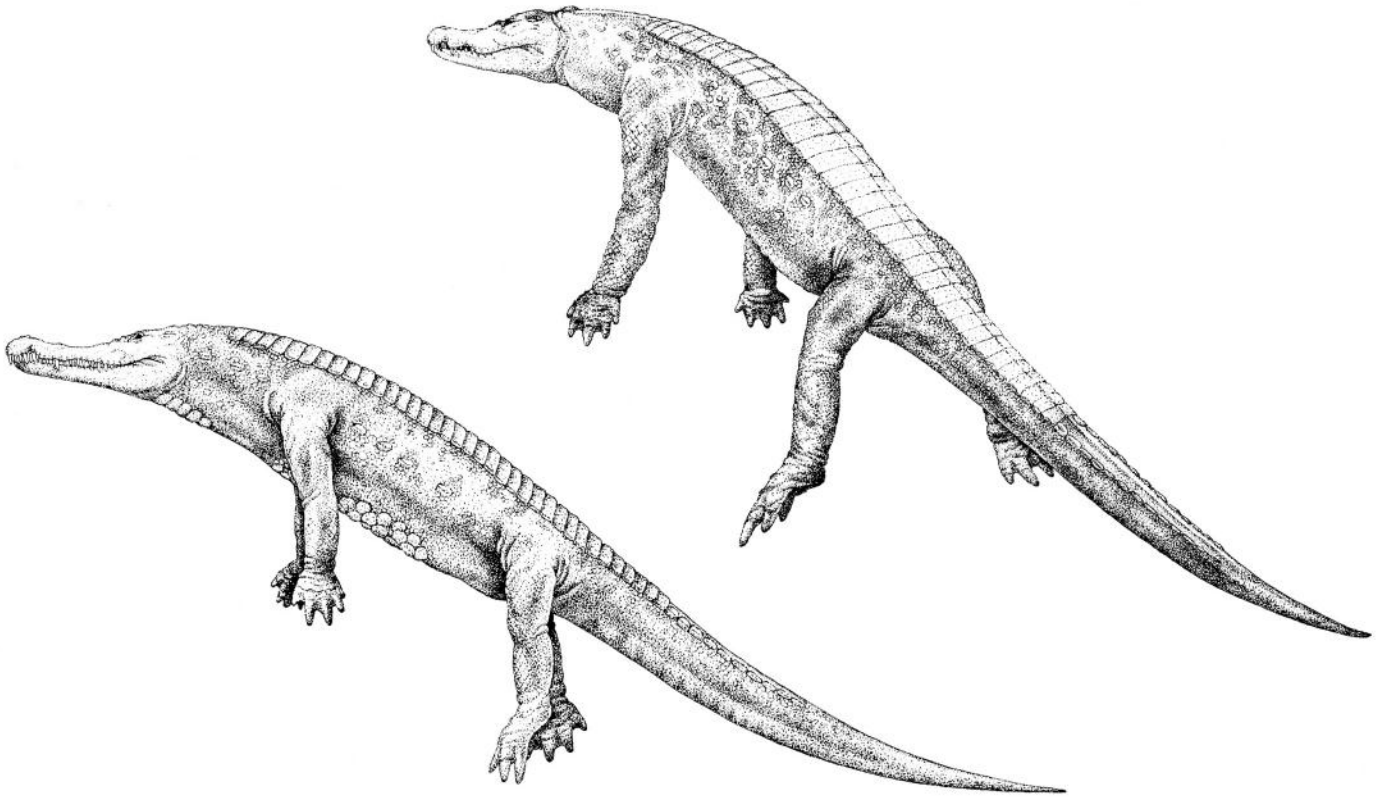
A NEW SKELETON OF THE NEOSUCHIAN CROCODYLIFORM GONIOPHOLIS WITH NEW MATERIAL FROM THE MORRISON FORMATION OF WYOMING

by Bruce R. Erickson



MONOGRAPH VOLUME 10: PALEONTOLOGY

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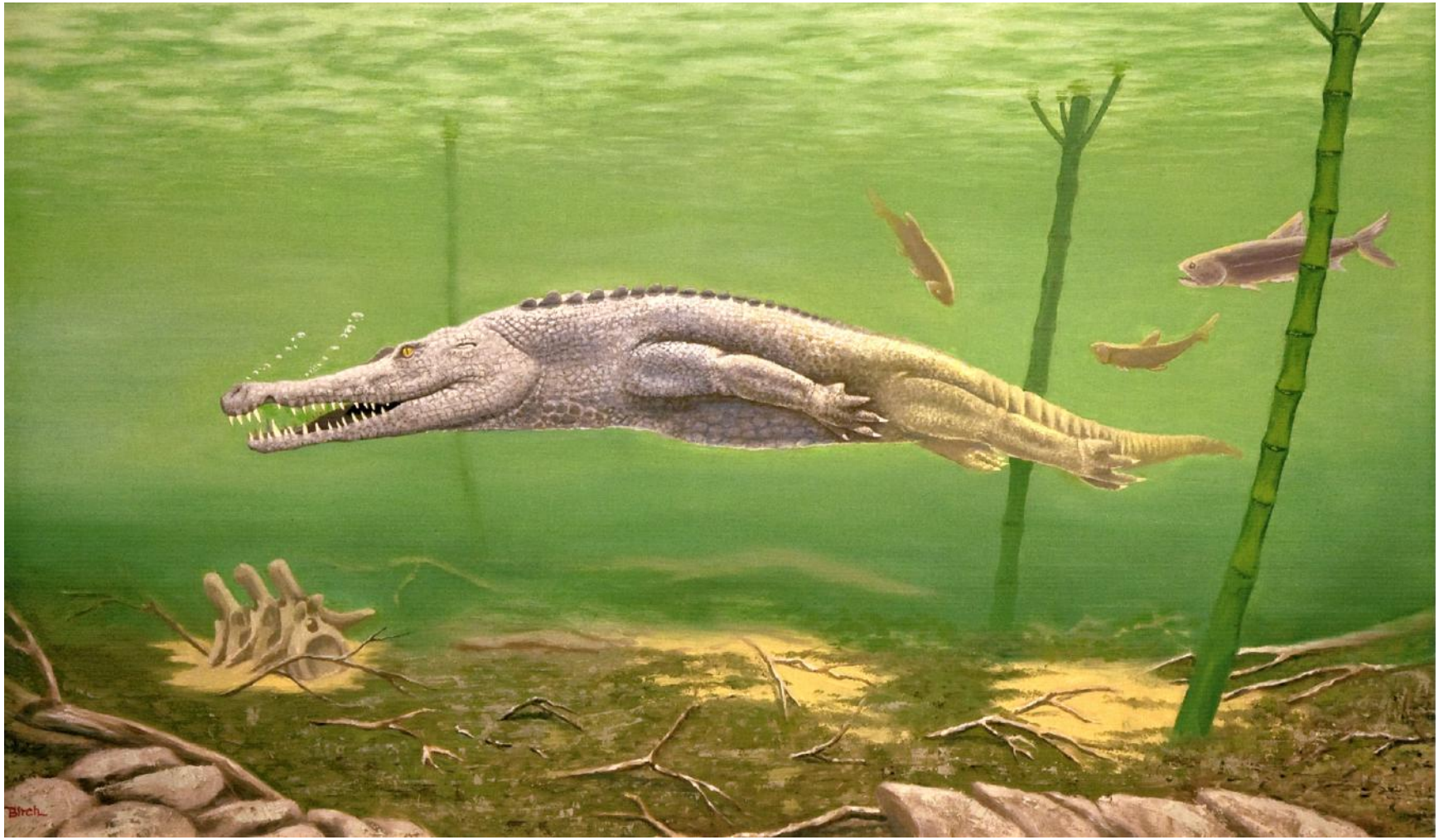

Frontispiece: Flesh restoration of *Goniopholis*.

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VOLUME 10: PALEONTOLOGY

International Standard Book Number: 911338-90-X

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VOLUME 10: PALEONTOLOGY

The Science Museum of Minnesota
120 West Kellogg Blvd.
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December 1, 2016

A NEW SKELETON of THE NEOSUCHIAN CROCODYLIFORM GONIOPHOLIS WITH NEW MATERIAL FROM THE MORRISON FORMATION OF WYOMING

ABSTRACT:

A new specimen of the neosuchian crocodyliform *Goniopholis* with most of its skeletal elements intact provides new information on its morphology. Skull features and overall osteodermal organization as well as taphonomic aspects are discussed in light of beach sand incursions that preserved the skeleton of its stranded carcass.

Key Words: *Goniopholis,* Jurassic crocodyliform, Taphonomy, Scutalation, salt glands.

INTRODUCTION:

The crocodyliform *Goniopholis* is represented in North America by four species: *Goniophois felix, G. lucasii, G. gilmorei, and G. stovalli.* The skulls of these named taxa show no unique characters which distinguish any of them as distinct from the type of *Goniopholis felix.* Their "unusual" characters fall within the range of variation in species morphology.

Unlike most material referred to Goniopholididae the present specimen (SMM P2003.20.1) has the important advantage over many specimens as it is that of a single individual, not a composite specimen of unassociated elements. This is an important value regarding related specimens. The evidence indicates that the skeleton was preserved without appreciable disturbance after it was stranded as a shoreline carcass. Subsequent wave swash episodes deposited sediments which buried the specimen in sand sediments.

