of Geological Sciences	http://www.geo.utexas.edu/
Texas Memorial Museum	http://www.utexas.edu/depts/tmm/
Vertebrate Paleontology Laboratory	http://www.utexas.edu/research/vprl/
NIH Image Home page	http://rsb.info.nih.gov/nih-image/
Adobe Home Page	http://www.adobe.com/

WEB SITE

The Digital Morphology Group is a University of Texas at Austin (UT) Web site (Table 2) that was developed in conjunction with the *Digital Atlas* CD-ROM. It presents a portion of the information and imagery contained on this disc over the Internet, along with data from other high-resolution X-ray CT studies conducted at UT. Most of the information on these pages was assembled at the Center for Instructional Technologies, in collaboration with the High-Resolution X-ray CT Facility, the Department of Geological Sciences, and the Vertebrate Paleontology Laboratory. Complete 3-D datasets for several other taxa are available on this Web site, but generally the imagery is of lower resolution than that presented here on the *Digital Atlas.*

In addition to serving a wider audience, one point of developing this Web site is to offer a comparison between the Web and CD-ROM as delivery media for large-volume digital datasets. Their relative merits are both debated and continually changing, and we hope that our experiment may help to better refine the roles of each, at least for the near future.

ABOUT THE ALLIGATOR

Fossils indicate that *Alligator mississippiensis* diverged from its closest living relative, the Chinese alligator, *Alligator sinensis,* by the Miocene (Mook, 1932; Malone, 1979). In historic times the American alligator occurred in North America along the Atlantic coastal plain from southern Virginia through eastern Texas. Earlier in the Quaternary it ranged as far north as Missouri (Preston, 1979; Holman, 1995), but it was exploited heavily for its hide and most populations were heavily depleted or extirpated earlier in this century (Groombridge, 1987; Thorbjarnarson, 1992). Enlightened conservation practices and intensive captive breeding programs have made *Alligator* one of the success stories of recent conservation biology, and limited hunting and commercial harvesting are now permitted. Indeed, captive breeding programs were so successful that crocodylian biologists are now provided with a readily available source of specimens. Because of its accessibility to Western researchers, *Alligator mississippiensis* has become the most frequently used exemplar for all living crocodylians in studies of morphology, behavior, developmental biology, physiology, and genetics.

The name *Alligator* has been used in a variety of contexts over the past two centuries (Brochu, this volume). As currently recognized this group first appears in the Oligocene of South Dakota (Matthew, 1918; Mook, 1932; Malone, 1979). *Alligator* is part of a much larger clade—Alligatoridae—that is presently most diverse in the Western Hemisphere, with a single living species, the critically-endangered Chinese alligator, in Asia. Caimans are the predominant alligatorids in South and Central America today, and caiman diversity was apparently high during the Tertiary (Langston, 1965). Monophyly of Alligatoridae relative to other extant taxa is not controversial and is independently supported by morphological and molecular data sets (Densmore, 1983; Norell, 1989; Norell et al., 1994; Hass et al., 1992; Gatesy et al., 1993; Kumazawa and Nishida, 1995; Poe, 1996). The Cretaceous and Tertiary geographic range of Alligatoridae and its closest extinct relatives includes much of Eurasia and, in North America, extends as far north as Ellesmere Island (Mook, 1921; Case, 1925; Patterson, 1931; Kuhn, 1938; Malone, 1979; Preston, 1979; Estes and Hutchison, 1980; Bartels, 1984; Norell et al., 1994; Berg, 1966; Wu et al., 1996; Buscalioni et al., 1997).

THE ALLIGATOR SKULL

Living crocodylians are highly distinctive and differ from other reptiles in several striking features. To introduce some of these features as they are presented in the *Digital Atlas*, we briefly describe them below with parenthetical reference to a slice number or an approximate range of slices that display these features in the *Slice by Slice* program on the *Digital Atlas* (see below). In bracketing ranges, we have chosen slice numbers divisible by 5, because every 5th slice is provided with anatomical labels via an on-screen label button (the exact limits of the structures may extend a few slices beyond either bound listed below). The numbering convention for these slices is as follows. Coronal (cor.) slices begin at the rear of the skull (cor. 1) and end at the front (cor. 869); transverse (tvs.) slices begin at the bottom of the skull (tvs. 1) and end at the top (tvs. 135); and sagittal (sag.) slices begin on the left side of the skull (sag. 1) and end at the right (sag. 387).

