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A new crocodilian from the Lower Cretaceous Crato Formation of north-eastern Brazil

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with 9 text-figures

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Zusammenfassung

Ein neuer Krokodilier der Unterordnung Mesosuchia aus dem Nova-Olinda-Member der Crato-Formation wird beschrieben. *Susisuchus anatocepts* gen. et sp. nov. ist der erste Krokodilier aus dieser Formation. Es handelt sich um ein unvollständiges teilartikuliertes Skelett: Schädel mit Unterkiefer, ein Teil des postcranalen Achsenskeletts, Vorderextremitäten und Teile des Osteodermenskeletts. Im Bereich beider Vorderextremitäten und der Finger der rechten Hand liegt Hauterhaltung vor. Der Erhaltungszustand des Stückes läßt vermuten, daß es als ausgetrocknete Leiche in die Lagune gelangte.

Susisuchus anatocepts ist einer der ältesten bekannten Krokodilier mit einem tetraserialen Paravertebralschild vom Eusuchiertyp. Der Paraventralschild ist beiderseits von zwei Reihen sagittaler akzessorischer Osteoderme flankiert. Das Tier besitzt außerdem amphicöle Thorax-, Lenden- und Schwanzwirbel. Eine derartige Kombination postcranialer Charakteristika wurde bislang bei keinem anderen Krokodilier beobachtet und rechtfertigt die Aufstellung einer neuen Familie innerhalb der Mesosuchier: Susisuchidae. Taxonomisch gesehen, ähnelt *S. anatocepts* einer Reihe anderer Unterkreide-Mesosuchier, die an die Basis der Eusuchier-Evolution gestellt wurden. Zu diesen gehören auch der „Glen-Rose-Krokodilier" und ein neuer bislang unbeschriebener Krokodilier aus der unterkretazischen Winton-Formation von West-Queensland (Australien). Eine erste Sondierungspräparation des Winton Krokodiliers hat gezeigt, daß er zu den Susisuchidae gehören könnte. Das würde die Annahme eines Wirbeltierfaunenaustausches zwischen Südamerika und Australien in der Unterkreide bestätigen.

Schlüsselwörter: Crocodilia – Mesosuchia – Susisuchidae – Unterkreide – Brasilien.

Summary

A new mesosuchian crocodilian from the Nova Olinda Member of the Crato Formation (Lower Cretaceous, Aptian) of north-eastern Brazil is described. *Susisuchus anatoceps* gen. et sp. nov. is the first crocodilian to be reported from this formation. It is represented by an incomplete, partially articulated skeleton: the skull and mandible, partial postcranial axial skeleton, forelimbs and portions of the osteodermal skeleton. Preservation of soft tissues includes the skin surrounding both forelimbs and the digits of the right hand. The state of preservation of the specimen suggests that it was incorporated into the basin as a desiccated carcass.

Susisuchus anatoceps is one of the oldest crocodilians with a eusuchian-type dorsal shield, comprising a tetraserial paravertebral shield and, either side of this, two sagittal rows of accessory osteoderms. It also possesses amphicoelous thoracic, lumbar and caudal vertebrae. This combination of postcranial features have never before been seen in a crocodilian and warrant the erection of a new family within Mesosuchia: Susisuchidae. Taxonomically, *S. anatoceps* is similar to a number of Lower Cretaceous mesosuchians previously considered to have given rise to eusuchians, most notably the Glen Rose crocodilian and a new, but as yet undescribed crocodilian from the Lower Cretaceous Winton Formation of western Queensland, Australia. Preliminary preparation of the Winton crocodilian indicates that it may belong to Susisuchidae, supporting the hypotheses of interchange between the vertebrate faunas of South America and Australia during the Lower Cretaceous.

Key words: Crocodilia – Mesosuchia – Susisuchidae – Lower Cretaceous – Brazil.

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Introduction

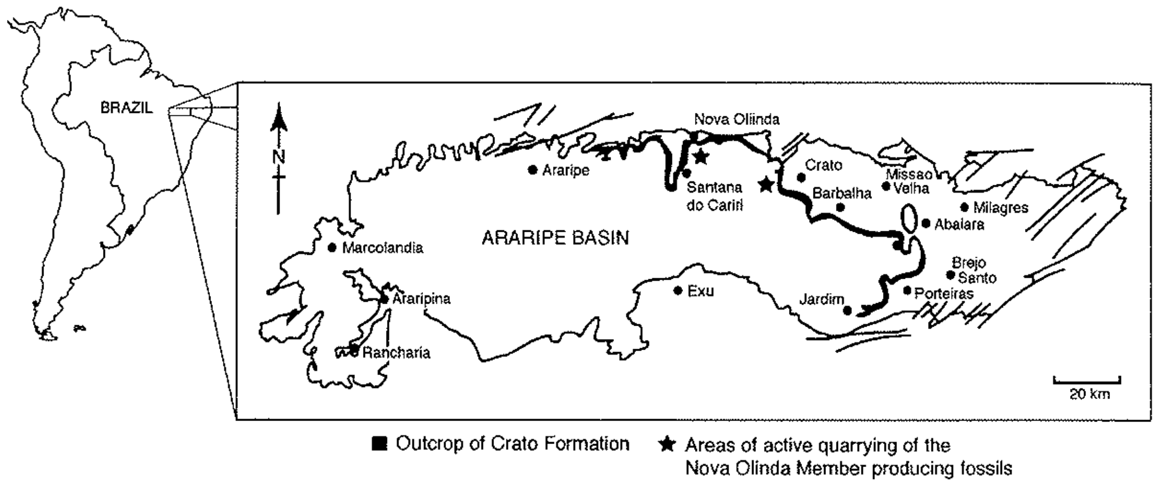
Herein, the remarkably well-preserved specimen of a new metamesosuchian crocodilian (sensu BUFFETAUT 1982) from Brazil is described. Although it was obtained from a commercial fossil dealer and lacked provenance data, the distinctive nature of the matrix associated with the new specimen, along with its preservational style indicates that it comes from the Lower Cretaceous (Aptian) Nova Olinda Member of the Crato Formation of the Araripe Basin, north-eastern Brazil. During field work in 1994, two of us (EF and DMM) were shown a portion of the columna vertebralis (vertebral column) of a second crocodilian from the Crato Formation, but this specimen has since disappeared. The new specimen therefore represents the first and until now only crocodilian to be reported from this formation. The only other crocodilian taxa known from the Araripe Basin are *Araripesuchus gomesii* (PRICE 1959, BUFFETAUT 1981) and *Itasuchus camposi* (KELLNER 1986, 1987, BUFFETAUT 1991), both of which were found in the younger Santana Formation.

Location and stratigraphy

The slab on which the specimen is preserved consists of a finely laminated, cream coloured limestone, with numerous elongate, reddish-brown pellet-like compressions on its bedding plane surfaces. Such characteristics are typical of the Nova Olinda Member of the Crato Formation of north-eastern Brazil. This formation outcrops on the flanks of the Chapada do Araripe in Ceará and Pernambuco, north-eastern Brazil (Text-fig. 1). It is a prolific source of fossils, but is only quarried commercially in Ceará (MARTILL 1993, WILSON & MARTILL 2001). It is therefore not possible to be more specific about the locality of the specimen, since the Nova Olinda Member has an extensive outcrop in the region and commercial fossil collecting is undertaken at several widely separate localities, including the region between Nova Olinda and Santana do Cariri, and to a lesser extent to the south of the city of Crato.

The Nova Olinda Member is the lowest member of the Crato Formation (MARTILL & WILBY 1993). Although the Crato Formation has been dated as Aptian (Lower Cretaceous) using palynomorphs (PONS et al. 1990), a precise date for the Nova Olinda Member is yet to be established. The Crato Formation comprises a series of laminated limestones interbedded with shales and sandstones within the Araripe Group. It rests conformably on the Batatieras Formation in the middle of the Araripe Basin, but at the basin margins it also rests unconformably on Lower Palaeozoic sandstones and Neoproterozoic rocks of the crystalline basement (MARTILL 1993).

The diverse suite of sediment types in the Crato Formation represents several distinctive palaeoenvironments, including freshwater lakes, saline lagoons, floodplains and deltaic settings (BRITO et al. 1998). The Nova Olinda Member represents a period of continual carbonate deposition under saline and perhaps anoxic lagoonal conditions. Palaeontological and sedimentological data indicate that little life persisted in the main body of water, but that a tongue of fresh, or brackish water above a halocline was populated by small fishes and larval ephemeropterans and odonatans (GRIMALDI 1990, MARTILL 1993, BRITO et al. 1998).



Text- fig. 1. Locality map showing the outcrop of the Crato Formation in the Chapada do Araripe, Ceará and Pernambuco states, north-eastern Brazil. The new crocodilian most probably was obtained from the region between Santana do Cariri and Nova Olinda, which is where most of the quarrying of the Nova Olinda Member limestone takes place.

The majority of fossil species from the Nova Olinda Member represent allochthonous forms, with volant species being the most diverse (MARTILL 1998). The Nova Olinda Member is a Konservat-Lagerstätte, famous for the high-fidelity preservation of its fossil assemblage, which includes plants, vertebrates and invertebrates (MAISEY 1991, MARTILL 1993, MARTILL & FREY 1998, FREY & TISCHLINGER 2000). The most abundant animal fossils are the gonorhynchiform fish *Dastilbe crandalli* (DAVIS & MARTILL 1999) and winged imagines, but larval ephemeropterans and odonatans are also common (GRIMALDI 1990, MARTILL 1993). Additional fish species are extremely rare (BRITO et al. 1998, BRITO & MARTILL 1999). Fragments of the gymnosperm *Brachyphylum* sp. are the most abundant plant remains (MAISY 1991, MARTILL 1993). Other terrestrial arthropods can be abundant (CAMPOS 1986, CAMPOS et al. 1988, GRIMALDI 1990, SELDEN & SHEAR 1996, MESQUITA 1996, MARTILL & BARKER 1998, DUNLOP 1999, WILSON 2001, WILSON & MARTILL 2001) and pterosaurs occur frequently (FREY & MARTILL 1994, MARTILL & FREY 1998, 1999, CAMPOS & KELLNER 1997, FREY & TISCHLINGER 2000). Vertebrates such as lizards, turtles, frogs and birds are very much rarer (MARTILL & FILGUIRA 1994, EVANS & YABUMOTO 1998, MARTILL & FREY 1998, MARTILL & DAVIS 2001), and in some cases are known only from single specimens. Soft tissue preservation may accompany preservation of skeletal remains, as either a goethitic stain of the body outline or a three dimensional phosphatisation. Many insect fossils also occur with colour patterning (MARTILL & FREY 1995).

Anatomical nomenclature

Throughout this paper we have followed the Latin anatomical terminology codified in the Nomina anatomica (NA 1989), Nomina anatomica veterinaria (NAV 1983) and Nomina anatomica avium (NAA, BAUMEL et al. 1993), as well as that used in FREY (1988a), RAUHE (1993), WITMER (1995), ROSSMANN (2000), SALISBURY et al. (1999), SALISBURY (2001) and SALISBURY & FREY (2001), all of which relate specifically to crocodilians. Further details concerning the use of this nomenclature are discussed in SALISBURY & FREY (2001). This terminology is used purely in topographic sense and we do not imply any homology in the sense that it relates to common ancestry.

Upon their first appearance in each section of the description or where they appear in sub-titles, all terms are followed by an English translation in brackets. An appendix of all anatomical terms that have been used in the text, their abbreviations used on figures and English translations is also provided.

Anatomical position of a crocodilian

The adjectives designating the relative positions of body parts, their locations or relationships, planes, axes or surfaces used in this paper are in accordance with the anatomical position of a crocodilian presented in SALISBURY & FREY (2001).

Crocodilian taxonomy

Following SALISBURY & FREY (2001), we have chosen to classify crocodilians using a 'traditional' Linnean taxonomy, as opposed to a phylogenetic taxonomic system (e.g. CLARK 1986, 1994, BENTON & CLARK 1988, WU & BRINKMAN 1993, WU et al. 1996a, b, 1997, BROCHU 1997b, RUSSEL & WU 1997–98, CLARK et al. 2000, SERENO et al. 2001, WU et al. 2001). Within most traditional classifications (for a comprehensive listing see STEEL 1973, BUFFETAUT 1982), Crocodilia is divided into four suborders: Eusuchia HUXLEY, 1875, Mesosuchia HUXLEY, 1875, Protosuchia MOOK, 1934, and Sphenosuchia HUENE, 1922. Within Mesosuchia, we have chosen to follow the classification outlined in BUFFETAUT (1982), and recognise five infraorders: Metamesosuchia, Notosuchia, Sebecosuchia, Tethysuchia BUFFETAUT, 1982, and Thalattosuchia FRASS, 1901.

Institutional abbreviations

Abbreviations used for institutions and collections are as follows: BMNH, Natural History Museum, London (formally the British Museum of Natural History); FMNH, Field Museum of Natural History, Chicago; IPMNHNP, Institut de Paléontologie, Muséum national d'Histoire naturelle, Paris; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MC, Museo de Cuenca, Cuenca, Spain; QM, Queensland Museum, Brisbane, Australia; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Germany; SMU, Southern Methodist University, Dallas, Texas, USA; TMM, Texas Memorial Museum, University of Texas at Austin, Austin, Texas; UAM, Universidad Autonoma de Madrid, Spain; USNM, US National Museum, Smithsonian Institution, Washington DC.

Systematic palaeontology

Ordo Crocodilia GMELIN, 1788

Subordo Mesosuchia HUXLEY, 1875

Infraordo Metamesosuchia HULKE, 1878

Familia Susisuchidae nov.

Diagnosis: As for the type genus (see below).

Genus *Susisuchus* nov.

Derivatio nominis: *Susi*, after Susanne Henssen, who prepared the holotype; *suchus*, Lat. Crocodile.

Diagnosis: As for the type species (see below).

Species *Susisuchus anatoceps* sp. nov.

Derivato nominis: *anas*, Lat. duck; *caput*, Lat. head. In reference to the duck-like nature of the caput (head), with its long, dorsoventrally flattened rostrum maxillae.

Holotype: SMNK 3804 PAL; an incomplete, partially articulated skeleton, comprising the cranium, mandibula (mandible) and skeleton postcraniale (postcranial skeleton) minus the terminal two thirds of the cauda (tail), the ossa coxarum et pubis (bones of the hips and the left and right pubic bones) and portions of the skeleton dermale (osteodermal skeleton).

Locus typicus: The precise locality from which the specimen was collected is unknown, but it is likely to have been somewhere within the quarrying region in the Caririucu Valley, south of Nova Olinda, Ceará, north-eastern Brazil.

Stratum typicum: Nova Olinda Member of Crato Formation (Lower Cretaceous, Aptian).