Due to the absence of articulated or associated dermal material of many specimens the proposed arrangements of the osteoderms may vary among researchers. An attempted reconstruction showing the various positions of osteoderms and groups of osteoderms proposed for the present specimen are indicated in figures 11, 12, frontispiece, and cover.

SYSTEMATIC PALEONTOLOGY:

ORDER CROCODYLIA Gmelin, 1789
FAMILY GONIOPHOLIDIDAE Cope, 1875
GENUS GONIOPHOLIS Owen, 1841
Goniopholis aff. *G. lucasii*

DESCRIPTION:

SKULL:

The skull has been altered during preservation, note the development of an earlier pathologic condition of the right quadrate. Many of the sutures are obscured especially on its highly sculptured dorsal surface (Figs. 1 and 15). The rostrum shows little distortion. The premaxillary region is typically like that of North American *Goniopholis* with 5 teeth and deep premaxillomaxillary notches. Dorsally the narial opening is nearly circular and partly divided by a premaxillary bar that extends about one third the distance to the anterior rim of the narial opening. Ventrally the premaxillae reach the posterior end of an elongate incisive foramen at the level of the fourth tooth.

A conspicuous feature on the lateral side of the skull near the base of the rostrum (lachrymal area) is a well-defined shallow, ovoid depression (lacrimal fossa of DeAndrade et

al. 2011), measuring 26 mm by 69 mm between maxillary alveoli 11 and 18 (Figs. 1, 2, 3). *G. lucasii* as noted by Foster (2007) has a depression on the lateral side of the rostrum (lachrymal area) like that in the present specimen. On this basis the present form has a tentative possibility of being assigned to *Goniopholis lucasii.*

The surface of the medial wall of the fossa undulates over the dental alveoli lying just beneath (Fig. 3). This feature in this freshwater crocodile is regarded as a probable vestigial space which historically housed salt glands.

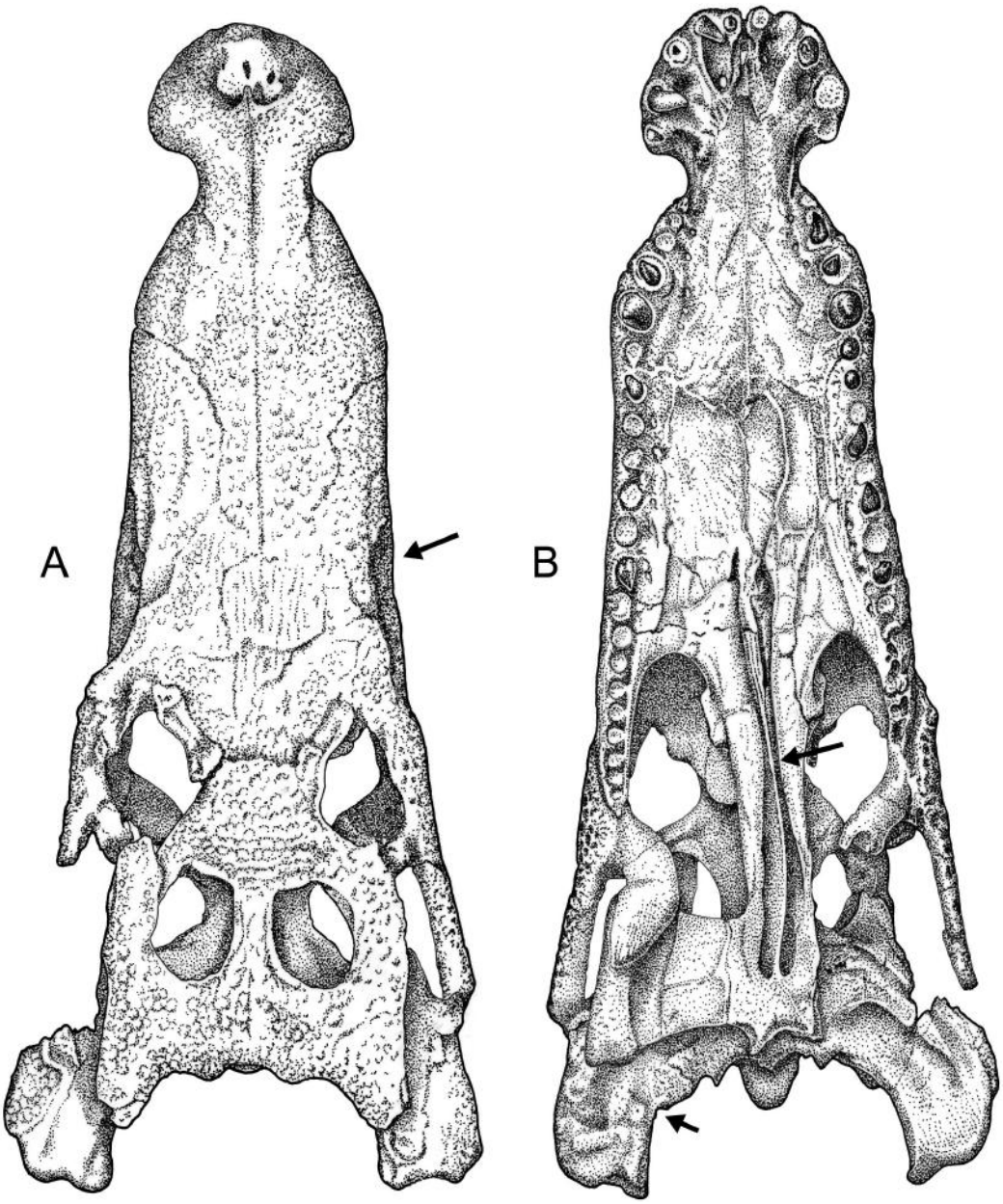

FIGURE 1. Illustrations of the skull of *Goniopholis* SMM P 2003.20.1. A, dorsal aspect showing lachrymal fossa (arrow); B, ventral aspect with bony septum separating choanae (long arrow) and pathology of right quadrate (short arrow).

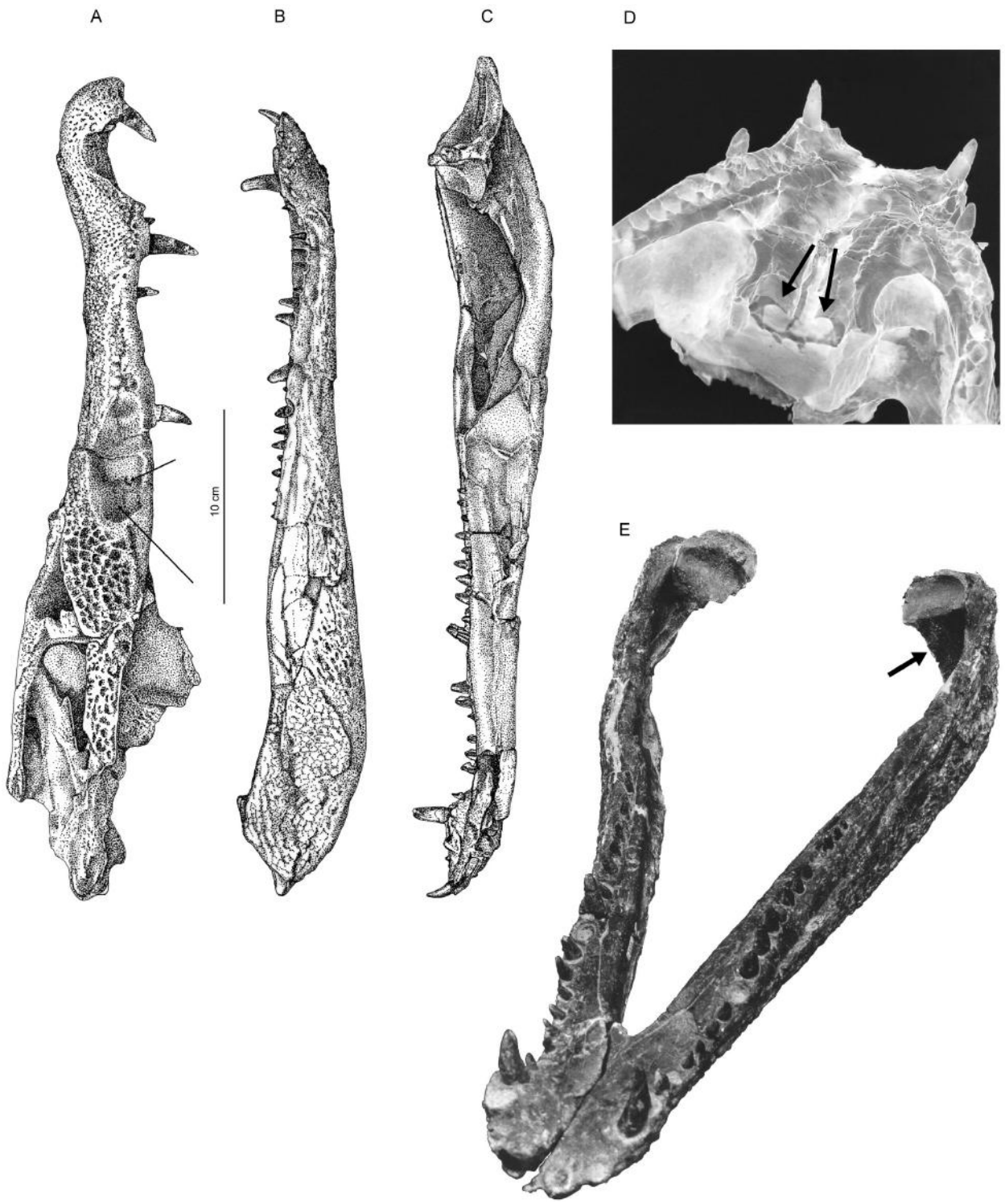

FIGURE 2. Illustrations and photographs of *Goniopholis* P 2003.20.1. A, Skull in right lateral aspect with lachrymal fossa (long line) and foramen (short line); B, mandible in right lateral aspect; C, right mandible in medial aspect; D, 3 d image of rostrum at level of the lachrymal fossa looking forward showing nasal passages (arrows); E, perspective view of complete mandible and adductor fossa (arrow).

