

A NEW NOTOSUCHIAN FROM THE EARLY CRETACEOUS OF NIGER

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In 1955 French geologists discovered a fossiliferous horizon of mid Cretaceous (Aptian–Albian) age in the southern Sahara in the Republic of Niger. The richest section, a narrow 45 km-long band of fluvial sandstone called Gadoufaoua, has yielded the most complete dinosaurian remains of Cretaceous age from Africa, including the iguanodontian ornithopods *Lurdusaurus* and *Ouranosaurus* (Taquet, 1976; Taquet and Russell, 1999), the diplodocoid sauropod *Nigersaurus* (Taquet, 1976; Sereno et al., 1999), and the spinosaurid theropod *Suchomimus* (Sereno et al., 1998). Crocodyliforms were among the first fossils recovered from Gadoufaoua (Faure, 1966), especially remains of the abundant long-snouted giant *Sarcosuchus imperator* (Broin and Taquet, 1966; Sereno et al., 2001). Contemporaneous smaller-bodied crocodyliforms include *Araripesuchus wegneri* (Buf-fetaut, 1981) and the peirosaurid *Stolokrosuchus lapparenti* (Larsson and Gado, 2000). Here we describe an unusual new small-bodied notosuchian crocodyliform from Gadoufaoua that adds an important new link to Cretaceous crocodyliforms from South America.

Institutional Abbreviation—MNN, Musée National du Niger, Niamey, Niger Republic.

SYSTEMATIC PALEONTOLOGY

CROCODYLIFORMES Benton and Clark, 1988

NOTOSUCHIA Gasparini, 1971

COMAHUESUCHIDAE Bonaparte, 1991

ANATOSUCHUS MINOR, gen. and sp. nov.

(Figs. 1 and 2)

Holotype—MNN GDF603, nearly complete skull with articulated lower jaws.

Locality and Horizon—Preserved in a hematitic nodule in regolith near exposures of the GAD 5 level of the Tegama Group (Taquet, 1976), corresponding to the upper and lower portions of the Elrhaz and Echkar formations, respectively (Sereno et al., 1999), Agadez Prefecture, Republic of Niger (16° 46' N, 9° 23' E); Late Aptian or Early Albian in age (Faure, 1966; Taquet, 1976).

Diagnosis—Small crocodyliform (total adult body length estimate 0.7 m) with short shallow snout, as broad as it is long (maximum snout width across maxillae nearly equals the maximum width across jugals); maxillary margin with lateral cor-



FIGURE 1. Stereophotographs of the holotypic skull (MNN GDF603) of *Anatosuchus minor* in dorsal view. Scale bar equals 5 cm.