An elongated snout with an extensive secondary palate is one of the most obvious distinctions of crocodylians. The secondary palate is formed by palatal laminae of the premaxillae (''pm'' in cor. 760–785), maxillae (''m'' in cor. 370–720), palatines (''pal'' in cor. 305–550), and pterygoids (''pt'' in cor. 195–410), that grow medially to join into a broad sheet before hatching (Parker, 1883; Voeltzkow, 1899; Shiino, 1914; Ferguson, 1981, 1984, 1985). This structure encloses a long nasopharyngeal duct (''npd'' in cor. 270–835) that opens into the pharynx through the internal choanae (secondary choanae *sensu* Witmer, 1995), which are displaced so far caudally (''ic'' in cor. 240–270) that they lie behind the orbits (''orb'' in cor. 295–435).

On either side of the nasopharyngeal passage is a box-work of thin bony walls that enclose large paranasal pneumatic sinuses, which fill much of the volume of the broad snout (tvs. 35–70, cor. 390–755). The elongated secondary palate is correlated with the evolution of a flattened (platyrostral) snout, and it may contribute strength to the rostrum (Busbey, 1994; Witmer, 1997).

The crocodylian braincase is also distinctive in being surrounded by an extensive system of pneumatic channels and cavities of complex form (Owen, 1850; Wettstein, 1937; Colbert, 1946; Tarsitano et al., 1989). From either side of the braincase, the pneumatic system communicates with the pharynx via a pair of epithelial eustachian tubes that pass between the basisphenoid and basioccipital through the eustachian foramina (''mea'' in tvs. 70–80), and which merge into a common eustachian duct that opens into the pharynx (Owen, 1850) through a single median opening (''meu'' in tvs. 60–70) and a pair of lateral openings (''leu'' in cor. 190) between the basioccipital and basisphenoid. The function of this pneumatic system remains unclear, in part because the anatomy of the system has been so difficult to observe. Similar structures exist in modern birds (Walker, 1990) and some non-avian dinosaurs (Currie, 1985; Currie and Zhao, 1993). On both phylogenetic and structural grounds, the pneumatic system of the braincase in crocodylians is non-homologous with the system in birds and their extinct theropod relatives (Gauthier, 1986; Gauthier et al., 1988; Witmer, 1997; Dingus and Rowe, 1997; Rowe et al., 1998).

In crocodylians, these features are broadly correlated with major changes in the orientation of the braincase floor. In archosaurs ancestrally, the basisphenoid was shaped as a broad plate anterior to the basioccipital. In contrast, in mature living crocodylians, the basisphenoid and basioccipital project ventrally, extending the osseous eustachian channels and giving the occipital plate what is known as a 'verticalized' appearance (Tarsitano, 1985). This is visible in the CT slices close to the midline (e.g., sag. 195), which show laminae of the basioccipital and basisphenoid projecting ventrally along the path of the median eustachian opening.

The skull of *Alligator mississippiensis* is distinctive among crocodylians in several features. Alligatorids generally are characterized by a dorsal extension of the nasopharyngeal duct in the vicinity of the internal choana (Müller, 1967; Norell, 1989), and the prefrontal pillars of *Alligator* are hollow (''prf.rec'' in cor. 390–455) (Witmer, 1995). Whereas non-alligatorid nasopharyngeal ducts generally lack a midline septum, that of *Alligator* projects to the rear of the duct and protrudes ventrally beyond the rim of the choana (''ics'' in tvs. 40–50).

ABOUT THIS SPECIMEN

The scanned skull (TMM m-983) is from the partial skeleton of a young *Alligator mississippiensis* from the Florida Everglades that is housed in the collections of the Vertebrate Paleontology Laboratory of the Texas Memorial Museum. The specimen was flensed and dried, defleshed with dermestid beetles, and degreased in dilute ammonia. Sex of the specimen is unknown. A video of the specimen is presented in the ''*Real Alligator Skull Viewer.*'' A young specimen was chosen as part of a systematic comparison between juvenile specimens of modern crocodylian species, using high-resolution X-ray CT (Brochu, 1997a b, c, unpubl. data).