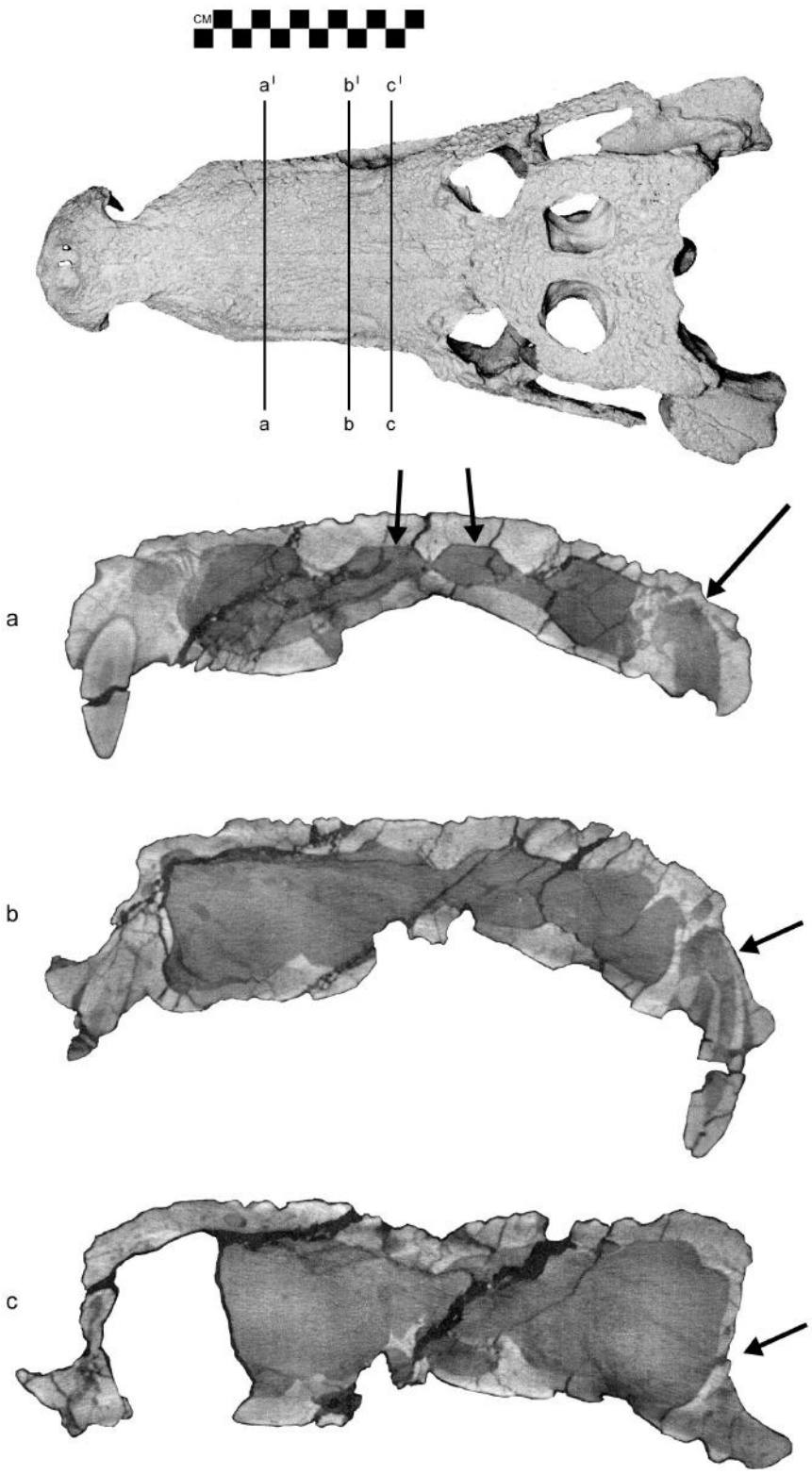

FIGURE 3. Axial C T (computed tomography) scans of rostrum. a-a, is anterior to lachrymal fossa showing nasal passages (short arrows) and vacant alveolus (long arrow); b-b, is at anterior end of fossa (arrow); c-c, is posterior through fossa and shows location of foramen (arrow) into antorbital space.

Among reptiles salt glands evolved independently at least 5 times (Dunson, 1976). Among crocodilians with their long history and extra-renal salt excreting methods, salt glands also arose independently several times. Salt glands in *Goniopholis* were evidently located in the depression described above. They may be likened in their location to those of the marine Goniopholid *Metriorhynhus supercilious* (Gandola, et al. 2006). If they were functional or not in *Goniopholis* is unknown.

Posteriorly the skull shows preservational alterations with loss of the left ectopterygoid, left pterygoid and fragments of the jugals and quadraojugals on either side. Palpebral elements were not located. Modification of the right quadrate is attributed to oblique fracturing with secondary osteomyelitis (Fig. 1 B). The skull table has nearly parallel lateral margins. The supratemporal fenestrae are slightly smaller than the orbits. Both pairs of those openings have irregular borders. The anterior border of the orbit is elevated in a prominent ridge (Fig. 15) that extends anteromedially and narrows the orbit anteriorly.

Ventrally (Fig. 1) the choanae (internal nares) are distorted but remain separated by a midline bony septum for their entire length to the level of the 12th maxillary tooth. The palate is intact forward of this without a secondary opening as noted for *Eutretauranosuchus delfsi,* (Mook, 1967) a goniopholidid from the Morrison Formation. The palatine fenestra is ovoid and broad anteriorly.

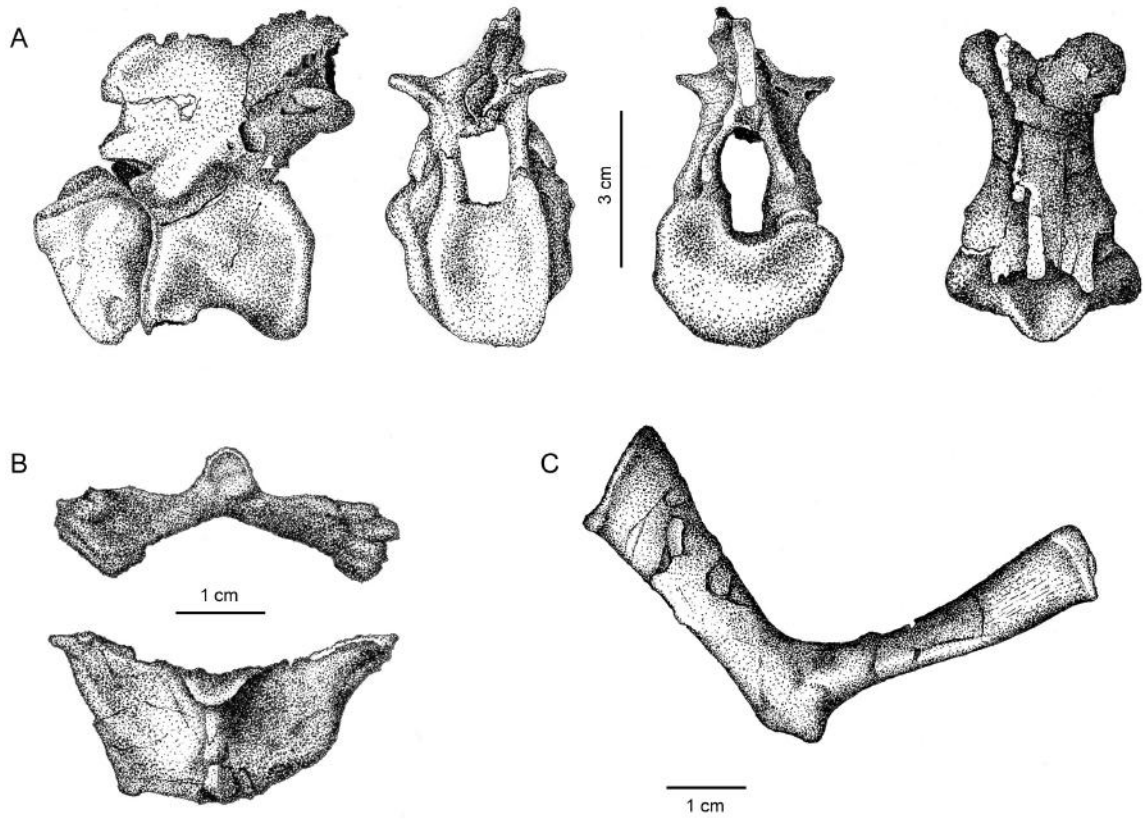

FIGURE 4. A, axis illustrations: In left lateral, posterior, anterior, and dorsal views; B, pro-atlas in posterior (above) and dorsal views; the first intercentrum and the first neural arch are like those of *Crocodylus*; C, first branchial horn of hyoid in lateral view.