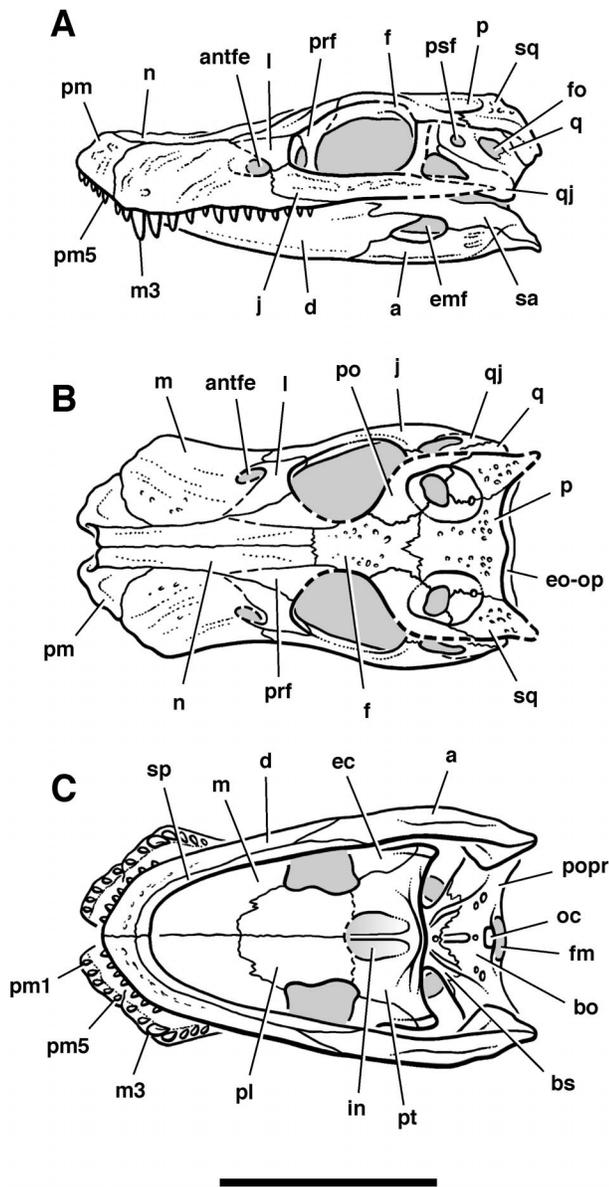


FIGURE 2. Reconstruction of the skull of *Anatosuchus minor* in (A) lateral, (B) dorsal, and (C) ventral views. Scale bar equals 5 cm. **Abbreviations:** a, angular; antfe, antorbital fenestra; bo, basioccipital; bs, basisphenoid; d, dentary; ec, ectopterygoid; emf, external mandibular fenestra; eo-op, exoccipital-opisthotic; f, frontal; fm, foramen magnum; fo, fenestra ovalis; in, internal naris; j, jugal; l, lacrimal; m, maxilla; m3, third maxillary tooth; n, nasal; oc, occipital condyle; p, parietal; pl, palatine; pm, premaxilla; pm1, first premaxillary tooth; pm5, fifth premaxillary tooth; po, postorbital; popr, paroccipital processes; prf, prefrontal; psf, preotic siphonial foramen; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sp, splenial; sq, squamosal.

ner; and anterior portion of maxillary tooth row set markedly lateral to dentary tooth row at the snout corner.

Etymology—Anas, duck (Latin); suchos, crocodile (Greek); minor, little (Latin). Named for its broad duck-like snout and its small body size.

DESCRIPTION

The nearly complete skull is characterized by a short, broad snout. Unlike most crocodyliforms, the width of the skull does

not taper anteriorly; maximum width of the skull across the jugals is approximately equal to that across the maxillaries (Figs. 1, 2B). A small antorbital fenestra is present between the maxilla and lacrimal (Fig. 2A). The external naris is small and undivided. As in *Notosuchus* (Gasparini, 1971; Bonaparte, 1991), the naris opens anteriorly rather than anterodorsally or anterolaterally. The dorsal (nasal) and ventral (premaxillary) borders of the external naris are inset from the anterior margin of the snout (Figs. 1, 2B), a very unusual condition shared only with *Comahuesuchus*, a small crocodyliform from the Late Cretaceous of South America (Bonaparte, 1991; Martinelli, 2000).

There are five premaxillary teeth and 15 maxillary teeth. The conical maxillary crowns curve lingually and have low, carinae fore and aft without serrations (Fig. 2C). The largest maxillary crowns are located at the lateral corner of the snout (maxillary teeth 3 and 4). The most unusual aspect of the dentition is a median diastema present in both upper and lower jaws (Fig. 2C). This condition is known elsewhere among crocodyliforms only in *Comahuesuchus* (Bonaparte, 1991:fig. 14C; Martinelli, in press). The anterior half of the maxilla overhangs the dentary, such that the anterior portion of the mandible is obscured in lateral view of the skull (Fig. 2A). In ventral view, the anterior portion of the dentary tooth row is also inset significantly from the maxillary tooth row (Fig. 2C). This condition is also present in *Comahuesuchus*, albeit to a lesser extent (Bonaparte, 1991; Martinelli, in press).

In dorsal view of the skull, the nasal is narrow and approaches the lacrimal posteriorly. Nasal-lacrimal contact may have occurred, but the skull is eroded in this region. Within the orbit, a prefrontal pillar is developed as a transverse sheet of bone. The jugal in *Anatosuchus* extends anterior to the orbit as in many other crocodyliforms but unlike *Comahuesuchus* (Fig. 2A). In lateral view, the broad anterodorsal ramus of the quadrate bears a shallow otic notch and a relatively large preotic siphonial foramen. The quadratojugal projects anterodorsally at a relatively shallow angle over the small subtriangular infratemporal fenestra to contact the postorbital.