Diagnosis: Differing from all other crocodilian taxa based on the possession of the following combination of osteological features: processus caudalis (caudal process) of the os maxillare (maxillary bone) separating the os lacrimale (lacrimal) from os nasale (nasal); os lacrimale extends rostrally beyond the rostral limit of the os prefrontale (prefrontal); dentes (teeth) needle-like and homodont; ten or eleven vertebrae thoracicae (thoracic vertebrae) and four vertebrae lumbicales (lumbar vertebrae); minimum width of the costae sacrales (sacral ribs) in a craniocaudal direction exceeds the maximum width of any of the processus transversi (transverse processes); postzygapophyses of vertebrae caudales VI–XI (the vertebrae terminal to vertebra caudalis XI are not preserved) unite medially to form a flat, horizontally aligned shelf, which extends terminally over the foramen vertebrale (vertebral foramen); maximum width of the extremitas proximalis (proximal extremity) of the ulna equivalent to that of the extremitas distalis, and slightly less than twice the minimum thickness of the corpus ulnae (ulnar shaft); absence of a tuberculum craniale (cranial tubercle) on the extremitas proximalis of the ulna; phalanx unguis (claw phalanx) present only on digiti manus I et II; scutum dorsi comprising a tetraserial scutum paravertebrale and two left and right sagittal rows of dermostea accessoria; amphicoelous vertebrae thoracicae, lumbicales et caudalis.

Description of the specimen

The specimen comprises the incomplete, partially articulated skeleton of a once *circa* 500 millimetre long crocodilian, preserved on a 400 × 520 mm slab of finely laminated, cream coloured limestone (Text-figs. 2 and 3). It arrived at the SMNK in a partially prepared state, and although the majority of bones currently exposed were visible, portions of many were obscured by matrix. Mechanical preparation, presumably with a pneumatic chisel, had been carried out to the extent that the general outline of the skeleton could be discerned. Minimal attention had been paid to the removal of matrix from between individual bones preserved in close association. Soft tissue and integumentary structures were not visible, and in the case of the right brachium (upper arm), cubitus (elbow) and antebrachium (forearm), may even have been removed unwittingly (see below). Further preparation of the specimen was carried out at the SMNK by Susanne Henssen. The slab was set in a wooden frame using polyester glue, after which dental tools and a pneumatic chisel were used to remove matrix from around the bones and clean the already partially exposed surfaces. The following description of the specimen refers to its condition following this second phase of preparation.

The elements preserved include the following: the cranium, mandibula and most of the skeleton postcraniale. The latter comprises the following elements: vertebrae cervicales, thoracicae, lumbicales, sacrales et caudales; arcus haemales (haemal arches); costae cervicales, thoracicae, sacrales et caudales; dermostea nuchae, dorsi, gastralia et caudae (nuchal, dorsal, gastral and caudal osteoderms); the right and left scapulae, humeri, ulnae and radii; the right coracoideum (coracoid); the right ossa carpi (carpal bones); all the right and left ossa metacarpi et digitorum manus (bones of the middle hand and fingers), except the left ossa digitorum manus IV et V. The ossa coxarum, pubis et membri pelvici (bones of the hip, both pubic bones and the bones of right and left hind limbs) are not preserved.

All the bones are either light or dark brown in colour. There has been some slight dorsoventral compaction of the rostrum maxillae (maxillary rostrum) and several of the bones are fractured. Soft tissues are preserved in a number of places (see Taphonomy for more details).

1. Skeleton axiale (axial skeleton)

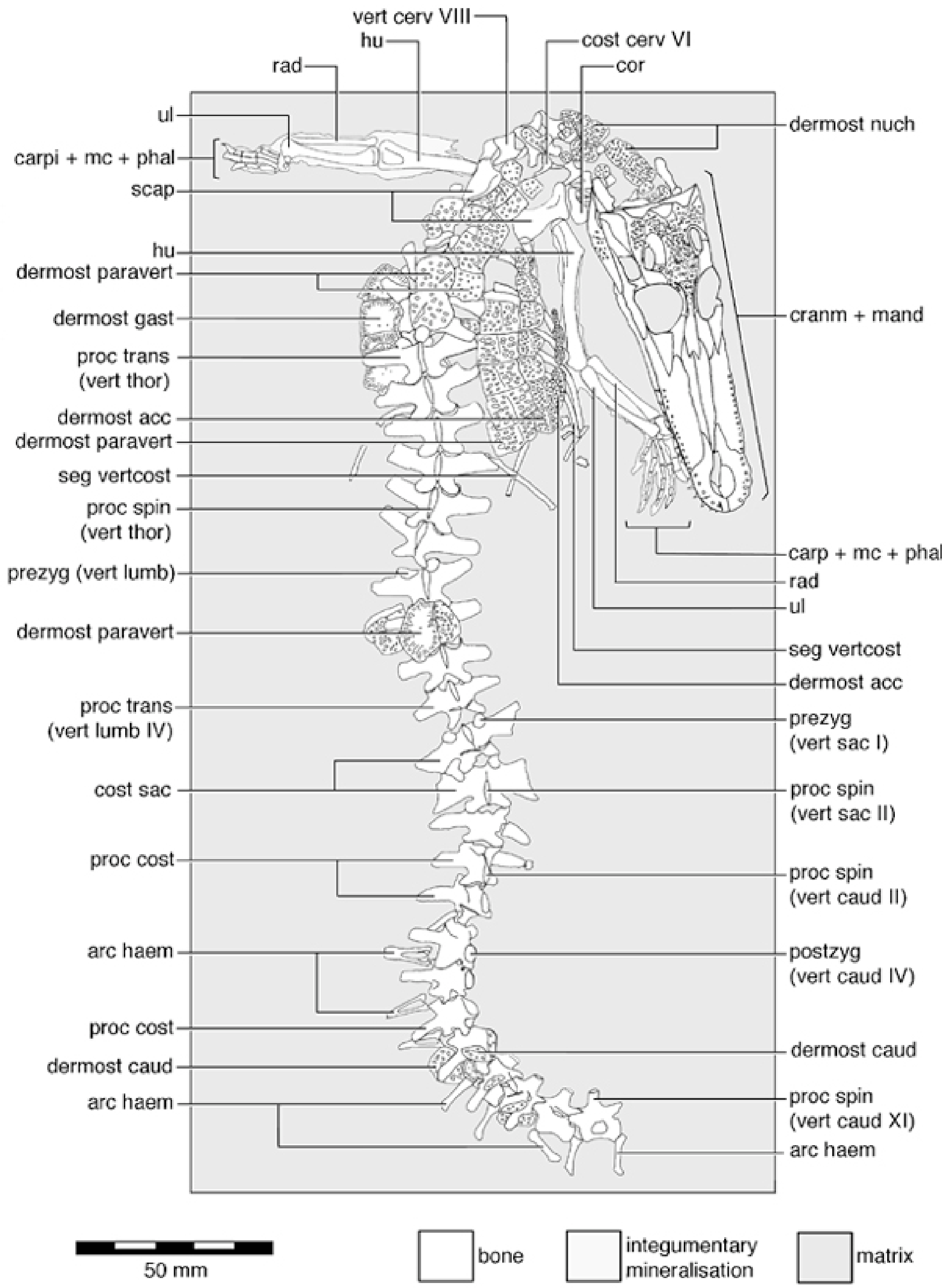
Cranium (skull) (Text-figs. 2 and 4)

The cranium is complete, but exposed only in dorsal and right lateral aspects. The ventral half of the occiput below the level of the processus paroccipitales (paroccipital processes) is obscured by overlying dermostea nuchae, and most of the left infraorbital bones are still obscured by matrix or missing. Portions of the facies dorsalis of the ossa palatina et pterygoidea (palatines and pterygoids) and facies medialis of the right os ectopterygoideum (ectopterygoid) are visible through the orbitae (orbits), but are badly fractured. The facies interna of the palatal part of the left os premaxillare (premaxilla) is also visible through the naris (external nasal aperture). The only dentes that are exposed are those of the right os maxillare and os premaxillare, all of which are still in their respective alveoli. The cranium is flattened dorsoventrally, with concomitant fracturing of the ossa maxillaria, frontalia et nasalia. The left os postoccipitale (postoccipital) is partially disarticulated, overhanging the rostrolateral corner of the left foramen supratemporale (supratemporal foramen).

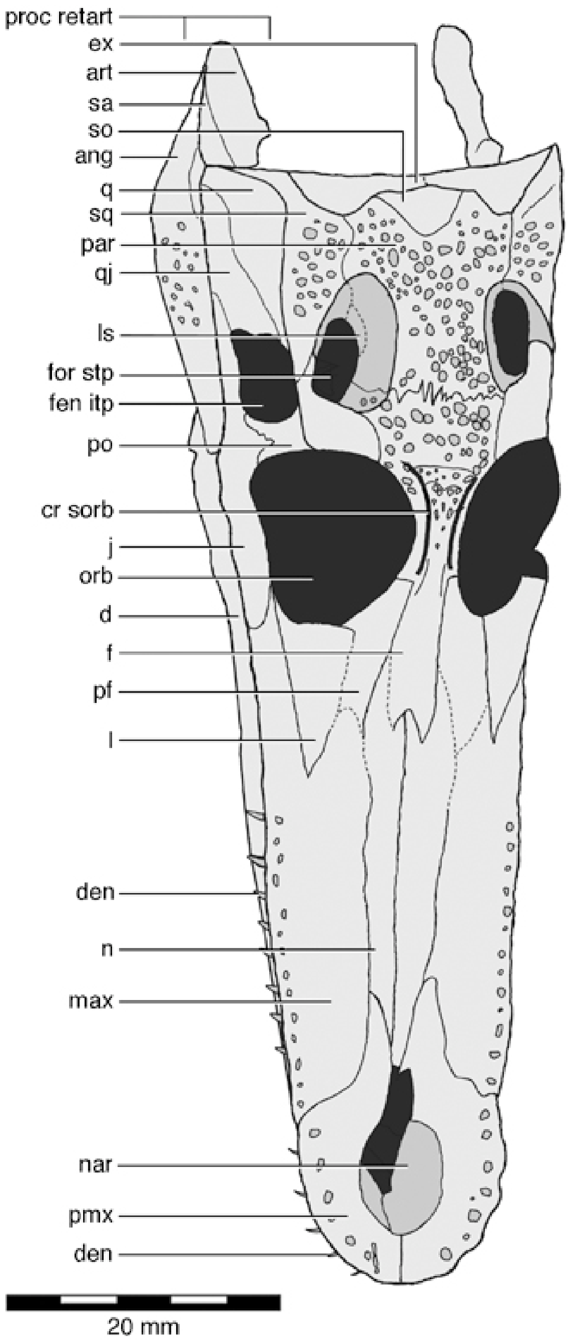
Mandibula (mandible) (Text-figs. 2 and 4)

The mandibula is preserved in articulation and is almost in occlusion with the cranium, but only the facies dorsalis of the processus retroarticularis (retroarticular process), dorsal half of the facies lateralis of the right ramus mandibulae (mandibular ramus) and facies dorsalis of the processus retroarticularis of the left ramus mandibulae are exposed. The ossa supraangulare et angulare (supraangular and angular) of the right ramus are disarticulated,

Text-fig. 2. *Susisuchus anatoceps* gen. et sp. nov.; holotype (SMNK 3804 PAL). See Text-fig. 3 for a schematic interpretation. Scale bar equals 50 mm.



Text-fig. 3. *Susisuchus anatoceps* gen. et sp. nov.; schematic interpretation of SMNK 3804 PAL (Text-fig. 2). The ossa cranii et mandibulae are labelled in Text-fig. 4. Anatomical abbreviations are listed in the appendix.



Text-fig. 4. *Susisuchus anatoceps* gen. et sp. nov.; schematic interpretation of the ossa cranii et mandibulae of SMNK 3804 PAL (Text-fig. 2). Anatomical abbreviations are listed in the appendix.

with the former element having collapsed medial to the latter. Only a small portion of the facies dorsocaudalis of the right os supraangulare is exposed beneath the condylus mandibularis (mandibular condyle) of the right os quadratum (quadrate), with the remainder being obscured by the right side of the rostrum maxillae and right os angulare.

Columna vertebralis (vertebral column) (Text-figs. 2 and 3)

The columna vertebralis is preserved in articulation with the cranium and includes a total of 32 visible vertebrae, most of which are in articulation with one another. The vertebrae thoracicae, lumbicales, sacrales et caudales I–II are exposed in dorsal aspect. Due to a slight dextral twisting of the columna vertebralis, only the facies laterales of the remaining vertebrae caudales are exposed. No skeletal elements are present terminal to vertebra caudalis XI. The columna vertebralis is bent through approximately 160 degrees, so that the cranium is lying sub-parallel to the skeleton axiale, with the main axis of bending passing through the regio cervicoprothoracica (cervicoprothoracic region).

Vertebrae cervicales (cervical vertebrae): Most of the vertebrae cervicales are obscured by overlying dermostea nuchae. The right arcus atlantis (neural arch of the atlas) is preserved adjacent to the right side of the occiput, and is exposed in caudolateral aspect so that the zygapophysis and facies articularis dentalis (dental articular surface) is visible. The processus spinosus (neural spine) of vertebra cervicalis III, exposed in left lateral aspect, is visible to the left of the right processus retroarticularis and right from the second and third articulated dermostea nuchae. Only the apex of the processus spinosus of what, based on its position, is interpreted as vertebra cervicalis V, is exposed. The only other vertebrae cervicales that are visible are VI, VII and VIII, which, although in close association to each other, are not preserved in articulation. A small portion of the left side of the arcus neuralis (neural arch) of vertebra cervicalis VI is exposed, lacking the dorsal half of the processus spinosus. Most of the left side of the arcus neurales, including pre- and postzygapophyses, of vertebrae cervicales VII and VIII are exposed, but the processus spinosus of the former is obscured partially by an overlying dermosteum nuchae, and that of the latter is broken off just dorsal to its base. The left diapophysis of each of these vertebrae is also apparent.

Vertebrae thoracicae et lumbicales (thoracic and lumbar vertebrae): The most cranially situated portion of a vertebra thoracica that is visible is the broken processus spinosus of what can be interpreted as either vertebra prothoracica I or II, which protrudes between the suturae medianae (median suture) of the left and right dermosteum from the third transverse row comprising the scutum dorsi (dorsal shield). Caudal to this is a second processus spinosus, followed by the left and right processus transversi of what are presumably the next two subsequent vertebrae in the series respectively. Four more vertebrae thoracicae follow, all of which are preserved with their pre- and postzygapophyses in articulation. All have their corpus vertebrae (vertebral bodies) and facies ventrales of the processus transversi embedded in matrix, and lack the dorsal half of the processus spinosus. The next two vertebrae preserved in the series possess processus transversi with straight margines laterales (lateral margins), suggesting that they may have articulated with short, spine-like costae thoracicae. If this is the case, then these represent the caudal-most vertebrae thoracicae. Caudal to these two vertebrae are four vertebrae lumbicales, the second of which is almost completely obscured by three overlying dermostea dorsi. These vertebrae are preserved in a similar manner to the proceeding vertebrae thoracicae, with their pre- and postzygapophyses in articulation. All lack the dorsal half of their processus spinosi and have their corpus vertebrae and facies ventrales of the processus transversi embedded in matrix. There is a slight dislocation of the columna vertebralis between the first of the aforementioned vertebrae lumbicales and caudal-most vertebrae thoracicae. As a result, the fossa vertebralis caudalis (caudal articular fossa) of the latter and fossa vertebralis cranialis of the former are exposed, as are their pedunculi arcus neurales and foramen vertebrale.