Mandible:

Both mandibular halves are preserved in articulation with splenials joined in broad contact at the posterior end of a long mandibular symphysis joining the dentaries (Fig. 2). The dentary is straight ventrally and festooned along the alveolar surface with 23 alveoli. Nearly all of the teeth are in place. Posteriorly the mandible is moderately curved dorsally and terminates in a short rounded retroarticular process. It has a low silhouette and a narrow ovoid shaped external fenestra. Internally the lower extension of the articular stands away from the medial surface of the angular being separated by a wide adductor fossa (Fig. 2). The right coronoid, or a fragment of it, remains as a wedge in the suture between the lateral surfaces of the angular and surangular. The coronoid was evidently separated from the splenial and displaced in the preservation process. Its general form as far as visible is not unusual. Figure 2D is a 3D image of the rostrum at the level of the lachrymal depression.

Hyoid:

The preserved hyoid portion consists of the first branchial horn. This small flat element has two branches of subequal length in slightly different planes. Where they are joined there is an irregular shaped node (Fig. 4).

Dentition:

A total of 21 alveoli are located in the maxilla. Many of those still hold teeth. The dentary contains 23 alveoli. Teeth are present in all except 7 alveoli. The loosely socketed teeth still in place attest to the relatively undisturbed position of the skull and mandible after separation from the carcass and loss of connective tissue.

Vertebral Column:

Vertebrae are fully articulated between the first dorsal and third caudal. All of the neural arches are intact within this section but show incomplete closure of the neurocentral sutures. All of the centra are flat-ended. The complete vertebral series consists of 9 cervicals, 12 dorsals, 2 sacrals, and an estimated 35 caudals.

Of the cervical pro-atlas, neurocentra, and first intercentrum make up a complete atlas. The axis is complete as well (Fig. 4). The axis centrum is short, opisthocoelous, and narrow posteriorly with small paired hypapophyses anteroventrally. The neural canal is twice as high as it is wide. The neural arch has a short, bluntly pointed prezygapophysis that fits into a shallow groove on the medial surface of a posteriorly projecting process of the neurocentrum.

Closure of neurocentral sutures in crocodilians during ontogeny indicates the age of the individual (Brochu, 1996). The mostly open sutures of both the axis – odontoid and the neurocentral contact in the present fossil crocodile suggest a mature age for it.

Cervicals 3 – 6 are displaced with their arches separated from their respective centra. Cervicals 7 – 9 are semi articulated anterior to the first dorsal *in situ.*

The dorsals are fully articulated and without ribs. Neurocentral sutures do not show closure.

The sacrum is complete with two vertebrae (Fig. 5), each equipped with heavy ribs that are broadly expanded distally for contact with the ilia. The second rib is fully as long as the iliac blade. Both anterior and posterior zygapophyses are wide and situated low on the neural arch.

Within the associated caudal vertebral series the first 3 show complete closure of the

neurocentral sutures. All of the other associated caudals have total closure of the sutures as well.

Ribs:
Cervical ribs are scattered in close association with many fragments of dorsal ribs. Those fragmented dorsal ribs were available for assembly of at least 10 pairs of ribs (Fig. 6). As noted, 2 sacral ribs are in articulation with the sacrum (Fig. 5).

Only 3 complete chevrons were recovered with this skeleton. They represent different sections of the tail and assist with estimating the number of vertebrae originally present. Among 10 or less caudal vertebrae and fewer chevrons there is less than good information about the number of caudals, but the likely positions of those elements indicate that a total of 32 – 38 vertebrae is a probable estimate. A total of 35 are displayed in the restored mount (Fig. 13).

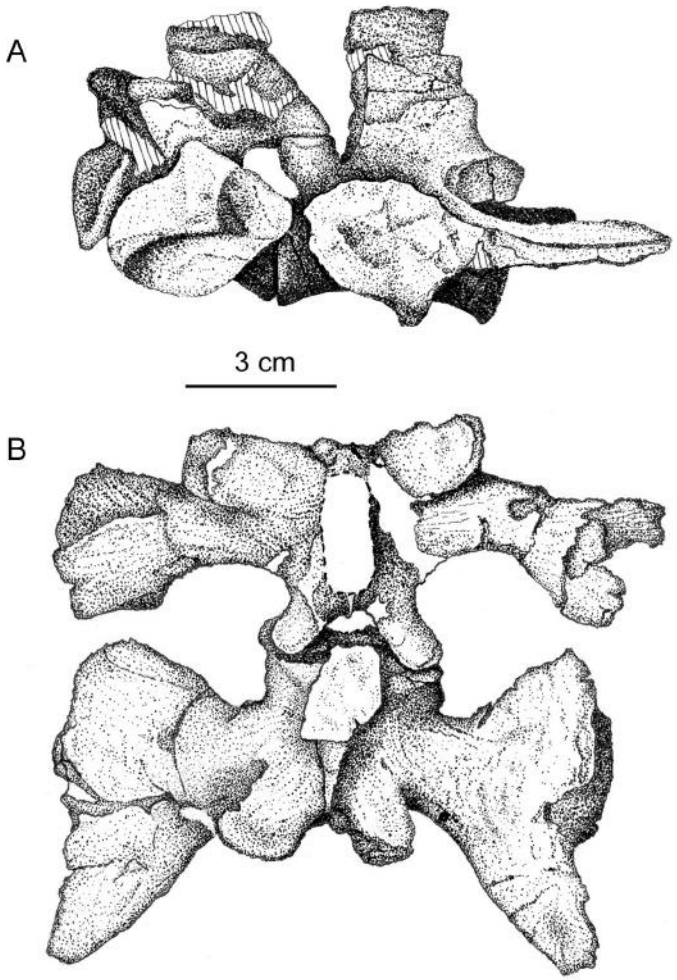

FIGURE 5. illustrations of sacrum. A, left lateral view (anterior to left); B, dorsal view of same.

Shoulder Girdle:

The shoulder girdle is incomplete lacking scapulae and coracoids. The interclavicle is present as a complete element. It is flat, widened at mid-length, narrowed to a blunt point posteriorly, and has a spatulate anterior end. Slight dorsal depressions occur at midshaft for cartilaginous attachments (Fig. 6).

Forelimb:

The front limb consists of the left humerus, radius, ulna, as well as the radial of the carpus (Fig. 7). The ulnar is missing, and the available metacarpals are like those of *Crocodylus.* A strong deltoid crest and expanded proximal and distal ends characterize the humerus along with its sigmoid form. Its total length is slightly less than that of the femur (Table 3). The radius is straight with enlarged extremities. The ulna is represented by a bone that has been modified by a greenstick fracture. Its ends are otherwise normal. Of the carpus only the radial is present. It is elongate with a narrow shaft and only a slightly expanded distal extremity. Its articular facets for radius and ulna are of nearly of the same size unlike *Crocodylus.*

Pelvic Girdle:

The pelvis comprises right ilium, left pubis (epipubis), and left ischium. The sacrum is described under vertebral column above. The ischium has lost much of its distal blade and part of its pubic facet. The pubis is missing the edge of its anterior margin (Fig. 8). All of those elements are essentially like those of living crocodilians.

Hind Limb:

Both femora, tibia, fibula, right astragalus and calcaneum, as well as 3 metatarsals represent the hindlimb and pes (Figs. 9, 10). The femur is sigmoid in shape and expanded at each end. The fourth trochanter is modestly developed and the length of the femur is only slightly greater than that of the humerus. The tibia and fibula are of near equal length. The right astragalus and calcaneum are shown in articulation with each other (Fig. 10). The calcaneum and 3 metatarsals represent the foot.

SCALATION:

Twenty six pairs of imbricating, median dorsal osteoderms were associated with the skeleton. Those are distinguished "right" or "left" by their morphology (Fig. 11). Anterior to the first pair a single osteoderm (scute) spans the breadth of the first pair (Fig. 11) that are joined by suture along midline. This single element overlaps the first pair and bears an imbricating surface on its leading margin indicating that another element was present anterior to it. In the absence of this