The ontogenetic immaturity of the specimen at time of death is indicated by many features. Most obviously, the skull length (217 mm from snout tip to back of jaws) is less than half that of the largest known skulls. The laterosphenoids, which arise early in ontogeny from paired ossifications on either side of the braincase (de Beer, 1937), approach each other but remain separated in this specimen (''ls'' in tvs. 85–120). In fully mature individuals the two bones are in contact along the midline of the skull. In addition, the basioccipital remains separated from the exoccipitals by a widely open suture (cor. 150–185), whereas in the largest known specimens these bones are fused. In gross shape, larger skulls also have relatively broader snouts (Mook, 1921; Kälin, 1933; Hall and Portier, 1994). In the postcranium, the neurocentral sutures are open throughout the presacral column and as far back as the sixth caudal vertebra, another indication of immaturity (Brochu, 1996). The vomers and both stapes are missing from this skull, presumably an artifact of preparation. We note that some rostral structures are not bilaterally symmetrical and this may complicate interpretation of some slices.

ANATOMICAL LABELS

In the *Slice by Slice* navigator on the CD-ROM (Table 1, below), anatomical labels are provided for every 5th slice in each serial section stack. Labels can be turned on or off by clicking the label button (marked by an orange flag bearing the letter 'L'). Major bones are labeled in red, and subsidiary structures (e.g., processes, nerve foramina, the mandibular symphysis, pneumatic structures) are labeled in yellow.

In choosing anatomical terminology, we generally followed the conventions of Iordansky (1973), Walker (1990), and Witmer (1995, 1997). Primary anatomical references for rostral structures are Bertau (1935), Wegner (1957), and Witmer (1995, 1997). Primary references for otic structures are Hasse (1873), van Beneden (1882), Wever (1978), and Walker (1990). For circumcranial pneumatic structures, our terminology follows Colbert (1946) and Walker (1990). For the braincase and cranial nerve passageways, we follow Iordansky (1973) and Walker (1990). Details of mandibular innervation passageways were derived from Nilsson (1944) and Poglayen-Neuwall (1953). Vascular structure terminology follows Hochstetter (1906) and Walker (1990). Other important discussions on the identities of cranial structures are provided by Owen (1850), Simonetta (1956), Busbey and Gow (1984), Tarsitano (1985), and Tarsitano et al. (1989).

We coin three names here. The first is the 'parietal antrum' (yellow label 'pa' in cor. 210–245), which probably corresponds with the 'neural pocket' of Tarsitano et al. (1989). The second is the 'articular antrum' ('aa' in cor. 60–90), which is a cavity within the articular that communicates with the quadrate via the foramen aereum. Third, the 'surangular channel' ('sc' in cor. 280–370) is a prominent canal passing through the surangular. Its entrance lies within the Meckelian canal, immediately anterior to the external mandibular fenestra. Its exit lies externally between the anterior processes of the surangular. We also note that the crocodylian opisthotic and exoccipital fuse together before hatching (Parker, 1883; Shiino, 1914; de Beer, 1937; Klembara, 1991). In the labels for this dataset, the term opisthotic is used in reference to the tympanic bulla and subcapsular buttress; we acknowledge that the paroccipital processes are partly of opisthotic derivation.

CT SCANNING

Visualizing and measuring complex 3-D anatomical structures are among the most fundamental processes of vertebrate morphology, and the most difficult. For more than 300 years, dissection and maceration have been the dominant techniques of morphology, and even today detailed dissection remains the mainstay of vertebrate morphology and anatomy. Serial sectioning offers an even more informative way of studying complex 3-D biological structures, and the basic techniques of sectioning were refined more than a century ago (de Beer, 1937). But this knowledge has been very costly. Serial sectioning is highly labor-intensive and it results in the destruction of the specimen itself. Moreover, it is generally difficult to quantify areas and volumes from mechanically cut or ground sections. The resulting preparations are commonly fragile and many unfortunate instances can be cited where irreplaceable histological collections were lost through mishandling or administrative fiat (e.g., Rowe 1996a). Nevertheless, nearly two centuries of knowledge gained from serially sectioned biological specimens is now fundamental to a vast spectrum of biological studies (de Beer, 1937; Olson, 1993).