Vertebrae sacrales and costae sacrales (sacral vertebrae and ribs): Both vertebrae sacrales are present, and have their corpus vertebrae and facies ventrales of the costae sacrales embedded in matrix. The latter are preserved in articulation with their respective vertebrae. Although they are in close association, the pre- and postzygapophyses of these vertebrae are not preserved in articulation with each other. Additionally, both lack the dorsal half of their processus spinosus. A break running through the slab, perpendicular to the long axis of the columna vertebralis, passes through the left costa sacralis I, left prezygapophysis of the vertebra sacralis I, right prezygapophysis of vertebrae sacralis II and costa sacralis II. With the exception of the latter, of which the craniolateral half is missing, the specimen appears to have sustained little damage as a result of this breakage, and both parts of the slab have been glued together accurately with resin. Because both vertebrae sacrales are not in articulation with one another, the fossa vertebralis cranialis of vertebra sacralis II has been exposed.

Vertebrae caudales and costae caudales (caudal vertebrae and ribs): Vertebrae caudales I–XI are preserved in partial articulation in a sinistrally convex arc. The first and second have their corpus vertebrae and facies ventrales of their respective costae caudales embedded in matrix. They are also not in articulation and each lacks the dorsal half of its processus spinosus. The prezygapophyses of vertebra caudalis I are in articulation with the postzygapophyses of vertebra sacralis II. A small portion of the corpus vertebrae of vertebra caudalis II is exposed. Vertebrae caudales III–V are preserved in left dorsolateral aspect, with the corresponding right costae caudales projecting into the slab. Nevertheless, as is the case with most of the other vertebrae, they are not exposed ventral to their processus transversi and each lacks the dorsal half of its processus spinosus. Although vertebrae caudales III et IV are not preserved in articulation, all vertebrae terminal to vertebra caudalis IV are. The degree to which the columna vertebralis has been twisted dextrally increases gradually in a terminal direction from vertebra caudalis III, so that the last vertebra in the series is fully exposed in lateral aspect. This rotation also means that as opposed to the case of the vertebrae thoracicae, lumbicales et sacrales, along with the first two vertebrae caudales, the degree to which the corpora vertebrarum are exposed gradually increases caudally, though portions of those belonging to vertebrae caudales VII–IX are obscured partially by overlying dermostea. The processus spinosi of vertebrae caudales VIII–XI are intact, with their left facies lateralis fully exposed. With the exception of those belonging to vertebrae caudales II et XI, all of the costae caudales on the right side are preserved intact, and are exposed in dorsal aspect; from the left side, only costae caudales I et II are exposed.

Assuming a length ratio of the caput + cervix + truncus (trunk) : cauda equivalent to that in extant crocodilians (1:1; WERMUTH 1964), the missing portion of the cauda of *Susisuchus anatoceps* constitutes approximately 65 per cent of its total length. At least 24 additional vertebrae caudales can be assumed to have been present, making the total number 35+.

Arcus haemales (haemal arches): Arcus haemales III–XI, of which all are complete, are preserved in association with the articulated series of vertebrae caudales. The first of these, arcus haemalis III, is exposed in right lateral aspect only, with its processus articulares obscured by the overlying costa caudalis IV. The processus ventralis of this element is preserved between the corpora of vertebrae caudales III et IV. Arcus haemalis IV is disarticulated and preserved between costae caudales IV et V, being visible in cranial aspect. The next two terminally following elements in the series are preserved in a similar position between costae caudales V et VI and VI et VII respectively, but are exposed only in terminal aspect. With the exception of arcus haemalis IX, which is slightly displaced terminally, arcus haemales VII, VIII, X et XI are exposed in left lateral aspect in close to what could represent an in situ position, with their processus articulares in intervertebral positions. All the latter elements have suffered some degree of mediolateral compaction, and the left processus articularis of each is fractured.

Costae cervicales (cervical ribs) (Text-figs. 2 and 3): Caudal portions of what appear to be the corpora of the right costae cervicales I, II et III are exposed in lateral aspect to the right of the right processus retroarticularis. Caudal to these elements, what are interpreted as the isolated right costae cervicales IV, V et VII are preserved in lateral aspect. The processus cranialis of each of these ribs is obscured by either matrix or overlying dermostea nuchae, and of their processus articulares vertebrales only the tubercula are exposed. The caudal half of the corpus of costa cervicalis IV is missing. What could be the caudal end of the corpus of costa cervicalis VI is preserved in articulation with the processus cranialis of costa cervicalis VII; the rest of this assumed costa being obscured by an overlying dermosteum nuchae and the tuberculum of costa cervicalis V.

Costae thoracicae (thoracic ribs) (Text-figs. 2 and 3): Of the costae thoracicae, at least nine of the right segmenta vertebrocostalia (vertebral rib segments), eight of which appear to be complete, are preserved. Although portions of the cranial seven of these segmenta are obscured by overlying dermostea dorsi, all are exposed in caudal aspect, with the axes of their corpora aligned parallel to the long axis of the articulated portion of the columna vertebralis. The remaining two are preserved caudal to the articulated portion of scutum dorsi. The capitulum and tuberculum of one of these is exposed in cranial aspect in partial articulation with the right processus transversus of the eighth vertebra (vertebra thoracica X or XI) in the series of exposed vertebrae thoracicae. The articular head of the other is obscured by the caudal-most dermostea of the articulated portion of the scutum dorsi. Although the capitula of all these ribs are obscured, the facies articularis of the tubercula of the second, third, fourth and fifth are visible. Only four segmenta vertebrocostalia from the left side can be discerned. Counting from cranial to caudal, the first of these, of which only a small portion of the broken corpus is exposed, is preserved to the left of the processus spinosus of the second of the exposed vertebra thoracica. Based on its position, this latter element can be interpreted as vertebra prothoracica II or vertebrae thoracica III. The capitulum and tuberculum of the next apparent segment are preserved beneath the processus transversus of the third vertebra thoracica in the exposed series (vertebra thoracica IV or V). The corpus and broken articular head of a third segment are preserved beneath the right processus transversi of the fifth and sixth of the exposed series of vertebrae thoracicae (interpreted as vertebrae thoracicae VI et VII or VII et VIII). The last segment from the left side comprises most of the corpus, the cranial half of which is preserved between the left processus transversi of the sixth and seventh vertebrae thoracicae in the exposed series (vertebrae thoracicae VI et VII or VII et VIII); the capitulum and tuberculum being obscured by the corpora of the latter vertebrae. A portion of the corpus of this segment is missing and has been replaced with what appears to be the same resin that was used to repair the large crack that splits the slab in two. Left of the last dermosteum comprising the articulated portion of scutum dorsi, a single isolated element is interpreted as a segmentum laterocostale (lateral rib segment).

2. **Skeleton appendiculare** (appendicular skeleton) (Text-figs. 2 and 3)

Ossa cinguli membri thoracici (bones of the pectoral girdle)

Scapula: Both the left and right scapulae are preserved in close to what could be regarded as their in situ position. The right element is exposed in lateral aspect, with its long axis aligned parallel to the portion of columna vertebralis beside which it is preserved. A small portion of the dorsocaudal corner of the ala scapulae (scapular wing) is obscured by an overlying right segmentum vertebrocostale, and the facies articularis coracoidea (coracoidal articular surface) contacts the facies medialis of the extremitas omalis (articular extremity) of the right coracoideum. The left scapula is also exposed in lateral aspect, but most of the extremitas omalis is obscured by matrix and the overlying left diapophysis of vertebra cervicalis VIII. The corpus scapulae of the left scapula is fractured.

Coracoideum (coracoid): Only the extremitas omalis (articular extremity) of the right coracoideum is exposed. The bone is preserved with its axis proximodistalis oriented perpendicular to the exposed surface of the slab, such that the facies articularis scapularis et humeralis are visible in dorsal aspect. The foramen coracoideum is visible only on the medial side; the rest of the corpus being obscured by the extremitas omalis of the right scapula.

Ossa membri thoracici (bones of the forelimbs)

Ossa membrum thoracicum dextrum (bones of the right forelimb). The bones of the membrum thoracicum dextrum are preserved in partial articulation parallel to the left margo lateralis of the cranium. The right humerus is exposed in lateral aspect, with the caput (proximal articular head) situated next to the margo caudalis of the right scapula. Only the lateral half of the facies cranialis et caudalis of the extremitas proximalis, corpus and extremitas distalis, including the condylus lateralis, is exposed. The exposed portions of the right ulna include the facies lateralis of the extremitas proximalis and facies lateralis et caudalis of the corpus and extremitas distalis (distal extremity). The right radius is preserved with its facies caudalis facing into the slab. Although almost all of the caput is exposed, the facies articularis carpalis (carpal articular surface) of the extremitas distalis is still embedded in matrix. The right os radiale (radiale), which is exposed in cranial aspect, is preserved in close association with the right os ulnare and extremitates distales of the skeleton antebrachii (forearm skeleton). A small portion of the lateral side of the corpus is obscured by the overlying os ulnare (ulnare). This latter element is preserved with its axis proximodistalis oriented obliquely to the slab, with its facies articularis metacarpalis embedded in matrix. In addition to this, only the facies lateralis of the corpus is exposed. A small round bone preserved between the right os radiale and os metacarpale I may represent the right os pisiforme (pisiform), but this cannot be determined with certainty. All the ossa metacarpi et digitorum manus are preserved in articulation in what could be considered a relaxed, in situ position, and are exposed in dorsal aspect only. There are five ossa metacarpi, and five digiti manus. Digitus manus I comprises a single phalanx and phalanx unguis. Digiti manus II, III et IV comprise four phalanges. Only phalanx 4 of digitus manus II can be regarded as a phalanx unguis. Digitus manus V comprises only two phalanges.

Ossa membrum thoracicum sinistrum (bones of the left forelimb). The bones of the membrum thoracicum sinistrum are preserved in partial articulation, the membrum being oriented caudolaterally slightly from the left regio omalis (shoulder region). The left humerus is preserved with the extremitas omalis beneath the left scapula; the rest of the bone being exposed in caudal aspect. The sulcus intercondylaris (intercondylar sulcus) and part of the condylus medialis of the extremitas distalis is obscured by the caput ulnae. Only the facies lateralis of the extremitates proximalis et distalis and facies lateralis et caudalis of the corpus of the left ulna are exposed. The cranial side of the extremitas distalis is in articulation with the extremitas distalis of the left radius, which, with the exception of the latter region, is exposed fully in lateral aspect. Due to the fact that the left ossa carpi, metacarpalia et manus are situated slightly caudal to their in situ position, most of the facies articularis carpalis of the ulna is exposed. Two small, round bones, preserved caudal to the extremitas distalis of the right ulna, may represent portions of the ossa radiale et ulnare. The ossa metacarpi et digitorum manus are preserved in partial articulation, but overlap each other in a lateral to medial manner, whereby os metacarpale I and the ossa digiti manus I are towards the matrix and os metacarpale V and the ossa digiti manus V are furthest away from it. All these bones are exposed in palmar aspect. All digiti manus are complete, with the exception of digiti manus I et II, which are missing.

3. **Skeleton dermale** (osteodermal skeleton) (Text-figs. 2 and 3)

Scutum nuchae (nuchal shield): At least 12 dermostea nuchae are preserved, all of which are exposed in external aspect. Five of these are round in outline, and approximately one quarter the size of the others, which appear to come from the right side of the scutum nuchae. The former are preserved in isolation immediately caudal to the occiput and medial to the series of exposed costae cervicales, while the latter are in partial articulation with one another, atop the vertebrae cervicales. The three cranial-most of these larger dermostea appear to be complete, but the remainder are both fractured and missing small portions.

Scutum dorsi (dorsal shield): A total of 34 dermostea dorsi are visible. The majority of these are preserved in partial articulation in the regiones prothoracica et thoracica. The remaining elements are preserved in disarticulation, but are still in close association with either the vertebrae lumbicales or the vertebrae caudales. Of those in the former region, all of which are exposed in external aspect, 23 come from the right side and seven from the left side of the scutum dorsi. Three transverse rows, each comprising two dermostea only, are preserved between the scapulae. These dermostea overlie what are presumably the processus spinosi of the caudal-most vertebrae cervicales and vertebrae prothoracicae, such that they are fractured in several places. The processus spinosus of what is interpreted as either vertebra prothoracica I or II is visible between the suturae medianae (median sutures) of the two dermostea that comprise the third transverse row. Caudal to these six dermostea, a large, articulated portion of the right side of the scutum dorsi is preserved. Only the first three median dermostea from this portion of the scutum dorsi are present, the cranial-most of which is preserved lateral to the second processus spinosus from the exposed series of vertebrae thoracicae (vertebra prothoracica II or vertebra thoracica III). A small fragment of the third dermosteum in this articulated row is preserved between the right processus transversi of the third and fourth vertebrae in the exposed series of vertebrae thoracicae (either vertebrae thoracicae IV et V or V et VI). Caudal and lateral to these three dermostea, three more articulated sagittal rows are preserved. The first comprises five sub-rectangular dermostea, extending caudally to a position level with the margo cranialis of the right processus spinosus of the eighth vertebra in the series of exposed vertebrae thoracicae (vertebra thoracicae IX or X). The facies articularis of the pars articularis cranialis of all but the first of these dermostea is obscured by the overlying pars articularis caudalis of that proceeding it cranially. The next sagittal row of dermostea dorsi comprises seven sagittally oval elements. With the exception of the cranial-most of these, which is situated just caudal to the right ala scapulae, each is sutured medial to the margo lateralis of the corresponding dermostea from the second lateral-most sagittal row. The lateral-most sagittal row of the dermostea dorsi comprises a series of five elements, all of which are sub-rhomboidal in outline, preserved in a row between and parallel to the right humerus and third lateral-most sagittal row of dermostea dorsi. These dermostea lie atop the corpora of the right series of segmenta vertebrocostalia.

The four dermostea from the left side of the scutum dorsi come from the medial-most sagittal row. The two cranial-most of these dermostea are preserved in partial articulation immediately caudal to the left ala scapulae. The next two, which are also preserved in partial articulation with one another, are situated on top of the second and third vertebrae from the exposed series of vertebrae thoracicae (vertebrae thoracicae III et IV or IV et V).

Three disarticulated dermostea dorsi are preserved in close association with vertebra lumbicalis II. Two lie atop this vertebra; one exposed fully in internal aspect on the left side, and the other, which the latter overlays partially, is exposed in external aspect on the right side. The third dermosteum in this agglomeration is exposed in external aspect, obscured partially by the left processus transversus. The side of the scutum dorsi from which these dermostea are derived cannot be determined.

Dermostea caudae (osteoderms of the tail): A second agglomeration of disarticulated dermostea is preserved in association with the terminal portion of the preserved series of vertebrae caudales. Two of these dermostea are of an equivalent size to those from the medial-most articulated sagittal row of dermostea accessoria (accessory osteoderms), and may belong to the squamae of either the latus caudae or venter caudae (scales on the lateral and ventral sides of the tail). The cranial-most of these two dermostea is obscured partially by matrix associated with the left costa caudalis VIII, and is exposed in external aspect. The second is preserved beneath the left costa caudalis IX, and both its facies interna et externa are exposed. The other five dermostea scattered around this region of the cauda appear to come from the squamae of the crista caudae pars duplicata (double tail crest). All except one are exposed in external aspect.