The frontals and parietals are fused as in most crocodyliforms. The large orbits are situated relatively close to the midline, although not as close as shown in at least one specimen of *Comahuesuchus* (Bonaparte, 1991). Palpebrals are not preserved nor is there an articular facet on the orbital margin of the postorbital. The postorbital forms about half of the lateral margin of the supratemporal fenestra; the remainder is formed by the parietal and squamosal (Fig. 2B). The postorbital bar is inset from the lateral margin of the skull roof; whether it is inset or not at its junction with the body of the jugal cannot be determined due to erosion.

In ventral view, the maxillae and palatines contribute to a broad secondary palate. The internal nares are retracted to the posterior margin of the palate. They are bordered by the palatines and pterygoids and divided by a slender pterygoid septum. Posteriorly the pterygoids are fused and form a thin transverse plate in the midline posterior to the internal nares (Fig. 2C). There are no distinct paired processes on this transverse plate unlike many other crocodyliforms; the ventral margin of the plate is slightly swollen to each side of the midline.

The ventral surface of the braincase is not steeply anteroventrally inclined as in most crocodyliforms. A prominent wedge-shaped median crest is present on the basioccipital (Fig. 2C). The basisphenoid is exposed ventrally between the basioccipital and pterygoid, and the small occipital condyle projects posterovertrally.

The lower jaws are U-shaped in ventral view with nearly horizontal dentary rami near the symphysis (Fig. 2C). The dentary rami have a similar form in *Comahuesuchus* (Bonaparte, 1991; Martinelli, in press) and several other crocodyliforms. There are at least eight dentary teeth, which do not appear to