With the invention of X-radiography near the beginning of this century, a non-destructive means of studying diverse internal anatomical structures became available. Unlike serial sectioning, however, conventional radiographs are unable to resolve the internal structures of objects in three dimensions because they are projections onto a 2-D plane. X-ray computed tomography emerged during the early 1970s as the first successful method to map non-destructively the internal structure of complex objects in three dimensions. It was invented in Great Britain in 1971 as a medical diagnostic tool, and its inventors, G. N. Hounsfield and the late A. M. Cormack, were awarded the Nobel Prize in 1979 for this accomplishment (Taube and Adelstein, 1987). In this technique, a specific plane of an object rotating on a turntable is illuminated by a thin fan of X-rays. After passing through the specimen, the X-ray energies are recorded by an array of detectors. Digitized information on attenuation of the X-rays as they pass through the illuminated plane at various angles during rotation is recorded and used to mathematically reconstruct a two-dimensional density map of that ‘slice’ of the specimen. By sequentially imaging and stacking all the two dimensional ‘slices’ of a specimen at proper distances, its entire 3-D density structure can be mapped (Selman, 1985; Carlson, 1993).

The utility of CT technology is strongly influenced by three issues: image resolution, the particular imaging conditions of each object scanned, and the ease with which data can be exported and analyzed. Resolution is itself a function of the thickness of the slice illuminated by the X-ray beam, the settings and properties of the detectors, and the physical properties of the specimen. Medical CT scanning facilities generally obtain slice widths of one to two millimeters on comparatively large, low-density specimens. Morphologists have now used medical scanners with considerable success on fossil and Recent specimens of human-sized and somewhat smaller vertebrates (e.g., Conroy and Vannier, 1984; Luo and Ketten, 1991; Currie and Zhao, 1993; Joeckel, 1992; Willis et al., 1995; Grine, 1997; Conroy et al., 1998). However, detailed imaging of the smallest vertebrates still remains generally beyond medical CT capabilities, and their lower X-ray energies fall short of the power needed for very dense natural materials such as the largest fossil vertebrates. Another common but repairable limitation of medical scanning facilities is that they generate digital files that are stored in proprietary or other formats that are difficult (and with some software illegal) to analyze off-site.

High-resolution industrial-grade CT scanners are the direct descendants of medical diagnostic CT scanners. Over the last decade, the development of high-energy micro-focal X-ray sources, and improvements and innovation in the design of X-ray detectors have produced a hundred-fold improvement in the spatial resolution of CT imagery. The latest generation of industrial X-ray CT scanners (Table 2) can be equipped with multiple interchangeable sources and detectors that provide resolution over a wide range of sample dimensions and densities. Resolution (slice thickness in this case) of ~5μm can be achieved for small objects (centimeter-scale) and sub-millimeter resolution can be achieved for larger objects (up to several tens of centimeters in maximum dimension).

These instruments have now been successfully tested on vertebrate fossils and Recent specimens at one- (Rowe et al., 1993, 1995, this volume) and two-orders (Cifelli et al., 1996; Rowe and Gans, unpubl. data) of magnitude finer resolution than conventional medical scanners. Furthermore, the greater X-ray energies produced by industrial scanners can penetrate dense objects like large, ancient fossil vertebrate crania. For the first time, almost the entire range of vertebrate skeletal materials and even the smallest vertebrate species can now potentially be studied with this technology. The greater part of vertebrate diversity has probably always resided among species too small to usefully inspect with medical equipment, so this new generation of high-resolution CT scanners offers a great leap in the potential utility of tomography to vertebrate morphology and anatomy.

CT IMAGES

X-ray CT produces two-dimensional images that show what an object would look like if it were to be sliced open along the image plane (Carlson, 1993; Carlson et al., 1995). Contrast in an X-ray CT image is generated by differences in X-ray absorption that arise mainly from differences in density within the object. A linear relationship associates the gray-scaled pixel values of the imagery with the varying densities of the object. In the dataset on this CD-ROM, black pixels are calibrated to the density of air, and the whitest pixels denote the densest bone. Digital X-ray CT imagery is generally presented in graytones to approximate the appearance of conventional X-radiograms, but any set of colors can be digitally mapped onto the density variations recorded in the imagery (Bottorff, 1993).

Despite their similar appearance, tomographic images are very different from standard X-ray images (Selman, 1985; Carlson, 1993; Carlson et al., 1995). Standard X-radiograms are shadowgraphs of an object, simple projections of parallel X-rays onto a single plane that show the amount of total absorption along the path of each ray. A certain amount of energy is absorbed from the incident X-ray beam as it passes through the object, but the depth at which each part of that absorption occurred is not recorded. In tomographic imaging, however, X-rays pass through the object along multiple paths in a single plane, as the object rotates within the stationary fan beam (in medical scanners the patient remains stationary while the X-ray source rotates). Mathematical formulas are used to determine the depth at which each part of the total absorption occurred along each X-ray path, and computer algorithms employ the formulas to generate a CT slice image. X-ray CT images display differences in density at each of several thousand points in a seemingly 2-D slice through the object.