Scutum gastrale (gastral shield): An articulated craniocaudal series of four dermostea gastralia are preserved beneath the processus transversi of the fourth, fifth and sixth vertebrae respectively in the exposed series of vertebrae thoracicae (vertebrae thoracicae V–VII or VI–VIII). They are all exposed in internal aspect, and have their margines mediales obscured by the corpora of the overlying vertebrae.

Osteology

1. Skeleton axiale (axial skeleton)

Cranium (skull) (Text-figs. 2, 3 and 4)

General form and proportions: Measured from the margo cranialis of the orbitae to the rostral terminus of the ossa premaxillaria, the rostrum maxillae forms approximately 60 per cent of the total length of the cranium in a rostrocaudal direction. In dorsal aspect, the cranium tapers only slightly towards the tip of the rostrum maxillae, the margines laterales almost parallel to each other. The minimum width of the rostrum maxillae, which occurs between the incisurae premaxillomaxillares (premaxillomaxillary notch), is 75 per cent the maximum width of the mesa cranii. Each orbita is approximately twice the size of the naris, and oval-shaped in outline, with its long axis aligned rostrocaudally. The size of each orbita is equivalent to that of the right foramina supratemporalia. External sculpture pitting comprises small (1 mm wide) pits and reticulations, developed best on the mesa cranii and around the margin of the rostrum maxillae.

Neurocranium (the part of the cranium enclosing the brain): Due to the way in which the cranium has been prepared, comments on the neurocranium are restricted to the facies externa of the mesa cranii, dorsal half of the occiput, regio infratemporalis (infratemporal region) and cavum typmpanicum (tympanic cavity).

Mesa cranii (skull table): In dorsal aspect, the mesa cranii is approximately square in outline. The margines laterales are gently convex lateral to the foramina supratemporalia, but become concave caudally. The margo caudalis is straight medially, and concave laterally, so that each caudolateral corner tapers to a blunt point dorsal to the processus paroccipitalis (paroccipital process). Each craniolateral corner is convex in outline, and the margines supraorbitales are rostrolaterally concave. The smooth foramina supratemporalia are rostrocaudally oval in outline, and are only gently demarcated from the facies dorsalis of the mesa cranii medially. The maximum dorsal length of each foramen in a rostrocaudal direction is equal to 80 per cent the length of the orbita, and the maximum width less than half. In dorsal aspect, minimum distance between them is 75 per cent of their maximum length in a rostrocaudal direction. The small, round apertura rostralis (rostral aperture) of the canalis postemporalis (postemporal canal) is situated at the caudal end of the fossa, being visible in dorsal aspect.

Occiput: The dorsal half of the occiput, which is the only portion that is exposed (see Description of the specimen), is visible in dorsal aspect, bulging out caudally either side of the os supraoccipitale and the crushed condylus occipitalis (occipital condyle). The same is true of the round aperturae occipitales of the canales posttemporales, which are of a similar size to their rostral counterparts within the foramina supratemporalia. In dorsal aspect, the blunt processus paroccipitalis is almost level with the condylus mandibularis (mandibular condyle) of the os quadratum. The dorsal outline of the foramen magnum cannot be discerned.

Ossa neurocranii (bones of the neurocranium)

Os frontale (frontal): The os frontale forms the entire medial border the orbita. In dorsal aspect, its minimum width between the orbitae is approximately 25 per cent of its maximum width on the facies dorsalis of the mesa cranii. Two prominent cristae supraorbitales (supraorbital ridges) are present, extending from the cranial extent of the smooth, rostrolaterally concave sutura frontopostorbitalis to the caudal-most contact between the ossa frontale et prefrontale. Cranial to this point, each ridge diverges into two smaller ones. The medial ridge follows the sutura frontoprefrontalis (frontoprefontal suture) to a point level with the cranial extent of the orbitae, while the lateral ridge follows the dorsal border of the orbita round to the contact between the ossa prefrontale et lacrimale.

The width of the os frontale increases cranial to the orbitae, with the processus rostralis contributing to the first ten per cent of the facies externa of the rostrum maxillae. This process is forked rostrally, being divided into two smaller, triangular-shaped rostral processes that contact the caudal margins of the ossa nasalia. The left process is slightly larger than the right one. A thin, triangular processus caudalis of the os nasale separates the rostral half of the processus rostralis from the rostral half of the os prefrontale.

Caudally, the os frontale forms the medial half of the mesa cranii rostral to the foramina supratemporalia, of which it forms the dorsal half of the rostromedial surface, but not to the extent that the os postorbitale (postorbital) is separated from the os parietale (parietal) within the foramen in dorsal aspect. The serrated sutura frontoparietalis extends between two points just caudal to the cranial apex of each fossa. The facies externa of the os frontale is covered with indistinct pits and depressions caudally, whereas within the foramina supratemporalia and between and cranial to the cristae supraorbitales it is smooth.

Os parietale (parietal): The facies externa of the os parietale forms most of the medial portion of the facies dorsalis of the mesa cranii and medial portion of each foramen supratemporale. The medial portion of its caudal end is excluded from the margo caudalis of the mesa cranii by the os supraoccipitale. Although indistinct, the suture between these two bones appears to be slightly serrated in places. The sinuous sutura squamosoparietalis (squamosoparietal suture) commences caudally dorsal to the apertura caudalis of the canalis postemporalis, and enters the foramen supratemporale medial to the apertura rostralis of the same canalis. The medial half of the latter aperture is formed entirely by the os parietale. Within the foramen supratemporale, the sutura laterosphenoidoparietalis (laterosphenoidoparietal suture) cannot be identified, suggesting that the os parietale may have formed the medial wall of the foramen supratemporale, at least in dorsal aspect. The facies externa of the os parietale is covered with indistinct pits and depressions, but is smooth within the foramina supratemporalia.

Os postorbitale (postorbital): In dorsal aspect, the os postorbitale forms the rostrolateral corner of the mesa cranii and foramen supratemporale. Caudally, it overlaps the os squamosum to a point halfway along the margo lateralis of the foramen supratemporale; the medial extent of this overlap being greater than the lateral one. The portion of the os postorbitale that contributes to the mesa cranii overhangs the columna postorbitalis rostrolaterally. This bar is mediolaterally flattened and has a width that is equivalent to the minimum width of the os frontale between the orbitae. The os postorbitale forms most of its facies lateralis, contacting the os jugale (jugal) just dorsal to the base. A small, spine-like processus rostralis is apparent two thirds of the way up the columna postorbitalis (postorbital bar). Dorsal to the columna postorbitalis, a foramen nutricium (nutrient foramen) is not visible on the facies lateralis of the os postorbitale. The entire facies dorsalis of this bone is weakly sculptured with small pits and depressions.

Os squamosum (squamosal): The os squamosum forms the caudolateral portion of the mesa cranii and foramen supratemporale. Cranially, it underlaps the os postorbitale, extending to a point just caudal to the dorsocaudal edge of the columna postorbitalis. Caudolaterally, it tapers to a point, below which it forms the dorsal half of the blunt processus paroccipitalis. Although most of the dorsal surface of this bone is sculptured with small, indistinct pits and depressions similar to those on other parts of the cranium, the latter region, above and contributing to the processus paroccipitalis, is smooth. The smooth, straight sutura squamosoexoccipitalis runs parallel to the margo caudalis of the mesa cranii, and is visible in dorsal aspect. Medial to this suture, the os squamosum forms the dorsal border of the apertura caudalis of the canalis postemporalis. Within the foramen supratemporale, the os squamosum forms the dorsolateral border of the apertura rostralis of this canalis. Rostral to this opening, the rostrocaudally aligned sutura squamosoparietalis is straight and smooth. It appears as if the os squamosum bordered the os quadratum medially within the caudolateral portion of the foramen supratemporale, though the suture between these two bones is difficult to discern.

Caudal to the cavum tympanicum, the os squamosum is sutured to the os quadratum. The nature of the facies lateralis of the os squamosum, dorsal to the cavum tympanicum, is not visible (see Description of the specimen).

Os supraoccipitale (supraoccipital): In dorsal aspect, the os supraoccipitale is a small, triangular bone that forms the medial portion of the mesa cranii caudal to the foramina supratemporalia. It is unsculptured and excludes the medial two thirds of the margo caudalis of the os parietale from contributing to the margo caudalis of the mesa cranii. In dorsal aspect, the part of this margin that is formed by the os supraoccipitale is triangular in outline, with the apex pointing caudally. Unlike the other bones that comprise the occiput, the facies occipitalis of the os supraoccipitale is not visible in dorsal aspect, being perpendicular to the facies dorsalis of the mesa cranii. Either side of a rounded, median ridge, a shallow fossa occipitalis perforates the facies occipitalis. Dorsolateral to this depression, the os supraoccipitale forms the medial border of the apertura caudalis of the canalis postemporalis. Caudal to this opening, a small, rounded bulla occipitalis (occipital bulla), formed entirely by the os supraoccipitale, is visible in dorsal aspect. Ventrally, the ossa exoccipitalia (exoccipital bones) exclude the os supraoccipitale from contributing to the dorsal border of the foramen magnum.

Os laterosphenoideum (laterosphenoid): Only a very small portion of the os laterosphenoideum is visible, forming the internal-most medial portion of the foramen supratemporale. The smooth, indistinct sutura parietolaterosphenoidalis (parietolaterosphenoid suture) circumscribes the medial border of the foramen supratemporale. Caudally, a small portion of the os laterosphenoideum contacts the os quadratum.

Os quadratum (quadrate): Portions of the os quadratum are visible in two regions of the neurocranium. The first, and most obvious area, includes the portion lateral to the cavum tympanicum and the condylus mandibularis, which is in articulation with the fossa articularis quadratica (articular fossa) of the mandibula. The width of this condyle in a mediolateral direction is equivalent to the minimum width of the os frontale between the orbitae. In occipital aspect, the long axis of the facies articularis of the condylus mandibularis is offset medioventrally 20–30 degrees to the facies dorsalis of the mesa cranii. In dorsal aspect, this condyle is gently concave medially. A foramen aërium is not visible on the exposed part of the facies dorsalis of the os quadratum, rostral to the condylus mandibularis. The suture between the ossa quadratum et squamosum is serrated, and situated immediately ventral to the main caudolateral expanse of the processus paroccipitalis. The sutura quadratoexoccipitalis (quadratoexoccipital suture) is not visible. The os quadratum forms the floor of the cavum typmpanicum, where it is smooth and gently concave. The sutura quadratoquadratojugalis (quadratoquadratojugal suture) is smooth, being rostrocaudally aligned caudally, but curving rostromedially as it approaches the fenestra infratemporalis (infratemporal fenestra) rostrally. The os quadratum is separated from the latter opening by the os quadratojugale. The contact between the os quadratum and os postorbitale is not visible, nor is the outline of the recessus tympanicus (tympanic recess) (see Description of the specimen and that on the regio infratemporalis below).

The second area where the os quadratum is visible is inside the foramen supratemporale, where it forms the caudolateral surface dorsal to the foramen supratemporale and ventral to the pars squamosalis. It does not appear to have contributed to the border of the apertura rostralis of the canalis postemporalis, being separated by a small contact between the ossa parietale et squamosum. The portion of the sutura quadratolaterosphenoidalis (quadratolaterosphenoidal suture) that is visible inside the foramen supratemporale is rostrocaudally aligned, entering the foramen supratemporale at its caudal-most extent.

Os exoccipitale (exoccipital): In dorsal aspect, the os exoccipitale forms almost all of the visible occipital surface of the cranium, extending caudally beyond the margo caudalis of the mesa cranii. Its surface in this region is smooth and gently convex lateral to the apertura caudalis of the canalis postemporalis and medial to the processus paroccipitalis, of which the os exoccipitale forms the ventromedial portion. Medially, the ossa exoccipitalia contact each other dorsal to the foramen magnum, excluding the os supraoccipitale from contributing to its dorsal border. The os exoccipitale forms the ventral border of the apertura caudalis of the canalis postemporalis. No foramina are visible on the exposed surface of the os exoccipitale.

Orbita (orbit)

In dorsal aspect, the orbita is concave medially, with a straight, caudorostrally aligned margo lateralis. Its maximum diameter is one and a half times the maximum length of the foramen supratemporale in a rostrocaudal direction. The dorsal border of each orbita is formed by the os frontale medially, os prefrontale rostromedially, os lacrimale rostrally, os jugale laterally and os postorbitale caudally.

Regio infratemporalis (infratemporal region)

The fenestra infratemporalis is longer in a rostrocaudal direction than it is wide, and oval in outline in dorsolateral aspect. Its external border is formed by the os postorbitale rostrally, os jugale rostrolaterally and laterally and os quadratojugale dorsocaudally. A spina infratemporalis (infratemporal spine) is absent on the os quadratojugale, though may have broken off during preparation or early diagenesis. Both the left and right recessus tympanici are filled with matrix.

Splanochnocranium (facial skeleton)

Maxilla (upper jaw). The maxilla, which includes the rostrum maxillae and arcus jugalis (jugal arch), is only slightly wider caudally than it is rostrally, with almost parallel margines laterales. Although crushed slightly, the rostrum maxillae does not appear to have been very deep dorsoventrally, being flat medially and gently convex laterally. The insicura premaxillomaxillaris is a shallow concavity in dorsal aspect, and dens dentalis IV may not have been visible during occlusion. The partes alveolaris maxillaris et premaxillaris (maxillary and premaxillary tooth rows) are not festooned vertically. It is therefore concluded that the dentes premaxillares et maxillares occluded in a overbite fashion with the dentes dentales. With the exception of the rostral extensions of the crista supraorbitales on the os frontale and ossa prefrontalia, along with some faint pitting around its margins, the external surface of the rostrum maxillae is smooth. Portions of the palatum osseum secundare (bony secondary palate) are visible through the orbitae, but the bones comprising it are crushed to such an extent that little can be said about their relationship to one another, or, for example, the size of the fenestrae suborbitales (suborbital fenestrae). What is apparent, however, are the margines rostrales of these fenestra, which are situated caudal to those of the orbitae. The fenestra premaxillaris (incisive foramen) is visible through the naris, and appears to have been rostrocaudally oval in outline, with a pointed rostral apex extending to a point halfway along the length of the vestibulum nasi (nasal vestibule) in dorsal aspect. The naris is teardrop-shaped in outline, rounded rostrally and pointed caudally, and of an equivalent size to the foramen supratemporale. In dorsal aspect it is positioned in the middle of the ossa premaxillaria, which together form its entire dorsal border. In lateral aspect it is not raised above the rest of the facies externa of the rostrum maxillae.

Ossa splanochnocranii (bones of the facial skeleton)

Os premaxillare (premaxilla). With the exception of the facies palatina (palatal surface), the os premaxillare can be described in full (see Description of the specimen). In dorsal aspect, the portion of the rostrum maxillae comprising the ossa premaxillaria is almost as broad as that comprising the ossa maxillaria et nasalia. Rostral to the naris, which is dorsally oriented, the ossa premaxillaria unite to form a small rugose ridge; the remainder of the margin of each bone is lobate in dorsal aspect. The ossa premaxillaria exclude the ossa nasalia from the dorsal border of the naris. A triangular process, which extends to a point level with dens maxillaris IV (IV maxillary tooth), separates the rostral extent of the os nasale from the os maxillare rostrally. External sculpturing is restricted to indistinct pits and lobations on and around the margin. A small foramen situated between the sutura premaxillaris and dens premaxillaris I may represent the reception pit for dens dentalis I. There are a total of five dentes premaxillares (premaxillary teeth), each of which is gracile, needle-like and of an equivalent size. Vertical festooning between the alveoli premaxillares is minimal. The ossa premaxillaria form the walls of the cavitas nasalis (nasal cavity) and at least the rostral borders of the fenestra premaxillaris.