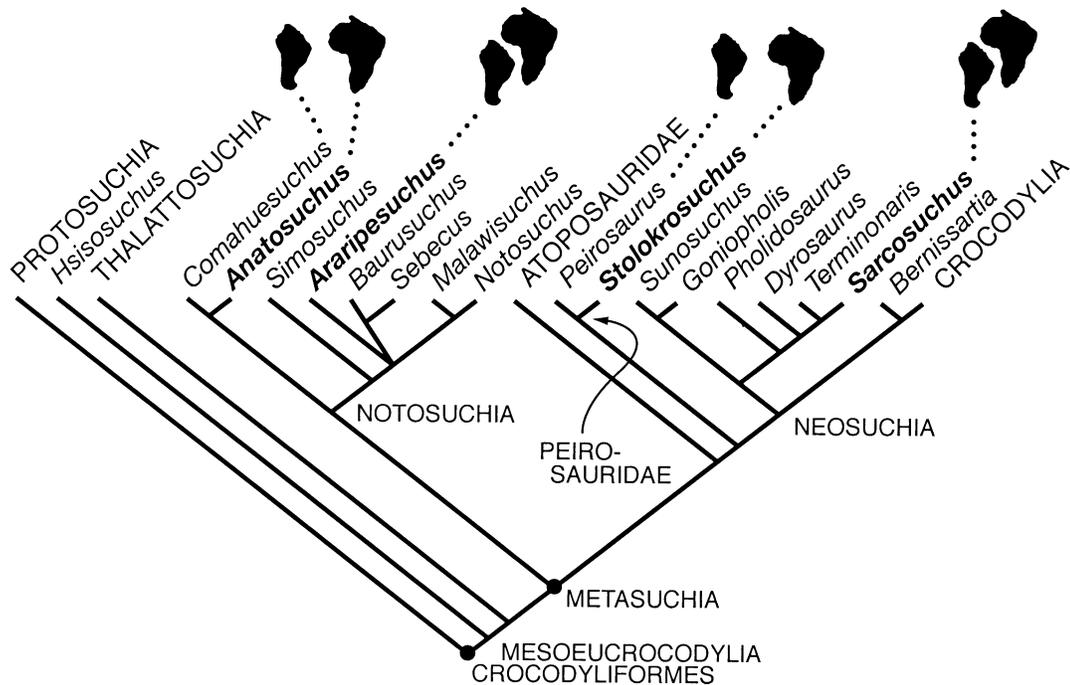


FIGURE 3. The position of *Anatosuchus minor* within Crocodyliformes was determined by maximum-parsimony analysis of 75 characters in 22 crocodyliform taxa, using *Hsisosuchus* and Protosuchidae as successive outgroups. This strict consensus tree is based on two 207-step, minimum-length trees (CI = 0.51, RI = 0.61) derived from data in Sereno et al. (2001) (Appendix). *Anatosuchus* and *Comahuesuchus* are sister taxa within Notosuchia, a clade with weak character support that includes a broader range of taxa than traditionally conceived (for phylogenetic definitions of Notosuchia and other higher crocodyliform taxa shown, see Sereno et al., 2001:1519). Continental icons identify taxa that share trans-Atlantic distribution, including species pairs within a single genus (*Araripesuchus*, *Sarcosuchus*) or among genera (*Comahuesuchus* and *Anatosuchus*; *Peirosaurus* and *Stolokrosuchus*). Contemporary genera on Africa shown in bold. Dots at nodes for Crocodyliformes and Metasuchia signify node-based definitions of node-stem triplets (Sereno, 1999).

increase in size unlike the opposing teeth in the upper jaw. A moderately-sized external mandibular fenestra is present, bordered by the dentary, surangular, and angular. The prearticular is absent. The jaw joint is a simple hinge that would not have allowed the propalinal movement inferred in some other notosuchians (e.g., Wu and Sues, 1996; Gomani, 1997). The well developed retroarticular process projects posteriorly and slightly ventrally (Fig. 2A). The lateral aspect of the process is smooth, suggesting that it served as an attachment surface for the pterygoideus musculature.

DISCUSSION

We used the character data in Sereno et al. (2001) to assess the phylogenetic relationships of *Anatosuchus minor* (Appendix 1). Because of the unusual similarities we have noted between *Anatosuchus minor* and *Comahuesuchus brachybuccalis*, we added the latter species and three additional characters to the analysis (Fig. 3). Our analysis indicates that *Anatosuchus* and *Comahuesuchus* are most closely related and that both taxa fall within a monophyletic Notosuchia that includes both the widespread, well known genus *Araripesuchus* as well as *Sebecosuchia* (Sereno et al., 2001) (Fig. 3).

The timing of the isolation of Africa during the break-up of Gondwana remains controversial. A recent hypothesis proposes that Africa broke away from other southern landmasses as early as 120 Ma during the Early Cretaceous (Sampson et al., 1998; Hay et al., 1999). Terrestrial fossils of mid Cretaceous age (ca. 112 Ma, near the Aptian–Albian boundary) provide critical evidence (Maisey, 2000), and crocodyliforms, in this regard, have played an important role (Buffetaut and Taquet, 1979; Buffetaut, 1981; Bonaparte, 1991; Gasparini et al., 1991; Larsson and

Gado, 2000; Ortega et al., 2000; Sereno et al., 2001). The discovery of *Anatosuchus minor* and its close relationship with *Comahuesuchus brachybuccalis* provide new evidence linking crocodyliforms of mid-Cretaceous (Aptian–Albian) age on Africa and South America, which suggests that subaerial connections between these landmasses may have existed until the end of the Lower Cretaceous (Fig. 3).

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APPENDIX 1

Three characters (73–75) and two crocodyliforms (*Anatosuchus*, *Comahuesuchus*) were added to a previous phylogenetic analysis (Sereno et al., 2001). For the three added characters, the original taxa were scored with the primitive character-state (0) with two exceptions (*Sarcosuchus imperator* 75:1 and *Simosuchus clarki* 75:?). The complete character list and taxon/character-state matrix are given below. There are 11 multistate characters, four of which are ordered (18, 30, 34, 61).

The majority of characters come from previous analyses, although our coding and scoring of these characters may differ. Character citations indicate first use in an explicit phylogenetic analysis. Ingroups include three suprageneric taxa of undoubted monophyly (e.g., Thalattosuchia, Atoposauridae, Crocodylia) that were coded according to basal relationships within each group, as inferred from previous phylogenetic analyses. In this way, we reduced the number of characters extraneous to understanding the relationships of *Anatosuchus minor* and other crocodylians from the El Rhaz Formation (*Sarcosuchus imperator*, *Araripesuchus wegneri*, *Stolokrosuchus lapparenti*).