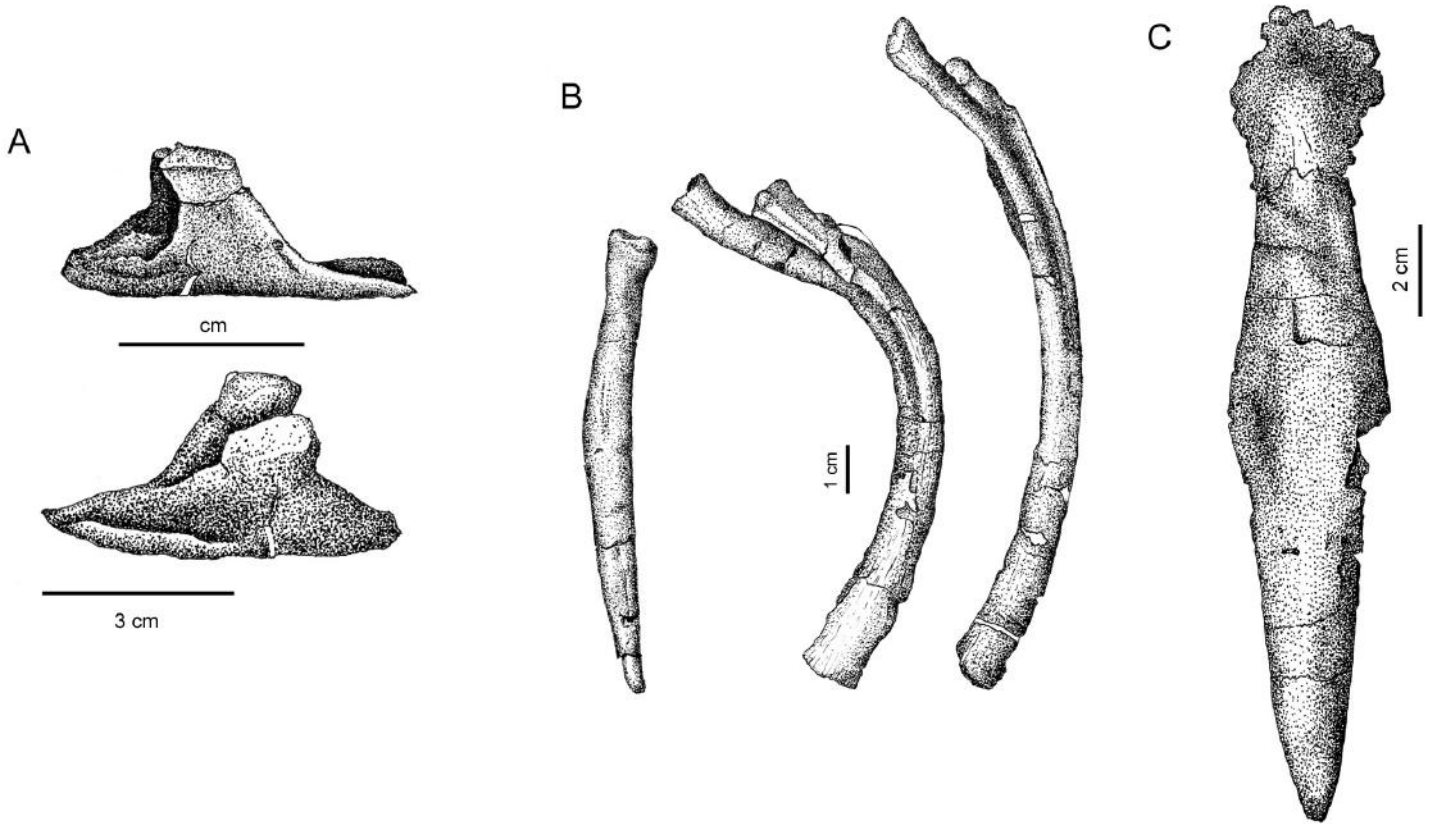

FIGURE 6. Ribs and interclavicle. A, mid cervical ribs in lateral and medial views; B, first cervical and 2 trunk ribs; C, interclavicle in dorsal view.

missing osteoderm an attempted facsimile of it was produced. Together those two most anterior single scutes form a postcranial "nuchal plate" (group) having a similar position to that found in extant crocodiles. Ventrally a group of five or more rings of scutes have imbricate relationships. The individual scutes are united by sutures to form a "gular plate" (Fig. 12). Median, paired osteoderms continue posteriorly to the base of the tail as shingled elements. From here they extend posteriorly as separate osteroderms or scales that diminish in size.

A cluster of 33 or more articulated, polygonal osteoderms comprise a plate on the left flank of the ribcage. All of those have sutural contacts with their neighbors making up a "flank plate" (Fig. 12) which remained intact after collapse of the carcass. A similar number of individual scutes that were located on the right flank were separated from one another during breakdown of the carcass and settled in the sand nearby.

Some individual scutes cannot be positioned reliably and may be referred to as nuchomarginals or postnuchals. For example those shown in Figure 11 A evidently represent midline elements as indicated by their shape and margins fully sutured. Those are scutes with a bony core as compared to "scales" lacking bone. As mentioned by Webb and Manolis (1989) some non-bony scutes may have been highly vascularized and assisted in thermoregulation in crocodiles. Only bony osteoderms are identified in this fossil. Vascularized non- bony scales as well as gaping behavior (Spotila and Terpin, 1977) may well have been a part of thermoregulation with *Goniopholis.* For further discussion of the scalation (plates and shields) of a North American Crocodile see Mehl (1941).

The articulated skeleton (Fig. 13) is mounted as if poised at the air/water interface. One purpose of this natural posture reflects a characteristic position of various living species of crocodilians while submerged just below the surface (pers. obser.). More specifically this body attitude best demonstrated the different groupings (clusters) of osteoderms determined for the present specimen. Figure 14 also shows in left posterior visceral view the flank plates and posterior aspects of the rib cage.

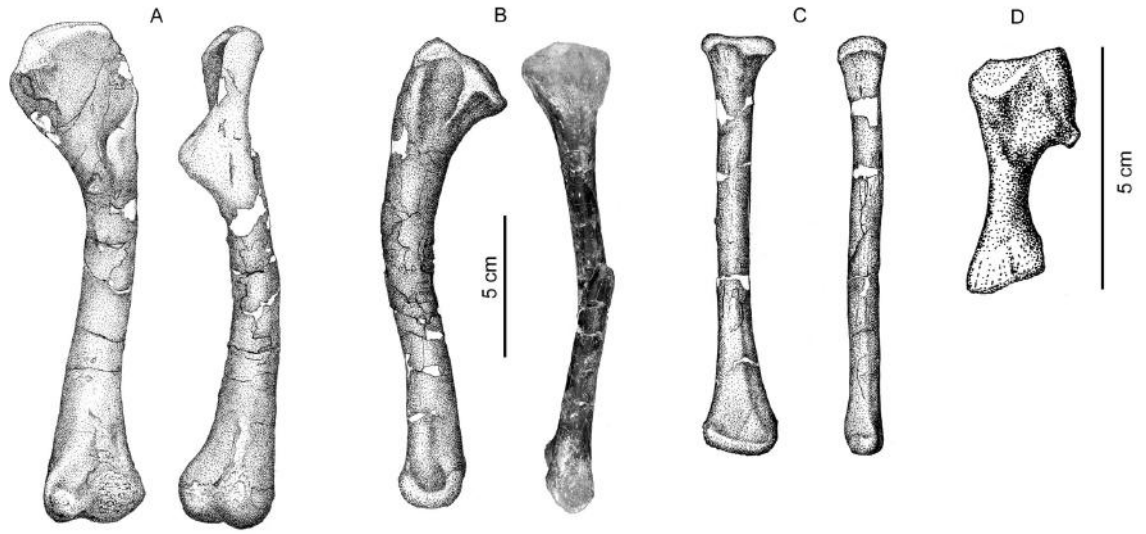

FIGURE 7. Illustrations and photograph of elements of the forelimb of *Goniopholis* P 2003.20.1. A, left humerus in ventral and anterior views; B, left ulna showing greenstick fracture (right); C, left radius; D, radial in posterior view.

TAPHONOMY:

This specimen is remarkable as a partly intact skeleton. Some loss of elements occurred, however the preserved elements provide a most useful *specimen* for analysis. Few of the bones show modification as vertical displacement of the skeleton *in situ* was measured at 190 mm. On close examination of the left radius it appears that the left radius also suffered a midshaft fracture along with that of the left ulna to which it was juxtaposed in life. It is further likely that this fracture of the left radius was mended during its preparation in the lab.

Taphonomic history of this mostly complete, adult specimen indicates that it became stranded "beached" as a probable cadaver on a point-bar in a Morrison stream channel. As characteristic of present-day crocodilians it likely died, became bloated and washed ashore to strand in a "bellyup" position. Subsequent to stranding the carcass experienced some dismemberment and disarticulation. There is no evidence that the carcass was relocated after it stranded. An argument for a high rate of deposition at the site is the fine preservation of the bones.

During preservation the skull was detached along with most of the cervical vertebrae which were individually scattered in close association with one another about the skull. Subsequent to its detachment from the vertebral column the skull and mandible were separated from each other and remained next to the rib cage (Fig. 16). Few teeth were lost from their alveoli. Further shoreline conditions like wave swash, undetected scavengers, and desiccation affected small bones, ribs, and scutes. Nearly half of the "free " scutes were inverted before burial and some were undoubtedly lost as were most phalanges. Figure 16 exhibits the concentration of bones of early stages in the preservation of the skeleton before final preparation was completed in the lab.