Os maxillare (maxillary bone). Only the facies externa of the os maxillare is visible (see Description of the specimen). This element is flat medially, but becomes dorsolaterally convex towards its margo lateralis, and, with the exception of a few indistinct pits close to its margo lateralis, is devoid of any sculpture pitting. Caudomedially, a short, triangular caudal process separates the caudal extent of the os nasale from that of the os lacrimale. The os maxillare is excluded from the dorsal border of the orbita by a contact between the ossa jugale et lacrimale, best evident on the left side of the maxilla. The os maxillare extends caudally beneath the os jugale to a point halfway along the margo lateralis of the orbita.

Only dentes maxillares I–IX are visible. Each is needle-like and of a similar size to the dentes premaxillares. With the exception of a slight diastema between dentes premaxillaris V et maxillaris I, interalveolar spaces are uniform throughout this portion of the toothrow, being approximately equal in length to each dens.

O s p r e f r o n t a l e (prefrontale): The os prefrontale forms the rostromedial portion of the dorsal border of the orbita. Medially it contacts both the ossa frontale et nasale, and rostrally it separates the caudal extent of the latter from the rostral extent of the os lacrimale, extending to a point that is level with the rostral extent of the os frontale. The lateral bifurcation of the crista supraorbitalis forms the medial half of the margo orbitalis of the os prefrontale. The medial bifurcation traces the caudal half of the sutura frontoprefrontalis (frontoparietal suture). Between these two ridges there is a shallow depression, here termed the sulcus prefrontalis (prefrontal suture). Apart from this feature, the rest of the facies externa of the os prefrontale is smooth.

O s l a c r i m a l e (lacrimal): In dorsal aspect, the os lacrimale is triangular in outline, extending rostrally to a point beyond that of the ossa frontale et prefrontale and level with dens maxillaris IX. The straight sutura lacrimoprefrontalis (lacrimoprefrontal suture) commences in the middle of the rostral portion of the dorsal border of the orbita, and is parallel to the sutura frontoprefrontalis. Laterally, the os lacrimale contacts the os jugale at the point where the straight margo lateralis of the orbita begins. The straight sutura lacrimojugalis (lacriomojugal suture) excludes the os maxillare from contributing to the dorsal border of the orbita. A foramen lacrimale (lacrimal foramen) is not visible on the exposed portion of the facies orbitalis of each os lacrimale.

O s j u g a l e (jugal): The os jugale forms the lateral portion of both the dorsal border of the orbita and fenestra infratemporalis. Rostrally, it overlaps the os maxillare, and contacts the os lacrimale, thereby excluding the os maxillare from the dorsal border of the orbita. The columna postorbitalis, of which the os jugale forms the base, is inset ventromedially only marginally from the facies lateralis of the os jugale. Lateral to this lip, the os jugale is sculptured with indistinct pits and depressions, similar to those on and around the margin of the rostrum maxillae. A foramen ductus is not visible caudoventral to the columna postorbitalis. The portion of the os jugale ventral to the fenestra infratemporalis, the arcus jugalis, is approximately half the width of the columna postorbitalis and straight in lateral aspect. Caudally, the os jugale contacts the os quadratojugale in a straight suture, which is located rostral to the caudolateral corner of the fenestra infratemporalis. It underlaps the latter bone to a point half way along the length of the cavum tympanicum.

O s q u a d r a t o j u g a l e (quadratojugal): The os quadratojugale forms the entire margo dorsocaudalis of the fenestra infratemporalis, excluding to os quadratum from entering this opening. Its facies caudodorsalis is smooth, and a spina infratemporalis is absent, though may have broken off during preparation or each diagenesis. Within the cavum tympanicum, the os quadratojugale appears to contact the os postorbitale immediately caudal to the dorsocaudal extent of the columna postorbitalis. The sutura quadratoquadratojugalis runs parallel to the margo dorsocaudalis of the fenestra infratemporalis for most of its length, before running rostrocaudally towards the condylus mandibularis of the os quadratum. Although it does not contribute to this condyle, the os quadratojugale forms the margo lateralis of the maxilla dorsal to the os jugale.

Ossa palati (bones of the palate)

The only part of the palatum osseum that can be discerned with certainty is part of the right os ectopterygoideum (ectopterygoid), which is visible through the right orbita. The portion constitutes the processus ventralis (ectopterygoid wing). It is smooth and of an equivalent width to the columna postorbitalis.

Mandibula (mandible) (Text-figs. 2, 3 and 4)

Due to the way it is has been exposed (see Description of the specimen), the complete outline of the right ramus mandibulae in lateral aspect cannot be discerned. A fenestra mandibularis externa (external mandibular fenestra) is not visible, though may be located ventral to the exposed portion of the ramus and therefore obscured by matrix. A caudodorsally directed processus retroarticularis is present, which, in a rostrocaudal direction, is of an equivalent length to the foramen supratemporale.

Ossa mandibulae (bones of the mandible)

O s d e n t a l e (dentary): The portion of the os dentale that is visible constitutes the ventral half of the facies lateralis caudal to what would have been dens dentalis IV. Caudally, it appears to have underlapped the os angulare, and a straight, rostrodorsally aligned sutura angulodentalis (angulodental suture) is visible immediately ventral to the columna postorbitalis. Its external surface is smooth.

Os angulare (angular): Most of the facies lateralis of the os angulare can be described. In lateral aspect, this bone forms the facies lateralis and margo caudoventralis of the processus retroarticularis, which is rostrodorsally concave in lateral aspect. The sutura angulosupraangularis (angulosupraangularis suture) is parallel to the margo ventralis of the arcus jugalis rostral to the fossa articularis quadratica in lateral aspect, but becomes caudoventrally concave towards its caudal end. The os angulare contacts the os articulare halfway along the processus retroarticularis dorsally, thereby excluding the os supraangulare from forming any part of the latter process in lateral aspect. Rostral to the processus retroarticularis, the facies lateralis of the os angulare is sculptured with well-spaced, indistinct pits and depressions, similar to those present on parts of the cranium.

Os supraangulare (supraangular): Only a small slither of the os supraangulare, caudal and lateral to the fossa articularis quadratica, can be described (see Description of the specimen). Of the processus retroarticularis, the os supraangulare forms the lateral third of the fossa retroarticularis, wedging out caudally between the ossa angulare et articulare. Although the fossa articularis quadratica is obscured by the os quadratum, this suggests that the os supraangulare formed at least the lateral half of this articular fossa. The portion of the os supraangulare lateral to this fossa is unsculptured.

Os articulare (articular): The os articulare forms the medial two thirds of the fossa retroarticularis, and presumably the medial half of the fossa articularis quadraticus, the caudal lip of which is shaped in a manner complimenting the condylus mandibularis of the os quadratum. The fossa retroarticularis is subdivided into two smaller concave fossae by a faint medial ridge, which extends caudally to a knobbly terminal process. The margo medialis of the os articulare, and therefore that of the processus retroarticularis, is not visible (see Description of the specimen).

Columna vertebralis (vertebral column) (Text-figs. 2 and 3)

Vertebrae cervicales (cervical vertebrae): The right arcus atlantis is a small crescent-shaped element, comprising a ventral articular extremity and flattened dorsal arch, between which the smooth, concave facies interna forms the lateral and dorsal walls of the foramen atlantum. The facies articularis dentalis is gently concave, and, in lateral aspect, the ventral articular extremity tapers to a sharp point. The zygapophysis of this bone is caudally triangular in outline.

The only portions of the processus spinosi of vertebrae cervicales III et IV that are visible are their dorsal apices (see Description of the specimen). These are of a similar width in a craniocaudal direction to the maximum width of the facies articularis dentalis of the arcus atlantis, and one third that of the same measurement on the processus spinosus on each of the vertebrae thoracicae. Cartilago apicalis (apical cartilage) is absent, and, in lateral aspect, the margo dorsalis of each of these processus is perpendicular to the margines cranialis et caudalis.

The facies articulares of the pre- and postzygapophyses of vertebrae cervicales V, VI et VII are inclined at 45 degrees to each vertebra's processus spinosus in cranial and caudal aspect respectively. Each facies articularis is flat and oval in outline, with the long axis aligned dorsolaterally. The distance between the centre of the facies articulares of the pre- and postzygapophyses of vertebrae caudales VI et VII is slightly greater than that between the centre of the facies articularis of each postzygapophysis and the facies articularis of each diapophysis. The facies externa of the pedunculus arcus neuralis (peduncle of the neural arch) of each of these vertebrae is flat caudally, but slightly concave cranially ventral to the prezygapophysis. In caudal aspect, this latter face is aligned at 90 degrees to the lamina arcus neuralis (dorsal lamina of the neural arch), which between the pre- and postzygapophyses is divided into two distinct concavities that are separated by low ridge, best evident on vertebra cervicalis VI. In lateral aspect, the margo cranialis of the processus spinosus of vertebra cervicalis VI is level with the caudal-most extent of the facies articularis of its prezygapophysis, whereas that of vertebra cervicalis VII is level with the midpoint of the same face on its process. Although their dorsal halves are missing, the processus spinosi of both of these vertebrae are of a similar shape to those of vertebrae cervicales III et IV, with vertically aligned, parallel margines cranialis et caudalis. In lateral aspect, the maximum basal width in a craniocaudal direction of that belonging to vertebra cervicalis VI is equal to minimum width of the facies articulares of its pre- and postzygapophyses. In comparison, the basal width of the processus spinosus of vertebra cervicalis VII is one and a half times this distance.

Vertebrae prothoracicae et thoracicae (prothoracic and thoracic vertebrae): The arcus neurales of all the visible vertebrae thoracicae, which include either vertebra prothoracica I or II and vertebrae thoracicae III–

X or III–XI, are all of an equivalent length in a craniocaudal direction to each of the dermostea from the two sagittal rows of the scutum dorsi. In dorsal aspect, the distance between the facies articularis caudalis of each vertebra's processus transversi is 2.2 times this distance. The basal width in a craniodorsal direction of all the processus transervsi is just under 20 per cent of the latter distance, and slightly less so in vertebrae thoracicae IX et X or X et XI. All the processus transversi are aligned at 90 degrees to the processus spinosus of each vertebra in either cranial or caudal aspect. The margines cranialis et caudalis of these processus, while parallel to each other, are offset 5–10 degrees cranially to the axis craniocaudalis of each vertebra's corpus. The facies dorsalis of the processus transversi is flat and smooth. The length in a craniocaudal direction of the facies articularis caudalis is slightly greater than that of the facies articularis cranialis. The distance along the facies cranialis between the two articular surfaces decreases from cranial to caudal along the columna vertebralis. In the case of the first vertebra for which it can be accurately measured, vertebra thoracica V or VI, it forms approximately 60 per cent of the total length of the margo cranialis. By vertebra thoracica IX or X, these two articular surfaces are confluent with each other, forming the entire margo lateralis. In all instances, the facies articularis cranialis et caudalis are straight in dorsal aspect, but the transition between them along the margo cranialis is not abrupt, forming a gentle craniolaterally concave arc. The total dorsoventral thickness of the processus transversi and their respective facies articulares is equal to the mediolateral thickness of the processus spinosi.

The facies articulares of the pre- and postzygapophyses of each of the vertebrae thoracicae are inclined horizontally, articulating in a plane that is only slightly dorsal to the facies dorsalis of the processus transversi. Where exposed, they are oval in outline, with their long axis aligned craniomedially. In dorsal aspect, the caudal- or cranial-most extent of the facies articularis of the pre- and postzygapophyses respectively is level with either the margo cranialis or margo caudalis of the processus spinosus. The basal width in a craniocaudal direction of this latter process is slightly greater than that of the processus transversus. Although their dorsal halves are missing, at their base the margines cranialis et caudalis are parallel to each other and vertically aligned. In cross-section each process tapers cranially and caudally to form a thin fin of bone. Areae interzygapophyses comprise thin, vertical slits that are visible in dorsal aspect. Each extends from the roof of the foramen vertebrale to the base of the processus spinosus, and has a maximum width in a mediolateral direction that is half that of the latter process.

The only vertebra thoracica that is exposed ventral to the processus transversi is vertebra thoracica X or XI, which is the last in the series. The foramen vertebrale has a flat ventral border, but is concave dorsally, with a maximum height that is half its width. The nature and position of the sutura neurocentralis (neurocentral suture) cannot be discerned. The caudal face of the corpus vertebrae, which is round in outline, is gently concave, and is therefore described as a fossa vertebralis caudalis. The entire surface of this fossa is rugose. The extent to which rugositates anulares (anular rugosities) were developed cannot be determined due to the fact that rest of the corpus is embedded in matrix.

V e r t e b r a e l u m b i c a l e s (lumbar vertebrae): Four vertebrae lumbicales can be distinguished from the vertebrae thoracicae based primarily on the morphology of their processus transversi, all of which have gently convex margines laterales that lack a facies articularis. In dorsal aspect, the processus transversi of vertebra lumbicalis I have straight margines craniales that are perpendicular to the axis craniocaudalis of their corpus vertebrae. The margines caudales, however, are offset cranially by approximately 20 degrees from a perpendicular alignment. The processus transversus of vertebra lumbicalis II has margines craniales et caudales that taper slightly laterally, whereas the margines laterales are gently convex. The margines craniales et caudales of the processus transversi of vertebra lumbicalis II are almost parallel to one another in lateral aspect. The last vertebra lumbicalis has a condition that mirrors that of the first; the processus transversi have straight margines caudalis that are perpendicular to the axis craniocaudalis of their corpus vertebrae, and the margines craniales are offset caudally by approximately 20 degrees.

Although also lacking their dorsal halves, the processus spinosus of the first three vertebrae lumbicales are similar basally to those of the vertebrae prothoracicae et thoracicae. That of vertebra lumbicalis VI, however, while having a vertically aligned margo cranialis, has a margo caudalis that is craniodorsally oriented in lateral aspect.

The only vertebra lumbicalis that is exposed ventral to the processus transversi is vertebra lumbicalis I. The foramen vertebrale of this bone is similar in outline to that of vertebra thoracica IX or X, and the corpus has a gently concave cranial end. It is therefore described as a fossa articularis cranialis. As is the case with the other exposed corpora vertebrarum in the series, the sutura neurocentralis of this vertebra is not visible, being obscured by matrix (see Description of the specimen).

The postzygapophyses of vertebra lumbicalis IV are slightly smaller than those of all the other vertebrae thoracicae et lumbicales, with facies articulares that are inclined at 70 degrees to the processus spinosus in caudal aspect.