Because each CT slice actually represents a certain finite thickness (determined by the imaging conditions), one can construct a continuous three-dimensional map of the density variations in the object by stacking up CT slices at proper distances. These volumetric maps or models can be manipulated in several different ways. For this CD-ROM, for example, the three-dimensional data set was re-sectioned digitally along two sets of planes perpendicular to the original CT slices, to produce coronal, sagittal, and transverse viewing options. Similarly, a 3-D digital rendering of the scanned *Alligator* skull was generated for this CD-ROM by stacking an entire set of slices and locating a digital surface enclosing the regions with densities corresponding to bone. We performed both of these tasks using homemade software, but a growing armament of commercial software and ‘freeware’ can now perform these functions on desktop-class computers equipped with a large amount of random-access memory (RAM) (Table 2).

The images stored on this disk were originally generated as the skull was scanned in 135 consecutive parallel horizontal planes, at a machine-calibrated increment of 250 μm between slice centers. Judging from independent measurements taken directly from the specimen itself, we estimate the true slice thickness to be 258 μm (we used this variable to calibrate the measuring tool). Slices in the coronal and sagittal planes were generated digitally using a homemade software tool. The geometry conventions adopted on the software and in organizing data storage are as follows. The transverse slices are those taken in a horizontal plane (XY plane). Sagittal slices are those taken parallel to the sagittal plane (XZ plane) and coronal slices are along planes (YZ plane) perpendicular to both the sagittal and transverse planes.

Owing to the orientation of the skull during scanning, the sagittal and coronal synthetic slices deviate from the true sagittal and coronal planes by approximately two degrees. For example, sagittal slice 195 passes directly through the midline at the back of the skull, where one can see the choanal septum, the anterior and posterior channels of the median eustachian opening, and the full extent of the basisphenoid rostrum. However, this slice passes through the right first dentary alveolus rather than the mandibular symphysis. The position of each slice with respect to a radiogram of the whole skull is marked by a red navigation bar in the navigation window.

The dataset used in *Alligator: Digital Atlas of the Skull* was generated in 1995 by Scientific Measurement Systems, Inc., of Austin, Texas, using an SMS 101 scanner that was built in the 1980s. During the scanning, the scanner evidently under went a shutdown-restart when the X-ray path reached approximately one centimeter ventral to the palate. This produced a shift in image contrast in some of the slices at this level, which is most obvious in the coronal slices passing through the lateral pterygoid flanges.

We are pleased to report that this outstanding dataset was generated with a CT scanner that now represents more than 10-year old technology; and that the newest generation of high-resolution CT scanners generate far better imagery, with greater spatial resolving power. We plan to begin very soon to distribute even better datasets for other taxa, using a new class of high-resolution X-ray CT scanner now in operation at the University of Texas at Austin (Table 2).

WHAT IS ON THE *DIGITAL ATLAS*

Some of the features on the CD-ROM were alluded to above, but for the sake of convenience they are all discussed below. The core program on this disc is the *Slice by Slice* navigator, which enables navigation through stacks of 1391 CT slices taken in consecutive coronal, transverse and sagittal planes. To run *Slice by Slice,* start the CD-ROM (Table 1) and click on the START button located on the title screen. *Slice by Slice* runs in its own window, and a menu bar across the top of the window has controls for the following:

- Navigation buttons for moving forward and backward through the stacks
- Navigation window, in which a red line shows the position of the current slice on a standard X-radiogram of the skull
- Control window for setting the number of slices stepped with each click on a navigation button
- On/Off button for anatomical labels (available only on every 5th slice, starting with slice 5 in each stack),
- Abbreviation index for anatomical labels
- Buttons for selecting transverse, coronal, or sagittal slice stacks
- Tool for measuring linear distances on individual slices

A series of animations provides 2- and 3-D visualizations around and through the skull. They are run from the ''*File*'' pull-down menu at the top of the computer screen. Animated sequences of consecutive slices (select ''*Open Animations*'') are provided for sagittal, coronal, and transverse stacks, and buttons at the top of the animation window provide control of both direction and speed of navigation through the stack. We note that there is often one empty (black) slice at the beginning and end of the skull in the slice stacks and animations, which provide assurance that the specimen was not clipped during scanning or image processing.