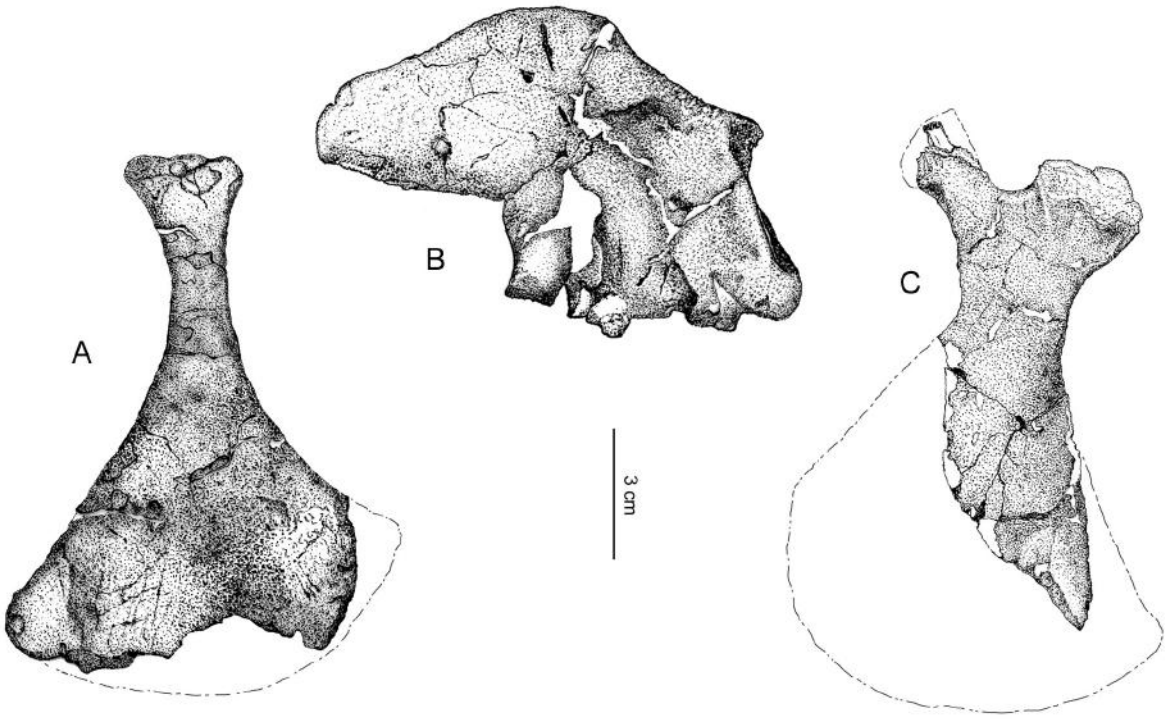

FIGURE 8. Illustrations of pelvic girdle elements. A, left pubis with anterior margin restored; B, right ilium in median view; C, right ischium with blade restored.

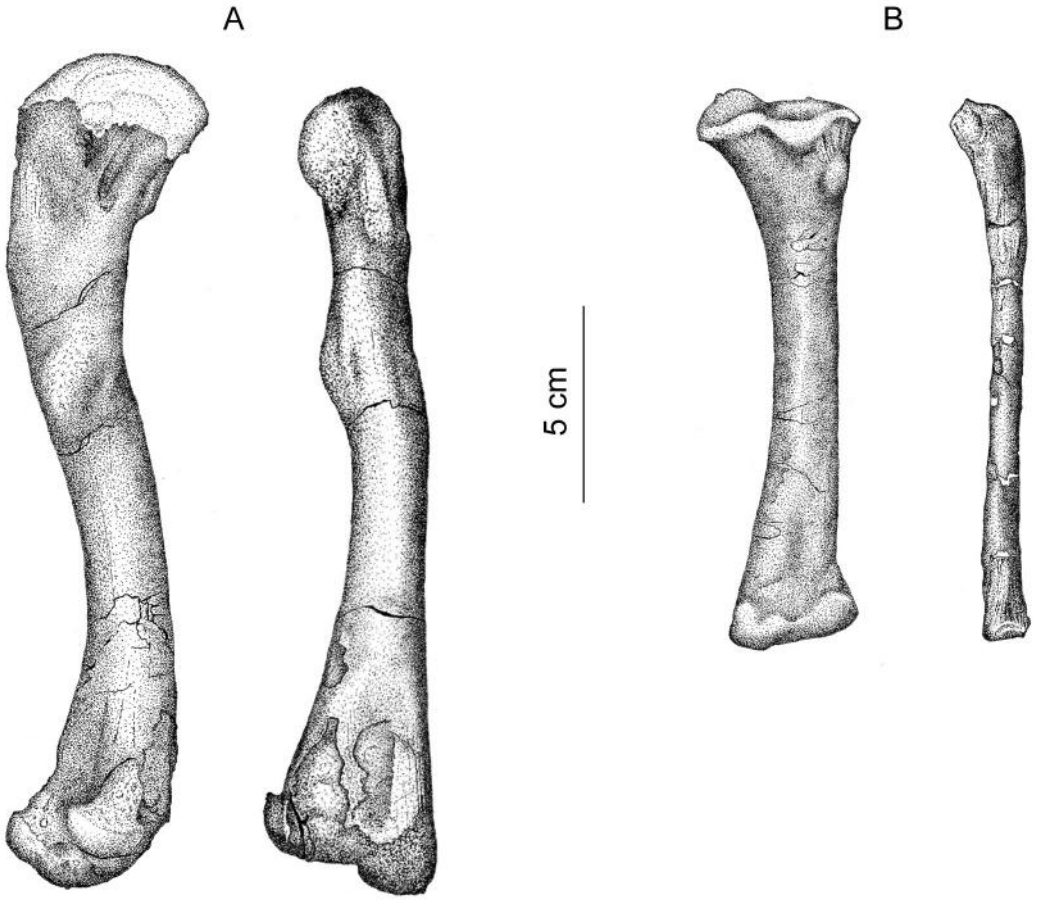

FIGURE 9. Illustrations of elements of the hindlimb of *Goniopholis* P 2003.20.1. A, left femur in ventral and anterior views; B, right tibia and fibula.

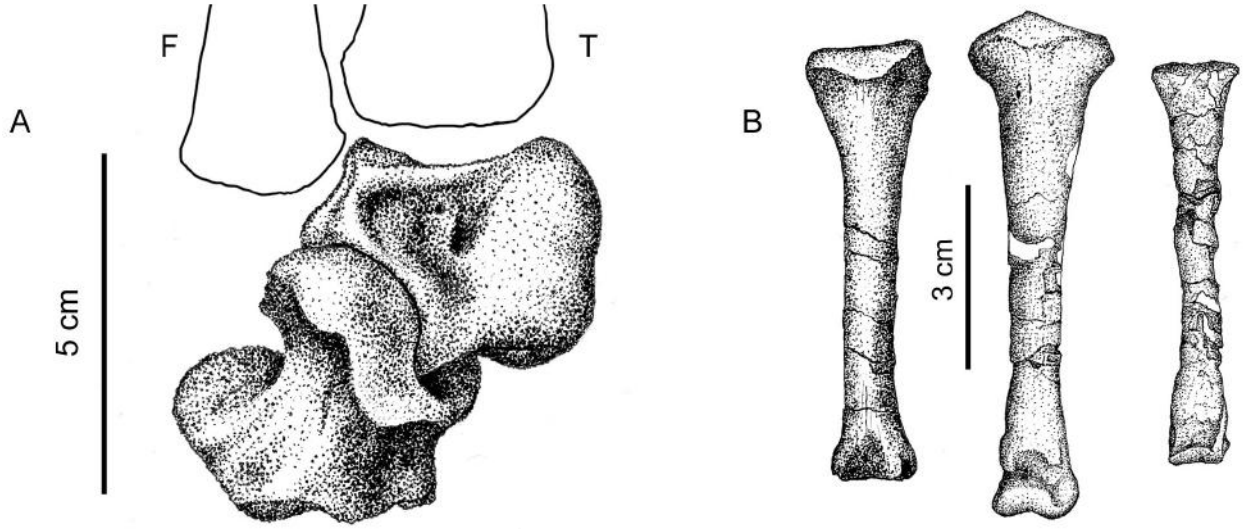

FIGURE 10. Illustrations. A, right astragalus and calcaneum articulated; B, metatarsals.

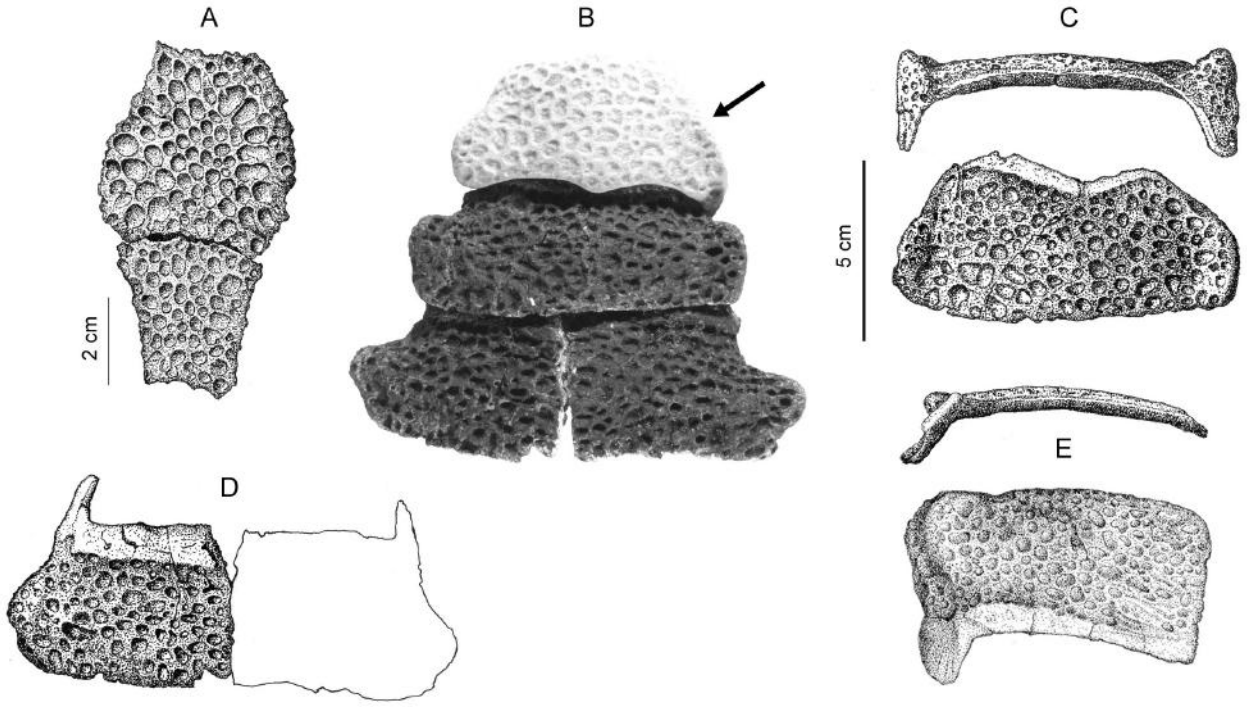

FIGURE 11. Illustrations and photographs of *Goniopholis* P 2003.20.1 osteoderms. A, "midline" elements; B, "nuchal plate" with restored anterior osteoderm (arrow); C, second single osteoderm of "nuchal plate" in dorsal and posterior views; D, paired median dorsal osteoderms; E, single median osteoderm showing imbricating anterior edge in anterior and dorsal views.