Vertebrae sacrales and costae sacrales (sacral vertebrae and ribs): The arcus neurales of vertebrae sacrales I et II are similar to each other, and in this respect, with the exception of their processus transversi, also resemble those of vertebrae lumbicales I–III. Although the basal width of the processus transversi of each vertebra sacralis in a craniocaudal direction is equivalent to that of the vertebrae thoracicae et lumbicales, these processus do not extent laterally beyond a point level with their vertebra's respective pre- and postzygapophyses in dorsal aspect. The facies articulares of the prezygapophyses of vertebra sacralis I are inclined at an angle of 70 degrees to the processus spinosus in cranial aspect. In comparison, those of its postzygapophyses, as well as the prezygapophyses of vertebra sacralis II, are inclined at close to 45 degrees to the processus spinosus of their respective vertebrae in either cranial or caudal aspect. Each pair of processus articulates with the next at a level that is slightly more dorsal in respect to their processus transversi than is the case in the vertebrae prothoracicae, thoracicae et lumbicales. In lateral aspect, the base of the processus spinosus of each vertebra sacralis is similar in outline to that of vertebra lumbicalis IV, with a vertically aligned margo cranialis and craniodorsally aligned margo caudalis. The former margin is level with the cranial-most extent of the prezygapophyses. The area interprezygapophysis (interzygapophysial area) of each vertebra sacralis forms a small, but nevertheless distinct, mediolaterally flattened, triangular process that overhangs the cranial extent of the foramen vertebrale. The outline of this latter foramen is similar to that of the exposed vertebrae thoracicae et lumbicales, being concave dorsally and flat ventrally. Although only the dorsal halves of each corpus vertebrae are exposed, each appears to have a gently concave cranial end; the caudal ends are not exposed.

Both pairs of suturae costocentrales between the vertebrae sacrales and their respective costae are difficult to discern with certainty. Where visible, they are strongly serrated and partially fused in several places. In dorsal aspect, each is approximately parallel to the long axis of the processus spinosus of the vertebra to which it belongs. The basal width in a craniocaudal direction of each costa sacralis is equivalent to that of the processus transversi of the vertebrae thoracicae. The margo cranialis of costa sacralis I is straight and aligned perpendicular to the processus spinosus. The length of this margin is one and a half times that of the gently convex margo caudalis, which has a length that is equivalent to the basal width in a craniocaudal direction of the latter process. The smooth facies symphysialis ilii (iliac symphysial surface) is therefore aligned craniolaterally to the processus spinosus in dorsal aspect. The facies dorsalis of each costa sacralis I, which is the only face that is exposed, is slightly concave medially.

The straight margines cranialis et caudalis of costa sacralis II diverge from each other laterally. The former is approximately two thirds the length of the latter, and the laterally concave facies articularis iliaca is twice as wide in craniocaudal direction as the costa is at the sutura centrocostalis (centrocostal suture). Laterally, the costae sacralis does not exclude the ilium from contributing to the lateral margin of the foramen pelvicum, which would have been approximately heart-shaped in dorsal aspect, with its apex pointing laterally.

Vertebrae caudales and costae caudales (caudal vertebrae and ribs): Although lacking their dorsal portions, in lateral aspect the basal width in a cranioterminal direction of each of the processus spinosi of vertebrae caudales I–V is equivalent to that of the processus spinosi of the vertebrae thoracicae et lumbicales. The margo cranialis of each of these processus is vertically aligned and parallel to the margo caudalis. From vertebra caudalis VI–X, however, the margo cranialis of the processus spinosus progressively becomes more craniodorsally aligned, such that by vertebra caudalis X the width towards the margo dorsalis is only one quarter the corresponding length of the corpus vertebrae, which remains constant throughout the entire preserved series of vertebrae caudales. This is also true for the processus spinosus of vertebra caudalis XI, though as in the cranial-most vertebrae caudales, the margines cranialis et caudalis are parallel to each other and aligned vertically. The only vertebrae caudales for which the margo dorsalis of the processus spinosus is preserved are vertebrae caudales VIII–XI, in which it is horizontally oriented and perpendicular to the margo caudalis in lateral aspect. The height of the processus spinosus in these vertebrae, measured from the top of the foramen vertebrale to the margo dorsalis, is equal to two thirds the length in a cranioterminal direction of the corpus vertebrae.

The pre- and postzygapophyses of the cranial-most vertebrae caudales are of an equivalent length to those of the vertebrae thoracicae et lumbicales, but only two thirds as wide. Measured from the maximum lateral extent of each facies articularis in dorsal aspect, the distance between the corresponding zygapophyses of each vertebrae decreases gradually in cranioterminal direction. In vertebrae caudales I et II it is slightly greater than the length in a cranioterminal direction of the corpus vertebrae, whereas by vertebra caudalis XI it is less than half. As a result, in the postzygapophyses of vertebrae caudales VI–XI unite medially to form a flat, horizontal shelf, extending terminally over the foramen vertebrale. The facies articulares of the pre- and postzygapophyses of vertebrae caudales I–VII are aligned at approximately 45 degrees to the processus spinosus in cranial and terminal aspect respectively. From vertebra caudalis VIII terminally, they become progressively more horizontally oriented, and on vertebra caudalis XI are perpendicular to the processus spinosus. In each case, however, this articular surface is oval in outline, being longer in a mediolateral as opposed to cranioterminal direction. Although slightly smaller than those of the vertebrae thoracicae, the maximum length of this articular surface is equivalent to that of the facies articularis on the same process on the vertebrae thoracicae et lumbicales. Ventroterminal to the prezygapophysis, there is a shallow concavity in the facies externa of the pedunculus arcus neuralis, which is otherwise smooth.

The areae interzygapophyses comprise distinct, mediolaterally flattened, triangular processus, which extend beyond the foramen vertebrale in lateral aspect, particularly in the case of some of the areae craniales. In some instances, for example on vertebrae caudales VIII – XI, the areae interzygapophyses of adjacent vertebrae appear to have contacted each other when the vertebrae were in a relaxed, in situ position.

Where exposed, the foramen vertebrale is of a similar shape to that seen in vertebrae thoracicae, but perhaps slightly deeper dorsoventrally and not as wide mediolaterally. Additionally, where exposed, the corpora vertebrarum are round in cranial and terminal aspect. Each corpus is hourglass-shaped in lateral and ventral aspect, with gently concave facies laterales. Rugostitates anulares can be clearly discerned in all cases, and in lateral aspect constitute approximately ten per cent of the total length of each corpus. Both ends of the corpus are gently concave, indicating these vertebrae were amphicoelous. The suturae neurocentrales are fused on all the vertebrae terminal to vertebra caudalis IV. The nature of this suture on the other vertebrae caudales cannot be commented upon because this portion of each vertebra is embedded in matrix (see Description of the specimen).

The margines cranialis et terminalis of all the costae caudales are parallel to each other dorsally. From costae caudales I–II, the former margin becomes progressively more convex laterally, so that a distinct margo lateralis is not present. Terminal to costa caudalis IV, both margines are parallel along their entire length, and perpendicular to the straight margo lateralis and axis cranioterminalis of each vertebra's processus spinosus in dorsal aspect. The maximum width of each costa is always less than that of its vertebra's processus spinosus, decreasing in a cranial to terminal direction until it is approximately equal to the width of the arcus haemalis cranial to it by costae caudalis X. The length of each costa caudalis in a mediolateral direction decreases only slightly in a cranial to terminal direction, and is equal to or slightly more than the corresponding length of the costa sacralis II. Serrated suturae costovertebrales are visible on all vertebrae. The cranial-most extent of this suture is situated terminoventral to the base of each vertebra's prezygapophyses. The gradual decrease in length of the costae caudales indicates that there would have been at least four or five more vertebrae with costae caudal to the last vertebrae in the series.

A r c u s h a e m a l e s (haemal arches): All the preserved arcus haemales bear two processus articulares. The length of the cranial-most arcus haemalis, arcus haemalis III, is slightly greater than the length in a cranioterminal direction of each of the corpus vertebrae. The length of the other arcus haemales decreases only slightly in a cranial to terminal direction, whereby it is equal to the length of each of the corpus vertebrae by arcus haemalis XI. Each processus articularis is mediolaterally flattened in cross-section and bears a flat facies articularis, which is round in outline. The medial portions of adjacent facies articulares almost contact each other medially. The maximum width of each processus articularis in a cranioterminal direction is approximately ten per cent the total length of each arcus haemalis. Ventral to the apex of the incisura arcus haemalis (haemal concavity) there is a shallow, triangular-shaped fossa, extending ventrally to a point approximately a quarter of the way along processus ventralis ventrally. At its base, this process is spatulate in outline, being twice as wide in cranial or terminal aspect as it is in lateral aspect; however, this characteristic is less pronounced in the caudal-most arcus haemales. The processus ventralis is convex ventrally in cranial/terminal aspect. In lateral aspect, the margo ventralis of arcus haemales III–VI is convex. In those arcus haemales terminal to this, this margin becomes progressively flatter and more cranioventrally aligned. By arcus haemalis XI, the concave margo terminoventralis of the processus ventralis is deflected terminally slightly.

Costae cervicales (cervical ribs) (Text-figs. 2 and 3): Only the corpora of costae cervicales I, II et III can be described. These are externointernally flattened, and taper to a sharp point caudally. The maximum width of each is equivalent to that of the other costae cervicales – costae cervicales IV, V et VII. The capitula of the latter costae cannot be described (see Description of the specimen). The tubercula, however, are all similar to each other. Each is about two and half times longer in a dorsoventral direction than it is wide, with gently concave margines cranialis et caudalis, such that they are wider towards the facies articularis than at their base. The minimum width of each tuberculum is slightly less than the width in a craniocaudal direction of the processus spinosus of vertebra cervicalis V. The outline of each facies articularis in lateral aspect is slightly dorsally convex.

In lateral aspect, the triangular corpus of costae cervicales IV et V is thicker at its base than that of costa cervicalis VII. Measured from the base of the margo caudalis of the tuberculum to their tip, all of these corpora are of a similar length to each other in craniocaudal direction, being one and a half times the length in a dorsoventral direction of their costa's tuberculum. The margines ventralis et dorsalis of each of these corpora are straight, tapering caudally to a rounded apex.

Costae thoracicae (thoracic ribs) (Text-figs. 2 and 3): With the exception of what can be interpreted as segmentum vertebrocostale X or XI, where they are exposed in full the remainder of the visible segmenta vertebrocostalia are of an equivalent length to each other. Their length is also equal to the proximodistal length of the right radius. The former segmentum is two thirds this length and has a externointernally flattened, almost straight corpus. The outline of the corpus of each of the other segmenta is gently convex laterally and concave medially, with the main point of flexion one third of way along its length ventrally. Immediately lateral to the tuberculum, the corpus is externointernally flattened, and approximately two thirds the width in a craniocaudal direction to the processus transversi of the vertebrae thoracicae. Ventrally, however, it becomes rounded in cross-section. The margo caudalis of the corpus of each of these segmenta forms a sharp ridge immediately lateral to the base of the tuberculum, extending to a point one third of the way along its length ventrally. The facies articularis ventralis is flat and perpendicular to the margines cranialis et caudalis in lateral aspect.

The maximum width of the tuberculum of each segmenta is equivalent to that of the facies articularis costalis caudalis of the processus transversi of each of the vertebrae thoracicae. The facies articularis of this process is also of an equivalent thickness to the corresponding articular surface on the processus transversi, and in addition to this, gently concave. In dorsal aspect, the margo ventromedialis of each costa is gently concave between the facies articularis of the tuberculum and base of the capitulum. Medial to this point further details on the morphology of the capitula of all the visible costae cannot be discerned. Nevertheless, the overall length of each can be gauged approximately based on the distance between the facies articularis costalis caudalis et cranialis of the processus transversi of the vertebrae thoracicae. All the visible segmenta vertebrocostalia have a smooth surface.

The single element interpreted as a segmentum laterocostale is approximately half the length of the left segmentum vertebrocostale X or XI. It is straight, with a rectangular cross-section and has rugose surface texture.

2. **Skeleton appendiculare** (appendicular skeleton) (Text-figs. 2 and 3)

Scapula: Only the facies lateralis of the scapula can be described. The maximum length of this bone is slightly less than half the proximodistal length of the right humerus. The maximum width of the extremitas omalis in a craniocaudal direction is approximately equal to that of the ala scapulae. In comparison, the minimum width of the corpus scapulae (scapular shaft) is half this distance, and one third of the proximodistal length of the entire scapula. The margo caudalis of the ala is gently concave, whereas the margo cranialis is straight close to the corpus, becoming gently convex towards the margo dorsalis. A tuberculum caudale is not visible on the exposed portion of the margo caudalis at the transition between the corpus and ala. A pronounced ridge is present on the facies lateralis of the extremitas omalis and corpus, extending from the cranioventral edge of the facies articularis coracoidea to the base of the ala. This highest part of this ridge, which is slightly rugose, is situated just cranial of the long axis of the corpus. Based on its topographical position, this ridge is therefore termed the crista craniolateralis. Cranial to the crista craniolateralis there is a broad, triangular-shaped facies cranialis on the extremitas omalis, the apex of which can be arbitrarily delimited by the highest part of the latter crest. The facies lateralis of the ala scapulae is smooth. The margo dorsalis is dorsally concave and slightly rugose in places. Because only one side of the scapula is exposed, comments on the thickness of the ala cannot be made.

Coracoideum (coracoid): The only portion of the coracoideum that can be described is the dorsal portion of the extremitas omalis. The width of this part of the coracoideum in a craniocaudal direction is equal to that of the extremitas omalis scapulae, with which it partially articulates. In dorsal aspect, the facies articularis scapulae has a minimum thickness of slightly more than ten per cent of the total width of the extremitas omalis. Cranially, the margo lateralis of the facies articularis is laterally concave in dorsal aspect, as opposed to the margo medialis, which is medially concave. Caudally, the latter margin becomes medially convex, but the former is continuous with the facies articularis humeralis of the processus glenoidalis. In dorsal aspect, the maximum thickness of this part of the extremitas omalis is at least three times that of the minimum thickness of the facies articularis scapulae cranially. Medially, where the coracoideum articulates with the scapula, the surface of the extremitas omalis is flat and slightly rugose. Laterally, however, the portion that formed the facies articularis humeralis is smooth and dorsolaterally convex. Immediately ventral to the point where the extremitas omalis begins to thicken, the foramen coracoideum is visible on the facies medialis. It is round in outline with a maximum diameter that is equivalent to the minimum thickness of the facies articularis scapulae. The lateral opening of this foramen is not visible on the exposed portion on the facies lateralis of the extremitas omalis. The exposed portions of both the facies lateralis et medialis of the extremitas omalis are devoid of any rugosities.

Humerus: The only portions of the humerus that cannot be described include the medial half of the extremitas proximalis and proximal portion of the corpus, the cranial half of the condylus medialis of the extremitas distalis and the sulcus intercondylaris. The proximodistal length of the this bone is slightly less than half the rostrocaudal length of the cranium, measured from the tip of ossa premaxillaria to the caudal extent of the condylus occipitalis (occipital condyle). The minimum width of the corpus humeri, which is round in cross-section, is only twelve per cent this distance. In lateral aspect, the corpus is slightly arched caudally. The entire extremitas proximalis is offset by approximately 5–10 degrees caudally from the axis proximodistalis of the corpus. The long axis of the smooth, proximally convex caput humeri is in the same plane as the line traced between the condylus medialis et lateralis of the extremitas distalis humeri.