Characters and Character-States

General Skull and Cranial Openings

1. Skull bone surface ornamentation (pits, grooves): present (0); absent (1). (Clark, 1994)
2. External nares, orientation: dorsolateral or dorsal (0); anterolateral (1); anterior (2).
3. Antorbital fenestra, size: half orbital diameter (0); very small (1); absent (2). (Clark, 1994)
4. Supratemporal fossae, length: subequal to or shorter (0), or longer (1), than orbital length. (modified from Clark, 1994)

Snout

5. Snout (preorbital) shape: narrow and rectangular (parallel-sided) (0), broadening gradually (subtriangular) (1); broad and rectangular (parallel-sided) (2).
6. Snout (midlength) depth: subequal to width (0); deeper than wide (1); wider than deep (2). (Clark, 1994)
7. Internarial bar: present (0); absent (1). (Clark, 1994)
8. Premaxilla contribution to internarial bar: about 50% (0); little to none (1). (Clark, 1994)
9. Premaxilla, width of margin anterior to external nares: narrower (0), or as broad as (1), narrowest margin lateral to external nares. (Clark, 1994)
10. Premaxilla-maxilla junction near alveolar margin, form: flat without depression (0); narrow slit or foramen (1); open notch (2). (Clark, 1994)
11. Nasal border of external nares: present (0); absent (1). (Clark, 1994)
12. Nasal-lacrimal contact: present (0); absent (by presence of maxilla-prefrontal contact) (1). (Clark, 1994)
13. Premaxillary narial fossa: poorly defined (0); well demarcated (1).
14. Maxillary fossa: absent (0); present (1). (Wu et al., 1997)
15. Alveolar margin, surface texture: sculptured (0); smooth (1). (Wu and Sues, 1997)

Posterior Skull Roof

16. Jugal anterior ramus, dorsoventral width: as broad (0), or twice as broad (1), as posterior ramus. (Larsson, 2000)
17. Jugal laterotemporal bar, form: transversely compressed (0); rod-shaped (1). (Clark, 1994)
18. Quadratojugal spine: absent (0); low crest (1); spine-shaped (2). (ordered) (Clark, 1994)
19. Quadratojugal dorsal ramus, width: dorsally broad with postorbital contact along most of postorbital bar (0); dorsally tapered, narrow postorbital contact (1). (Clark, 1994)
20. Frontal participation in supratemporal fossa: significant (0); very marginal or no participation (1). (Clark, 1994)
21. Postorbital bar, form: transversely flattened (0); subcylindrical (1).
22. Ectopterygoid, relation to postorbital bar: no support (0); contributes to base of bar (1). (Clark, 1994)
23. Postorbital foramen, lateral aspect of body: absent (0); present (1). (Clark, 1994)
24. Postorbital anterolateral process: absent (0); present (1). (Clark, 1994)
25. Postorbital, dorsal end of postorbital bar, form: gradually expands to body (0); bar and body well differentiated (1). (Clark, 1994)
26. Parietal roof between supratemporal fossae, form: flat sculpted surface (0); sagittal crest (1). (Clark, 1994)
27. Frontal anterior ramus, position of tip: posterior (0), or anterior (1), to tip of prefrontal. (Larsson, 2001)
28. Interfrontal suture: open (0); closed (1). (Clark, 1994)

Palate

29. Incisive foramen, bone meeting in midline along posterior margin: premaxilla (0); maxilla (1). (Clark, 1994)
30. Choanal position, bone forming anterior margin (joining opposite in midline): maxilla (0); palatine (1); anterior end of pterygoid (2); centered on pterygoid (3). (ordered) (Clark, 1994)
31. Choanal size: 20–30% (0), or approximately 10% (1), of cranial width across jugals. (adapted from Clark, 1994)
32. Choanal septum: absent (0); present (1). (Clark, 1994)
33. Maxilla, posterior ends of palatal rami, position: meet in midline (0); separated by palatines (1). (Clark, 1994)
34. Prefrontal pillar-palatine contact: absent (0); present, narrow (1); present, robust (2). (ordered) (Clark, 1994)
35. Quadrate fenestra(e): absent (0); one (1); more than one (2). (Clark, 1994)

Braincase

36. Basisphenoid ventral exposure: broad (0); mostly covered by pterygoid and basioccipital (1). (Clark, 1994)
37. Basal tubera (basioccipital), size: small (0); large, pendulous (1). (Clark, 1994)