Three distinct episodes of sand incursion A, B, C are in evidence. Those episodes can be distinguished by grain sizes of sand, shape of grains (rounded or angular) and the percentage of CaCO3, loss.

The first beach swash of sand "A" surrounded the bones of the skeleton covering some. This deposit contains sand grains of 0.5 mm (Fig. 17). The dark grains are fragments from decomposition of underlying bone debris. Personal observations note that a carcass lying on a beach will decompose on its underside while its upperside will dessicate. Such was evidently the condition found in the present skeleton. The CaCO3 of this level "A" is 16-20%.

A second sand incursion "B" above level "A" (Fig. 17) has rounded grains of 0.3 mm and consists of 36-40 % CaCO3. The samples "A" and "B" were recovered from an area at the base of the skull.

A third incursion of sand level "C" with angular grains 0.15 mm in size consists of 13-16 % CaCO3 covered the remaining exposed parts of the skeleton

Those 3 separate deposits of sand at the site indicates that burial of the skeleton was fairly rapid after the initial separation of the skull and some postcranials. The partial articulations observed in this skeleton of *Goniopholis* are reminiscent of those which occur with dinosaurs and other vertebrates found in the Morrison Formation of Wyoming (pers. obser.). A recent description of *Goniopholis* (Hups et al. 2006) shows characteristic preservation of partial skeletons from the Morrison Formation.

ACKNOWLEDGMENTS

I thank Brooks Britt, B Y University and Ron Mjos, Western Paleontological Laboratories, Lehi, Utah, for access to the collections in their care. I also thank R. Mjos for allowing me to make casts of various elements of *Goniopholis.* Becky Huset and Richard Benson, Science Museum of Minnesota reviewed the manuscript and offered suggestions for its improvement. North Star Imaging, Rogers, Minnesota, provided computed tomography and 3 – dimension images. Mark Ryan, SMM completed all photography; Timothy Erickson contributed redacting of all images; Jeffery Birch did the frontispiece painting and figures 4 – ll; Lee Hallgren, SMM contributed photomicrographs for figure 17, Lois Erickson furnished all manuscript processing; Richard Wolszon and Tom Ostertag mounted the cast of *Goniopholis* (Fig. 13). Gail Rector painted the cast. I am especially grateful to the Philip Fitzpatrick Research Fund which made this publication possible.

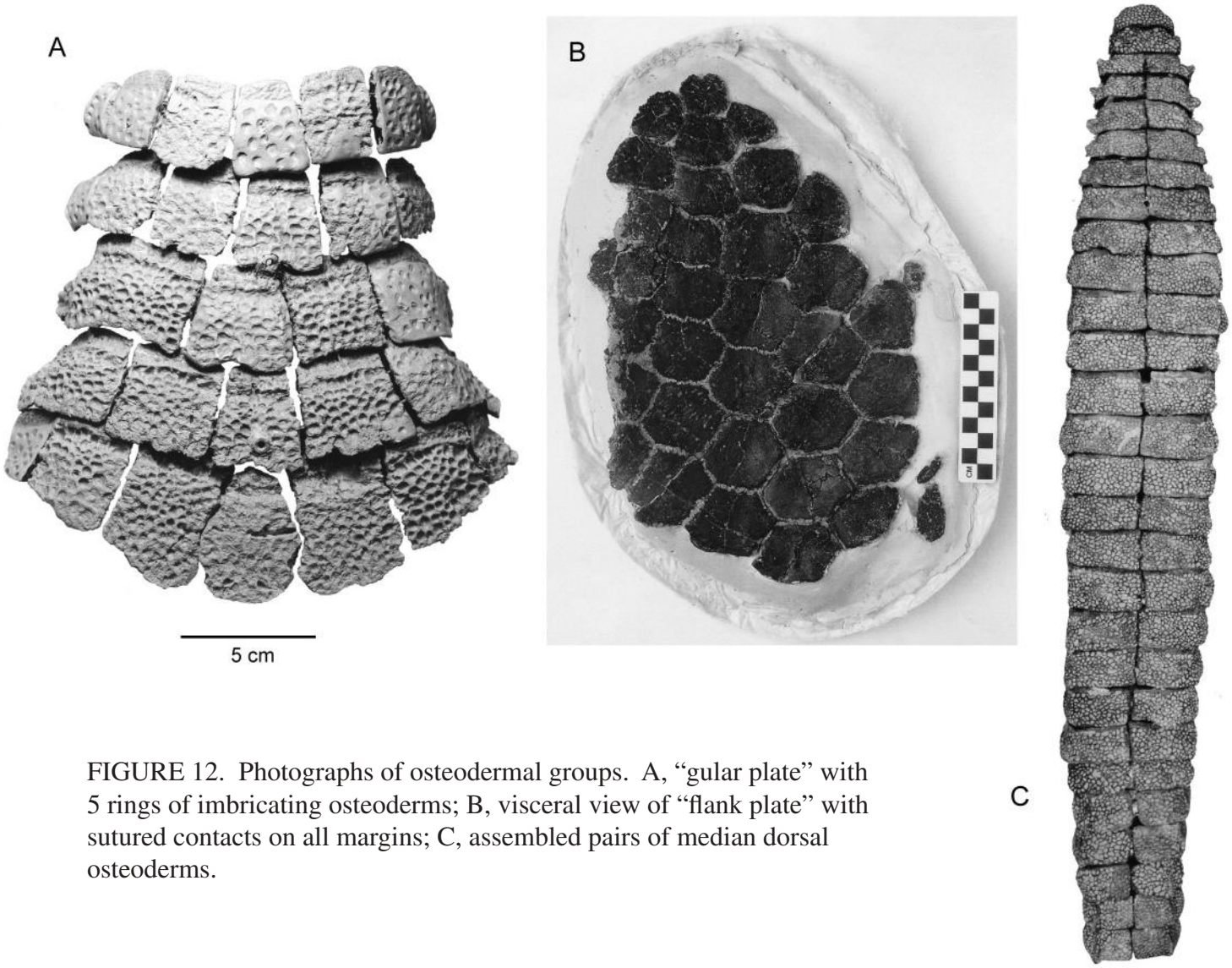

FIGURE 12. Photographs of osteodermal groups. A, "gular plate" with 5 rings of imbricating osteoderms; B, visceral view of "flank plate" with sutured contacts on all margins; C, assembled pairs of median dorsal osteoderms.

FIGURE 13. Photograph of mounted cast of *Goniopholis* P 2003.20.1 illustrating osteodermal groups in perspective view.

FIGURE 14. *Goniopholis* restored posterior trunk region in perspective aspect. A, left flank plate; B, xiphisternum; C, area of gastralia; D, median dorsal osteoderm showing imbricate relationship with fellow dorsal osteoderms.