Proximally, there is a distinct crista cranialis, extending from the tuberculum mediale of the extremitas proximalis to a point one third of the way along the corpus distally. The highest part of this ridge is slightly rugose, and based on its position is referred to as the tuberositas cranialis. The margo distalis of the caput is elevated above the gently concave facies caudalis of the extremitas proximalis. In lateral aspect, the distance between the latter face and tuberositas cranialis is one and a half times the minimum thickness of the corpus. Proximal and distal to the tuberositas cranialis, the outline of the crista cranialis in lateral aspect is straight, so that this part of the extremitas proximalis is triangular. In cranial aspect, the line traced by the crista cranialis is parallel to the facies medialis et lateralis of the corpus. Immediately cranial to the maximum distal extent of the crista cranialis there is a small rugose depression on the facies lateralis of the corpus, here termed the depressio caudolateralis. The exposed portions of the corpus are smooth.

The maximum distance between the condylus medialis et lateralis of the extremitas distalis is twice the minimum cross-sectional thickness of the corpus. Distinct epicondylus medialis et lateralis are absent. Each condyle is smooth and gently convex. Two ridges are present on the facies caudalis of the extremitas distalis, here termed the cristae proximalis lateralis et medialis. These extend proximally from the slightly raised proximal margin of each condyle to a point where the diameter of the corpus remains constant. Between these ridges, the facies caudalis of the extremitas distalis is gently concave.

Ulna: With the exception of the medial half of the extremitates proximalis et distalis and facies medialis of the corpus ulnae, the ulna can be described in full. The total length of this bone in a proximodistal direction is approximately 75 per cent that of the right humerus. In lateral aspect, the extremitas proximalis is offset cranially from the axis proximodistalis of the corpus ulnae by 20–25 degrees. In lateral aspect, the margo cranialis of the corpus and distal portion of the extremitas proximalis is caudally concave, whereas the outline of the facies caudalis of the corpus is caudally convex. The latter surface is more strongly curved that the former margin. The maximum width of the extremitas proximalis is equivalent to that of the extremitas distalis, and slightly less than twice the minimum thickness of the corpus, which gradually increases towards each extremity. The corpus is tear drop-shaped in cross-section, with the apex being formed by the margo cranialis. The planes of the extremitates proximalis et distalis intersect each other at an angle of 15 degrees, with the latter being aligned craniolaterally to the former.

The caput ulnae is gently proximally convex in both lateral and medial aspect. Distinct condylus cranialis et medialis are absent, as are tubercula craniolaterale et caudale. Immediately distal to the caput ulnae, the surface of the facies lateralis of the extremitas proximalis is covered in proximodistally aligned striations. Distal to these striations, there is also a small, rugose depression, here termed the depressio caudolateralis. Either side of the margo cranialis, there is a shallow depression on the proximal half of the corpus. These depressions, here termed the sulci lateralis et medialis, extend from the base of the extremitas proximalis to a point half way along the corpus distally. No other ridges are apparent on the visible portions of the corpus

In lateral aspect, the extremitas distalis ulnaris is craniocaudally expanded and slightly flattened mediolaterally. The facies articularis carpalis is gently distally convex and triangular-shaped in proximal aspect, with the apex pointing cranially. Immediately proximal to the facies articularis carpalis, the surface of extremitas distalis is covered in proximodistally aligned striations.

Radius: The only parts of the radius that cannot be described are the medial half of the facies caudalis of the corpus and extremitates proximalis et distalis. The total proximodistal length of the radius is slightly less than that of the ulna. The minimum thickness of the corpus radii, which is cylindrical and round in cross-section, is approximately 10 per cent this distance. In cranial aspect, the width of the extremitas proximalis in a mediolateral direction is twice the minimum thickness of the corpus, and slightly greater than the same measurement on the extremitas distalis. The latter extremity is flattened craniocaudally and in distal aspect its long axis is perpendicular to planum sagittale (sagittal plane); the outline of the caput radii being round in proximal aspect. The thickness of the corpus radii is uniform over most of its length, but widens proximally and distally towards the extremitates proximalis et distalis. No distinct ridges or rugosities are apparent on the exposed portions of the corpus.

The proximal outline of the caput radii is flat in lateral aspect, and aligned perpendicular to the axis proximodistalis of the corpus. In the centre of the caput, there is a shallow, concave cotyla capitis. Immediately distal to the caput radii, the surface of the extremitas proximalis is covered with proximodistally aligned striations. In cranial aspect, the flat facies articularis carpalis of the extremitas distalis is oriented ventrolaterally. The facies medialis of this extremity is slightly longer than the facies lateralis.

Ossa carpi (carpal bones): The os radiale is a small, craniocaudally flattened, hourglass-shaped bone, the proximodistal length of which is slightly less than 20 per cent that of the right radius and one and a half times that of the right os ulnare. The minimum width of the corpus ossis radiale in a mediolateral direction is 75 per cent that of the extremitas proximalis ossis radialis, which itself is slightly narrower than the extremitas distalis ossis radiale. Both the facies articularis radialis et metacarpalis are flat. The former is aligned perpendicular to the axis proximodistalis of the corpus, whereas the latter is oriented distolaterally slightly. A small, concave facies articularis ulnaris is apparent on the lateral side of the extremitas proximalis. This articular surface is continuous with the facies articularis radialis. Circumferentia articulares (wheel-like articular surfaces) are present around both the facies articulares radialis et metacarpalia. The facies cranialis of the corpus is smooth.

Only the cranial side of the extremitas proximalis, including the facies articularis ulnaris, and facies cranialis of the corpus of the os ulnare can be described. This bone is of similar shape to the os radiale, being hourglass-shaped, but only half its size. In proximal aspect, the proximally convex facies articularis ulnaris is round in outline. Both the corpus and extremitas distalis are flattened craniocaudally. The maximum exposed width in a mediolateral direction of the latter extremity is approximately one and a half times that of the extremitas proximalis. The nature of the facies articulares ossis metacarpalis, radialis et pisiformis cannot be discerned. As is the case with the os radiale, the exposed portion of the corpus is smooth.

The element situated between the facies articularis metacarpalis of the right os radiale and facies articularis carpalis of os metacarpale I that is interpreted as the os pisiforme is spherical in shape, with a smooth surface texture. The maximum diameter of this element is one third the length in a mediolateral direction of the basis (proximal articular base) of os metacarpale I.

Ossa metacarpi et digitorum manus (bones of the middle hand and fingers): The fact that the right and left manus are preserved in dorsal and palmar aspect respectively means that all the ossa metacarpi et digitorum manus can be described in full. There are five ossa metacarpi. Of these, the proximodistal length of os metacarpale II is the greatest, being slightly less than the proximodistal length of the right os radiale. Os metacarpale III is slightly shorter than the proximodistal length of the right os radiale, I is three quarters, IV two thirds and V one third. In lateral aspect, the corpus of each os metacarpale is arched dorsally. The minimum width of the corpus of os metacarpale I in cranial aspect is slightly greater than one third its maximum length in a proximodistal direction, and two thirds the maximum width of the caput (distal articular head) and basis, which are of an equivalent width to each other. In cross-section, the corpus is oval in outline, being flattened palmocranially. The corpora of the other ossa metacarpi are round in cross-section, and in comparison to os metacarpale I, their minimum widths can be described as follows: II = III = IV = V. In proximal aspect, the long axis of the basis of each os metacarpale is offset medially by approximately 35 degrees from that of its caput. The facies articularis carpalis of the basis of each os metacarpale, while differing in size, are all slightly concave. The lateral part of basis of all but os metacarpale V overlaps the medial corner of the basis of the os metacarpale lateral to it. Immediately proximal to the distally convex capitis of ossa metacarpi I, II et II, there is a shallow, rugose depression on the facies cranialis of the corpus.

The minimum width of the corpus of each of the phalanges digiti manus decreases gradually from proximal to distal, but in the case of the most proximal elements is slightly less than that of the os metacarpale with which they articulate. Phalanx 1 of digitus manus I is half the length of os metacarpale I. The length of each of the three phalanges of digitus manus II is equal to that of phalanges 1, 2 et 3 of digiti manus III and IV respectively. The third phalanx of the later digiti is slightly shorter than their respective second phalanx, and is of an equivalent length to phalanx 3 of digitus manus V. The fourth phalanx of digiti manus III et IV is the smallest of all the phalanges. The basis of each phalanx digiti is palmocranially concave towards its centre, whereas each caput is distally convex. In cranial aspect, the basis of each phalanx is slightly wider in a mediolateral direction than is the caput.

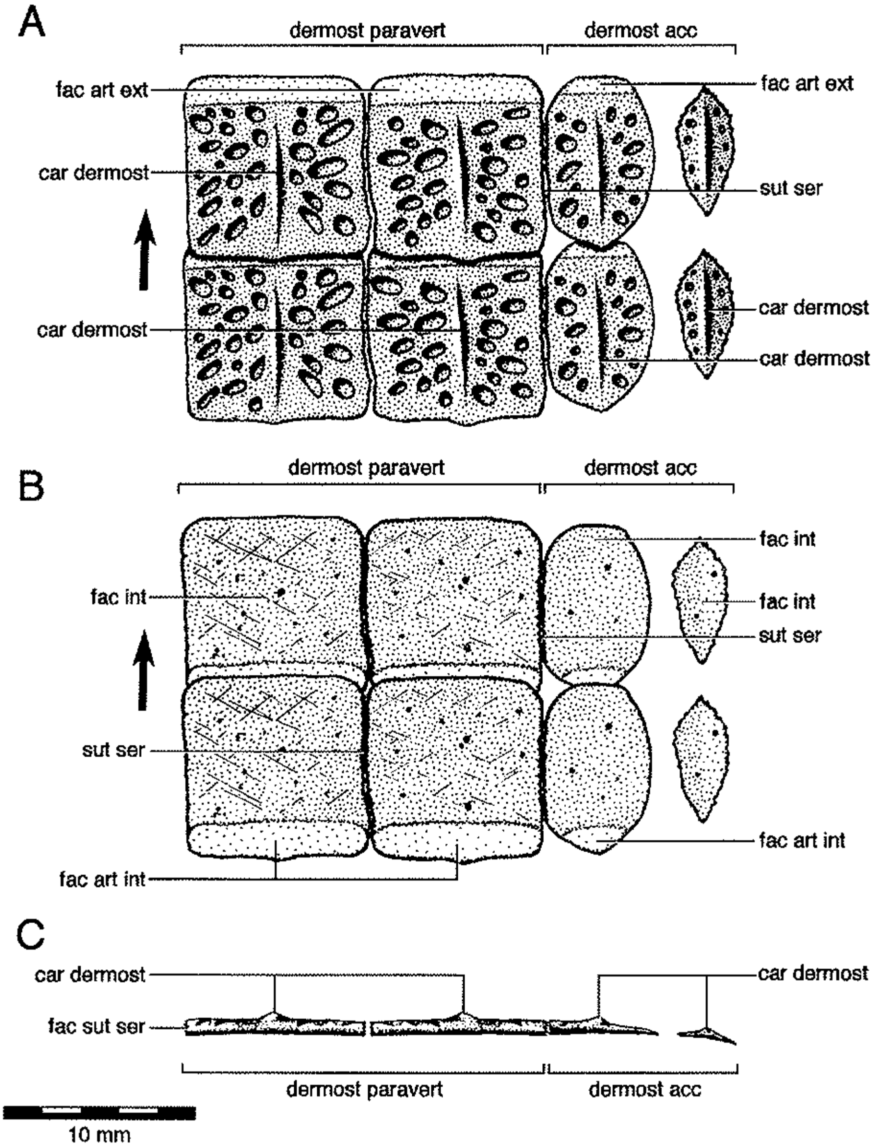
The phalanx unguis of digitus manus I is a blunt, robust element that, in medial or lateral aspect, has a convex dorsal and sinuous palmar outline. At its base, which is gently proximally concave, it is slightly wider than the caput of the phalanx with which it articulates. Its length in a proximodistal direction is equivalent to that of os metacarpale I. The phalanx unguis of digitus manus II is of a similar shape to that of digitus manus I, but smaller and slightly narrower in cranial aspect, with a sharp apex.

3. **Skeleton dermale** (osteodermal skeleton) (Text-figs. 2, 3, 5 and 6)

Scutum nuchae (nuchal shield): As preserved, the scutum nuchae includes at least twelve dermostea. Five of these are round in outline, and approximately one quarter the size of the others, which are of an equivalent size to those dermostea from the two cranial-most transverse rows of the scutum paravertebralia. The latter have a length in a mediolateral direction that is slightly less than on third the maximum width of the vertebrae thoracicae in dorsal aspect. The largest dermostea nuchae are sub-rectangular in outline, with a gently convex margo lateralis. Each is sculptured with small (0.5–1 mm) pits and lacks a carina dermostealis (osteodermal keel). A smooth facies articularis cranialis forms approximately 15 per cent of the total length of the facies externa in a craniocaudal direction. The presence of this feature on all but the cranial-most one in the preserved series indicates that these dermostea formed part of an articulated scutum; the other, smaller ones all lack a facies articularis cranialis. All the former dermostea also possess a sutured margo mediana on their left side, suggesting that they come from the right side of the scutum nuchae. When reconstructed, this means that the articulated portion of the scutum nuchae included a minimum of ten dermostea, arranged in two sagittal rows of five dermostea each. This scutum would have extended from just caudal to the margo caudalis of the mesa cranii, dorsal to a point between the axis and vertebra cervicalis III, to a point dorsal to vertebra cervicalis VIII. As such it would not have been continuous with the first transverse row of dermostea paravertebralia (see below).