Lower Jaw

38. Dentary alveolar margin, form: straight (0); sinusoidal (1). (Ortega et al., 1996)
39. Prearticular: present (0); absent (1). (Clark, 1994)
40. Mandibular fenestra: present (0); absent (1). (Clark, 1994)
41. Surangular, form of dorsal margin (especially anterior part): flat (0); dorsally arched (1). (modified from Clark, 1994)
42. Pterygoideus insertion on angular: ventral edge only (0); extends onto lateral aspect (1). (Clark, 1994)
43. Splenial participation in symphysis: short (0); extensive (1). (Clark, 1994)
44. Mandibular symphysis, depth: deep (0); shallow (1). (Wu and Sues, 1996)
45. Articular cup of lower jaw, shape: wider than long (0); longer than wide (1). (Wu and Sues, 1996)
46. Jaw articulation (quadrate condyle), position: above (0), or below (1), maxillary tooth row. (Wu and Sues, 1996)
47. Retroarticular process, orientation of base of process: posterior (0); posteroventral (1).

48. Retroarticular process, length: less (0), or more (1), than twice the length of the articular cotyle. (Larsson, 2000).

Dentition

49. Posterior premaxillary teeth, size: similar to anterior premaxillary teeth (0); at least one much longer (1). (Clark, 1994)
50. Mid to posterior maxillary teeth, crown-root junction: unconstricted (0); constricted (1). (Buckley et al., 2000)
51. Maxillary tooth number: more (0), or less (1), than 10.
52. Posterior maxillary teeth, crown form: subcylindrical (0); transversely compressed (1). (Buckley et al., 2000)
53. Ornamentation on carinae: smooth (0); denticles (1); serrations (2).
54. Dentary tooth opposite premaxilla-maxilla diastema: moderately enlarged (0); more than twice the length of adjacent dentary teeth (1). (Clark, 1994)
55. Dentary teeth posterior to premaxilla-maxilla diastema: gradually decrease in size posteriorly (0); increase and then decrease in size posteriorly (opposite trend in opposing maxillary teeth). (Clark, 1994)
56. Premaxillary teeth 1 and 2, position: separated like adjacent teeth (0); nearly confluent (1). (Larsson and Gado, 2000)

Axial Column

57. Cervical centra: amphiplatyan (0); procoelous (1). (Clark, 1994)
58. Dorsal centra: amphiplatyan (0); procoelous (1). (Clark, 1994)

Girdles and Limbs

59. Coracoid length: approximately half (0), or subequal to (1), scapular length. (Clark, 1994)
60. Iliac preacetabular process, length: subequal to (0), or 25% or less than (1), to postacetabular process. (Clark, 1994)

Osteoderms

61. Mid dorsal (trunk) paramedian osteoderms, shape: rectangular (up to 3 times wider than long) (0); strap-shaped (more than 3 times wider than long) (1); subquadrate (2); oval (longer than wide) (3). (ordered) (modified from Clark, 1994)
62. Dorsal (trunk) osteoderms, anterior process on anterolateral corner: present (0); absent (1). (Clark, 1994)
63. Dorsal (trunk) osteoderms, number of rows: two (paramedian) (0); four (two accessory rows) (1). (Clark, 1994)
64. Dorsal (trunk) osteoderms, anteroposterior keel: absent (0); present (1). (Clark, 1994)
65. Dorsal trunk osteoderms, anteroposterior keel position: median or paramedian (0); lateral margin (1).
66. Trunk ventral osteoderms: present (0); absent (1). (Clark, 1994)

Characters Uniting *Sarcosuchus* and *Terminonaris*

67. Premaxillary palate, circular paramedian depressions; absent (0); present (1).
68. Premaxillary, anterior alveolar margin and teeth, orientation: vertical (0); intumed (1).
69. Premaxillary tooth row, orientation: arched posteriorly from midline (0), angled posterolaterally (120 degree intervening angle) (1). (modified from Wu et al., 2001)
70. Last premaxillary tooth, position: anterior (0), or anterolateral (1) to first maxillary tooth.
71. Premaxillary tooth row, position relative to maxillary tooth row: level (0); ventrally offset (1). (modified from Wu et al., 2001)
72. Dentary distal end, shape: parallel-sided (0); transversely expanded (1).

Characters Uniting *Anatosuchus* and *Comahuesuchus*

73. External naris, position of dorsal and ventral margin: flush with (0), or inset posteriorly from (1), the anterior snout contour.
74. Median diastemata (upper, lower): absent (0); present (1).
75. Position of anterior portion of upper tooth row: adjacent to (0), or offset labially and ventrally from (1), dentary tooth row.