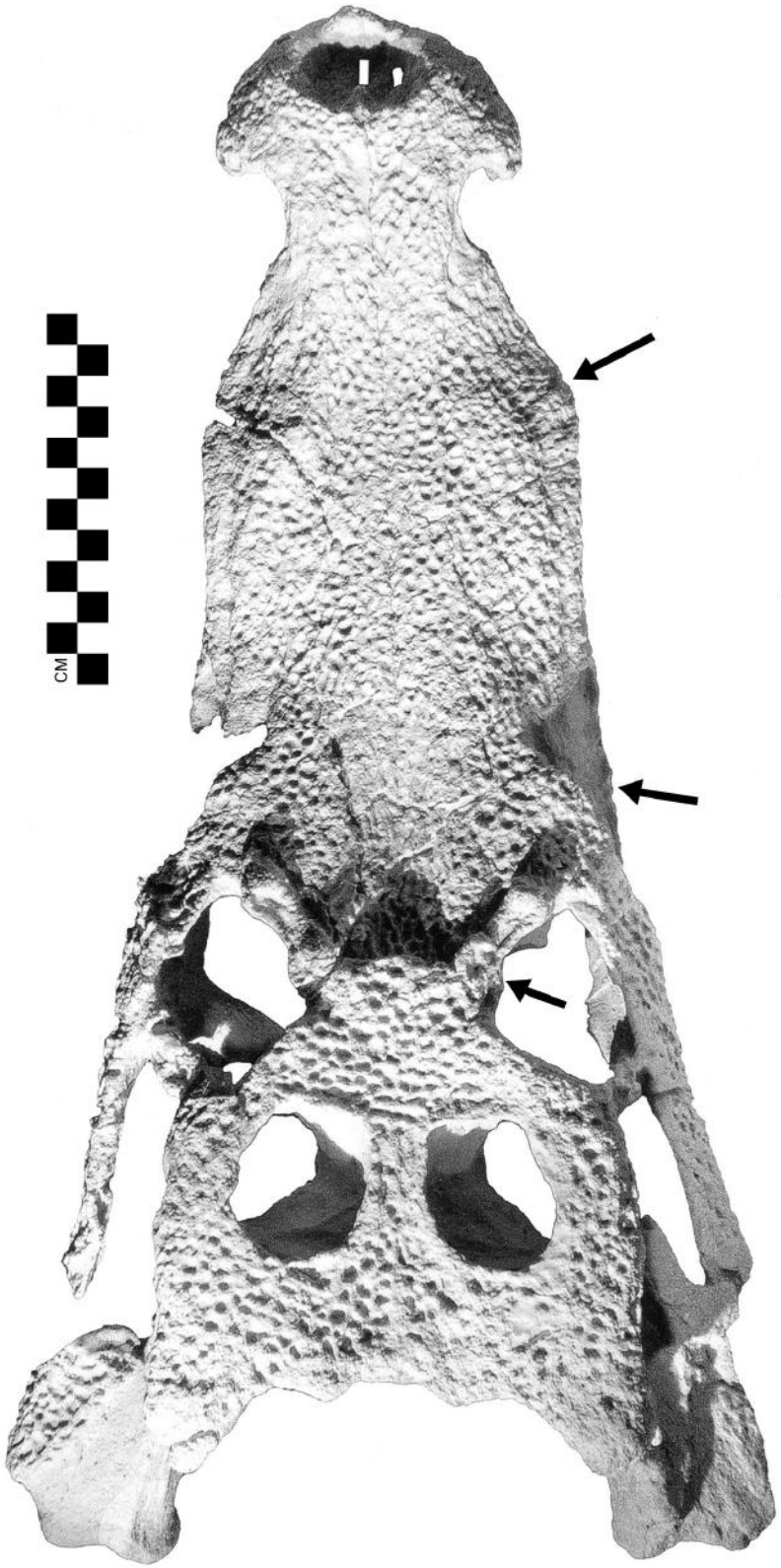

FIGURE 15. Photograph of *Goniopholis* skull P 2003.20.1 in high relief. A, Swelling above 5th alveolus and lachrymal fossa, high relief ridges at median margin and between orbits (arrows).

FIGURE 16. Photograph of the skeleton of *Goniopholis* SMM P 2003.20.1 from the Morrison Formation of Albany Co., Wyoming in field jacket during early stage of preparation.

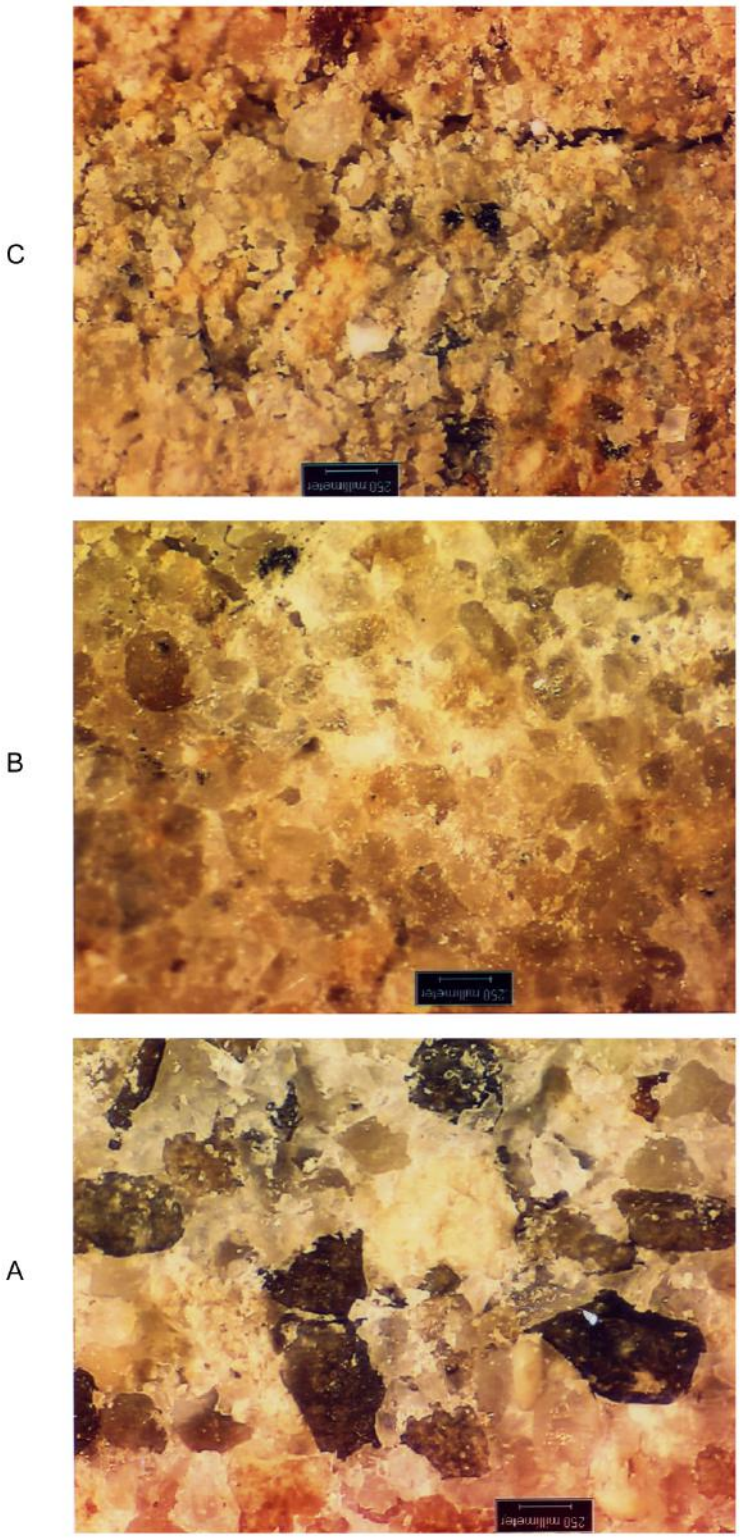

FIGURE 17. Profile of 3 sand incursions that sequentially buried the skeleton of *Goniopholis* SMM P 2003.20.1. A, Initial deposit of sand around skeleton; B, second deposit of sand over skeleton; C, final sand deposit covering the skeleton.

TABLE 1. Cranial measurements in mm. **mm**

Maximum length along midline, cranial table to tip of snout	375
Length of rostrum, anterior rim of orbit to center of premaxillomaxillary notch	190
Length between end of left quadrate and posterior edge of internal rostral dep	182
Maximum height of skull at cranial table and pterygoids	128
Length of lateral rostral depression	68
Height of lateral rostral depression	24
Length of cranial table, posterior edge to posterior rim of orbit	96
Width of cranial table, posterior edge	125
Width of rostrum at level of 5th maxillary tooth	110.7
Width of rostrum at level of 5th premaxillary tooth	90
Narrowest distance between premaxillomaxillary notches	50
Length of supratemporal fenestra	36
Width of supratemporal fenestra	34
Length of orbit	45
Width of orbit	38
Narrowest distance between orbits	50
Narrowest distance between supratemporal fenestrae	14
Width of anterior narial opening	32
Width across quadrates	200
Length of palatine vacuity	95
Length of internarial septum	150

TABLE 2. Mandibular measurements in mm. **mm**

Maximum length of left mandible, retroarticular to tip of snout	485
Length of symphysis to splenial	70
Length of dentary	320 (est)
Length of angular	250 (est)
Length of surangular	220 (est)
Length of dentulous portion of dentary	245
Length of external fenestra	34
Height of external fenestra	8
Length of articular-angular suture	125

TABLE 3. Postcranial measurements in mm. **mm**

Articulated vertebrae (first dorsal to posterior of Sacral 2)	590
Sacrum combined 2 vertebrae: Length	85
Height of second vertebra	63
Distance across ribs of second vertebra	98
Distance across ribs of first vertebra	120 (est)
Interclavicle: Length	177
Humerus: Length	205
Dia. of shaft	17
Width of prox. End (head)	40
Width of dist. End	40
Radius: Length	144
Ulna: Length (pathologic)	165 (est)
Ilium: max. Length	117
Length of superior edge	73
Height: acetabular base to superior edge	73
Pubis: Length (restored)	14.5 (est)
Dia. of shaft	12
Ischium: Length (restored)	16.5 (est)
Dia. of shaft	25
Femur: Length	216
Dia. of shaft	20
Width of prox. End (head)	46
Width of dist. End	45
Tibia: Length	159
Dia. of shaft	17
Width of prox. End	45
Width of dist. End	34
Fibula: Length	154
Dia. of shaft	10
Width of prox. End	27
Width of dist. End	18

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