The 3-D animations portray a surface model of the specimen from continuously changing perspectives. The animated model of the skull was made by surfacing an entire set of slices and producing a polygonal model that could be manipulated in 3-D animation software. Computer-generated animations of the model show the skull spinning about each of its three orthogonal axes. A ''VR'' (Virtual Reality) animation enables one to pivot the skull about its geometric center in any direction and to view it in 3-D from any angle. A video of the actual specimen is presented in the *Real Alligator Skull Viewer*, offering a simple means of evaluating accuracy of the computer-generated 3-D model. A series of text files provides help in operating the disc, along with a copy of most of this introduction. These files are accessed from buttons on the opening screen, and from pull-down menus that appear at the top of the screen once the program has been started.

ARCHIVE FILES

An Archive folder located on the CD-ROM contains many of the original digital files used to develop this memoir. These files are not directly accessible using the *Digital Atlas* navigator, but they can be accessed using standard word processors and image processing software packages like NIH *Image* (for raster graphics; Table 2). The organization of the archive folder is set out in the Table of Contents for this memoir. Among its other contents are the original (i.e., un-processed) transverse (XY-plane) slice images generated by the SMS 101 scanner. We include them here in the event that readers might wish to apply their own filtering, re-slicing, and surfacing algorithms to the data, or simply to inspect the noise levels or other properties of the original dataset while using this disc. The original images are saved as TIF (Tagged Image Format) files that can be opened by NIH *Image* software and by most off-the-shelf image processing software.

Included in the Archive folder is the 3-D surface model that we used to generate the 3-D animations on the CD-ROM. It is stored as an STL (stereolithography) file. Although we have not tested the performance of this model outside our own software, we believe it suitable for importation into most popular 3-D visualization software packages. It can also be rendered as a physical 3-D model in material ranging from paper to nylon, using the various solid modeling output devices now available. Thus, 3-D physical models of the specimen can be generated from the STL file located in the Archive.

Also within the archive folder, we include digital copies of both this article and Brochu's (this volume) monograph on Alligatoroidea, as Portable Document Format (PDF). These latter files can be opened in a standard Adobe Acrobat (R) reader, and the advantage of this is that they can be 'searched' for words or combinations of words, enabling quick scanning of this entire volume for specific points of information.

ABOUT THE PROJECT

The *Digital Atlas* was produced in a collaboration among students studying computer science, vertebrate paleontology, and biology in the UT College of Natural Sciences. Production of the *Digital Atlas* involved the departments of Geological Sciences and Computer Sciences, the Center for Instructional Technologies, and the Vertebrate Paleontology Laboratory of the Texas Memorial Museum. The venue for this collaboration was a course entitled 'Multimedia Production for Natural Sciences.' We highlight this aspect of the project because the fact that student labor played a major role in the development of the CD-ROM speaks to the feasibility of generating similar products on a larger scale in the future. Undergraduates can now master much of the technology and perform much of the labor that goes into building an interface for the data on a disc like this. Interpretation of anatomy and other issues pertaining to the 'expert content' of the imagery remain largely, but not exclusively, in the domain of more advanced graduate students and faculty.

This course was designed to simulate the environment of a commercial multimedia publishing workplace. The client, in this case a faculty member (Rowe), established specifications for the final product to be developed by a team of graduate students and undergraduates. In the course of a single semester production schedules and divisions of labor were determined, the various components of the CD-ROM and interface software were generated, and the final integrated product was assembled and tested.

To transform raw CT data into a publishable format, faculty and graduate students provided expert anatomical information and labels for the CT imagery, and graduate students and undergraduates performed basic image processing. The *Alligator* CT dataset used in the *Digital Atlas* was collected during dissertation research on the phylogenetic systematics of Crocodylia by Christopher Brochu (1997a, b, c, this volume), who directed the labeling effort and all the research that it entailed. The development of presentation software was undertaken by undergraduate Computer Sciences majors, who first evaluated authoring software, and then prototyped each of several software components. Once the final components were chosen and built, students assembled and tested alpha- and beta-prototypes. The list of class tasks also included the digital enhancement of raw CT images, digital generation of synthetic CT slices, management of large volumes of data, and library research on the identities of many anatomical structures.

Overall management of the project, which involved coordinating all the technologies and independent efforts of the protagonists was directed by Kyoko Kishi. The final result was a working prototype of the CD-ROM included in this memoir.

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