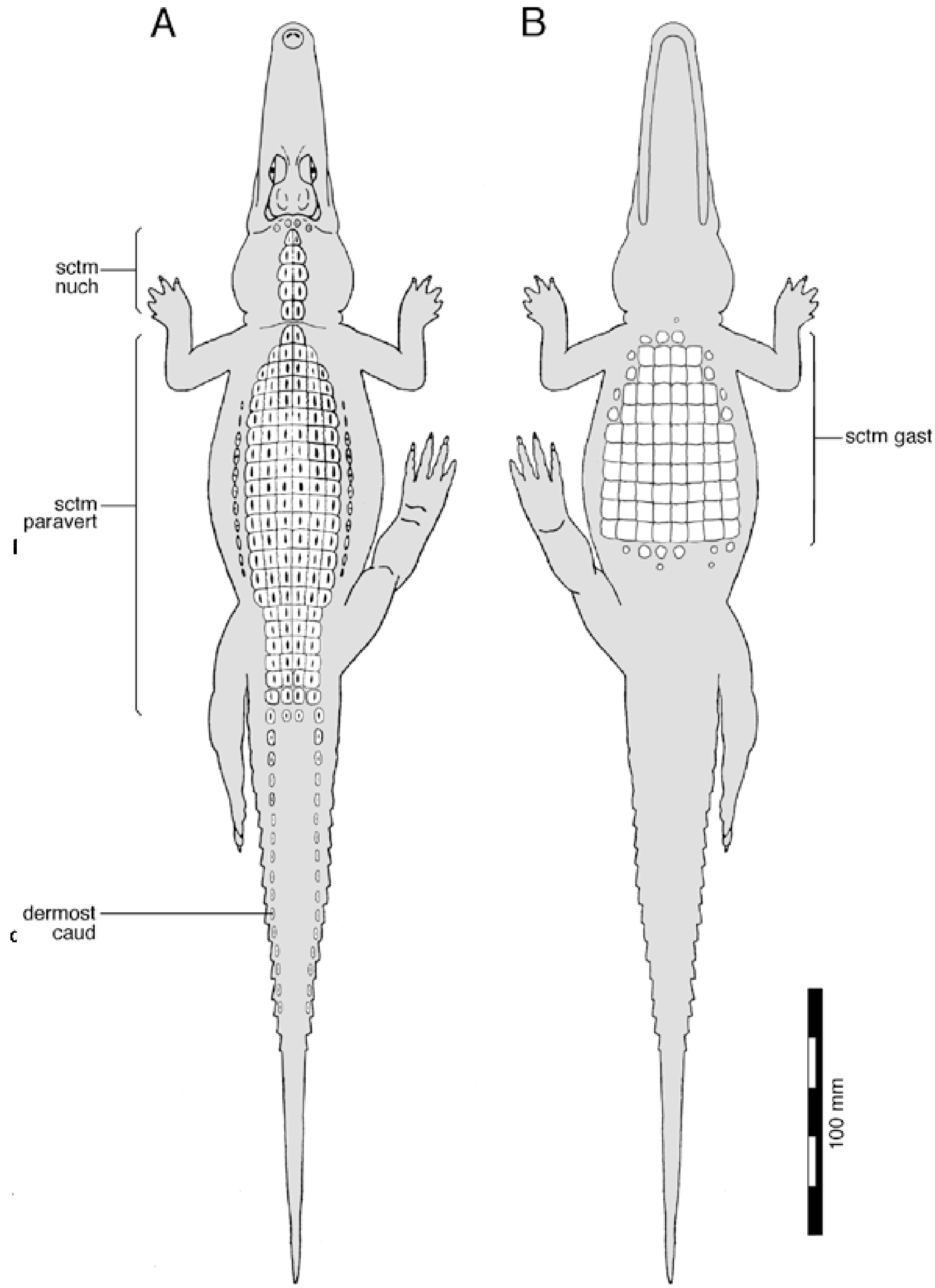
Scutum dorsi (dorsal shield): At its maximum width, the scutum dorsi comprises eight sagittal rows of dermostea. The scutum paravertebrale, which comprises the median four sagittal rows of dermostea from the scutum dorsi (Frey 1988a), commences cranial to the regio cervicoprothoracica, between vertebrae cervicales VIII et IX. The full extent of the scutum dorsi caudal to the regio lumbicalis cannot be determined. Counting from cranial to caudal, the medial-most sagittal row of dermostea accessoria commences lateral to the fourth transverse row of dermostea paravertebralia. This sagittal row comprises at least seven dermostea. A second, detached sagittal row of five dermostea accessoria commences lateral to the sixth transverse row of dermostea paravertebralia. As with the scutum paravertebrale, the full caudal extent of this sagittal row cannot be determined. All of the dermostea dorsi appear to have had a flat to gently transversely concave facies interna.

Each of the two cranial-most transverse rows of dermostea paravertebralia appear to have comprised only



Text-fig. 5. *Susisuchus anatoceps* gen. et sp. nov.; reconstruction of two articulating transverse rows of dermostea dorsi from the regio thoracica. A, from the right side of the scutum dorsi in external aspect. B, from the left side of the scutum dorsi in internal aspect. C, from the right side of the scutum dorsi in caudal aspect. Similar to many extant crocodilians, there are two sagittal rows of dermostea paravertebralia and, lateral to these, one contiguous and one detached sagittal row of dermostea accessoria. Based on SMNK 3804 PAL. Anatomical abbreviations are listed in the appendix.

two dermostea. The two dermostea from the cranial-most transverse row are squarish in outline and lack a well-defined facies articularis cranialis, suggesting that they were not contiguous with the caudal-most dermostea nuchalia. The two dermostea from the following transverse row are twice as long in a craniocaudal direction as they are wide, and in respect to the latter dimension, slightly wider than those dermostea from the first transverse row. The craniolateral and caudolateral corners of these dermostea are rounded. A smooth facies articularis cranialis forms approximately 20 per cent of the total length in a craniocaudal direction of the facies externa.



Text-fig. 6. *Susisuchus anatoceps* gen. et sp. nov.; schematic reconstruction in dorsal (A, basking position) and ventral (B, basking position) aspect, showing the configuration of the skeleton dermale. Based on SMNK 3804 PAL. Anatomical abbreviations are listed in the appendix.

Unfortunately, the margo lateralis of both dermostea from this second transverse row are not visible. Although the facies externa of each of the aforementioned four dermostea is sculptured with small (0.5–1 mm) wide pits, all lack a carina dermostealis.

It is unclear whether the third transverse row of dermostea paravertebralia comprised four or two dermostea. Only two are preserved – one from the left and one from the right of the scutum – and the margo lateralis of each is obscured, which means that the presence of a sutured margin and thus evidence for a second, lateral pair of dermostea cannot be determined. Both of these dermostea are of a similar shape to those from the proceeding transverse row, but about one and a third times as large. A smooth, well-defined facies articularis cranialis is present, separated from the rest of the facies externa by a shallow, transverse groove. Each is sculptured in a similar manner to the proceeding dermostea, except that towards their axis craniocaudalis, they possess a low, sagitally aligned carina dermostealis.

Each of the medial-most dermostea paravertebralia from the following transverse rows are all of a similar shape and size to each other, being sub-rectangular in outline. The margins of these dermostea are all of an equivalent length to the width of the processus spinosi of the vertebrae thoracicae in a craniocaudal direction. The facies articularis cranialis forms slightly less that 20 per cent of the total length in a craniocaudal direttion of the facies externa. All are sculptured in a similar manner to the other dermostea paravertebralia and possess a low, sagitally aligned carina dermostealis. Each one is sutured medially to the dermosteum adjacent to it in the medial-most sagittal row on the other side of the scutum paravertebrale, and laterally to the dermosteum adjacent it in second, lateral-most sagittal row.

Dermostea from the second sagittal row of the scutum paravertebrale are all of a similar size, shape and structure to those of the medial-most sagittal row, to which they are sutured. Although they may have contacted those dermostea accessoria from the sagittal row that is lateral to them, there is no indication of a sutural contact.

The three disarticulated dermostea dorsi preserved in close association with vertebra lumbicalis II are of an equivalent size and shape to those dermostea from the regio thoracica (thoracic region) of the scutum paravertebrale. The facies articularis cranialis of these dermostea is slightly raised in respect to the rest of the facies externa. In dorsal aspect, this articular surface forms approximately 15–20 per cent of the total length of the facies externa in a craniocaudal direction. The rest of this surface is sculptured with shallow pits, and a low, sagittally aligned carina dermostealis extends along the axis craniocaudalis. The one that is partially obscured beneath the left processus transversus has a sinuous margo sinistra. The facies interna of the dorsal-most of these three dermostea, which is the only dermostea dorsi preserved in internal aspect, is smooth.

Dermostea from the medial-most sagittal row of dermostea accessoria are craniocaudally oval- to diamond-shaped in outline, with irregular, serrated margins and a prominent, sagitally aligned carina dermostealis. They are approximately 75 per cent the length in a craniocaudal direction of the dermostea paravertebralia. External sculpturing on these dermostea comprises similar sized pits and depressions to those seen on the other dermostea dorsi. Cranially, where they taper to a rounded apex, all but the cranial-most of these dermostea accessoria possess a smooth facies articularis that underlaps the proceeding dermosteum. This surface comprises approximately 15 per cent of the total length in a craniocaudal direction of each dermosteum.

The lateral-most sagittal row of dermostea accessoria are detached from the rest of the scutum dorsi. These dermostea are craniocaudally oval-shaped in outline, tapering to point cranially and caudally. They are approximately twice as long in a craniocaudal direction as they are wide, and three quarters the length of those dermostea from the medial-most sagittal row of dermostea accessoria. A prominent, sagitally aligned carina dermostealis extends along the entire length of the facies externa. To either side of this crista, each dermosteum is sculptured with faint ridges and pits that are of a similar size to those on the other dermostea dorsi.

S c u t u m g a s t r a l e (gastral shield): All of the preserved dermostea gastralia are sub-rectangular in outline, with gently rounded craniolateral corners. Each is of an equivalent size to the dermostea from the lateral-most sagittal row of the scutum paravertebrale. The margines laterales show evidence of a sutured contact, suggesting that these dermostea did not belong to the lateral-most craniocaudal row of the scutum gastrale. In addition, they indicate that the dermostea gastralia were arranged in transverse rows.

The facies interna of each dermosteum gastrale smooth, and gently concave in either cranial or caudal aspect. The cranial quarter of each, the pars articularis cranialis, underlaps the caudal quarter of the proceeding dermosteum, the pars articularis caudalis. The facies articulares of these dermostea are not visible.

D e r m o s t e a c a u d a e (osteoderms of the tail): The two dermostea caudae that are of an equivalent size to those dermostea from the medial-most articulated sagittal row of dermostea accessoria are approximately one and a half times as long in a cranioterminal direction as they are wide, being rectangular in outline with rounded corners. Although serrated, the margines of these dermostea a too thin (less than .05 mm) to be interpreted as representative of a sutural contact. Both are sculptured in a similar manner to the dermostea accessoria and possess a low, cranioterminally aligned carina dermostealis along the terminal half of their axis cranioterminalis. The facies interna of the dermosteum caudae preserved beneath the left costa caudalis IX is smooth. Due to their position and shape, these dermostea are interpreted as belonging to the squamae of either the latus caudae or venter caudae (scales on the lateral or ventral sides of the tail).

The other five dermostea scattered around this region of the cauda are lobate in outline, with their long axis aligned cranioterminally. Each is of an equivalent size or slightly smaller to those dermostea from the lateral-most row of dermostea accessoria, and possesses a prominent carina dermostealis along its axis cranioterminalis. In lateral aspect, the maximum height of this keel is equal to each dermosteum's maximum width. All are sculptured with shallow (0.5–1 mm) pits and have a smooth facies interna. Combined with the position in which they are preserved, these features suggest that all these dermostea belong to the squamae of the crista caudae pars duplicata (double tail crest).

Ontogenetic stage of the specimen

Due to the scarcity of discrete size-independent osteological features in the crocodilian skeleton that are indicative of maturity (BROCHU 1992, 1994, 1995), comments on the ontogenetic stage of fossil crocodilians can only be regarded as tentative at best. *Susisuchus anatoceps* does, however, possess a number of osteological features commonly associated with juvenile individuals of all extant crocodilians, and mature individuals of dwarf taxa such as *Alligator sinensis*, *Osteolaemus tetraspis* and *Paleosuchus* spp. Within the cranium, these features include the short caudal extent of the ossa quadratica beyond the occiput; the large size of the orbitae in relation to the foramina supratemporalia; the elliptical and obliquely oriented foramina supratemporalia; the narrow, dorsally concave shape of the os frontale between the orbitae; the lack of any vertical festooning of the partes alveolaris premaxillaris et maxillaris; the gracile, needle-like, homodont dentes; and the indistinct nature of the sculpture pitting on the mesa cranii and rostrum maxillae (KÄLIN 1933). Within the skeleton postcraniale, addition juvenile characteristics include the lack of torsion of the extremitas distalis of the humerus in relation to the caput humeri (cf. BROCHU 1992) and the smooth facies articularis symphysialis ilii of the costae sacrales (BROCHU 1992). Unfortunately, fusion of the presacral suturae neurocentrales, a feature that can accurately be used to interpret the ontogenetic stage of extant crocodilians (BROCHU 1992, 1995), cannot be commented upon because most of the corpora of the presacral vertebrae are still embedded in matrix (see Description of the specimen). In all the vertebrae terminal to vertebra caudalis IV, however, the sutura neurocentralis is fused, though this is typical of even hatchlings of extant crocodilian taxa (BROCHU 1992, 1994). Distinct muscle scars are also absent on the corpora of the ossa membri thoracici.

Although the presence of these features may well indicate that *S. anatoceps* was a juvenile animal, the partial fusion of the serrated articulationes costovertebrales in the pelvis (BROCHU 1992) and heavy sculpturing on the facies externa of each dermosteum also suggest it may have been a subadult. In any case, the melange of juvenile and subadult osteological features on the specimen indicate that it was not a mature individual.

Comparisons

Taxonomic issues

The osteology of *S. anatoceps* compares best with those crocodilians that are currently referred to as 'advanced neosuchians'; the group from which eusuchian crocodilians are thought to have evolved. Erected by CLARK (1986), Neosuchia was first published in BENTON & CLARK (1988). As initially defined by BENTON & CLARK (1988), Neosuchia included Atoposauridae GERVAIS, 1871, Goniopholididae COPE, 1875, Pholidosauridae EASTMAN, 1902, Dyrosauridae DE STEFANO, 1903, *Bernissartia fagesii* DOLLO, 1883, *Shamosuchus* MOOK, 1924 and Eusuchia. With the exception of Eusuchia and Dyrosauridae, BENTON & CLARK's (1988) Neosuchia is essentially the 'traditional' mesosuchian infraorder Metamesosuchia HULKE, 1878 as conceived by BUFFETAUT (1982). Because their classification was based on the recognition of cladistically defined monophyletic groups, it was the exclusion of Eusuchia from Metamesosuchia by BUFFETAUT (1982) that prompted BENTON & CLARK (1988) to erect Neosuchia.

Following a reassessment of his original cladistic analysis, CLARK (1994) decided to substantially alter the content of Neosuchia sensu BENTON & CLARK (1988). In addition to all its previous taxa, he further included Thalattosuchia. In CLARK's (1994) classification, Thalattosuchia comprised *Pelagosaurus* BROWN, 1841, Metriorhynchidae FRITZINGER, 1843 and Teleosauridae GEOFFROY, 1831. CLARK (1994) also recognised an unnamed group of 'longirostrine taxa' within Neosuchia, comprising *Pholidosaurus*, Dyrosauridae and Thalattosuchia. CLARK's (1994) results have been supported by the analysis of BUCKLEY & BROCHU (1999). However, a subsequent cladistic classification of crocodilians by WU et al. (1997, 2001) excluded the 'longirostrine taxa' from Neosuchia, primarily due to the inclusion of Notosuchia DOLLO, 1924. In both of these analysis, Notosuchia comprised *Notosuchus* WOODWARD, 1896, *Libycosuchus* STROMER, 1914 and *Araripesuchus* PRICE, 1959. A similar arrangement was reached by BUCKLEY et al. (2000). CLARK (1994), on the other hand, considered Notosuchia to be paraphyletic.

Other taxa assigned to Neosuchia *sensu* BENTON & CLARK (1988), but not referred to in the cladistic classifications of CLARK (1994), WU et al. (1997), BUCKLEY & BROCHU (1999), BUCKLEY et al. (2000) and SERENO et al. (2001) include *Brillanceausuchus babouriensis* (MICHARD et al. 1990) and *Gilchristosuchus palatinus* (WU & BRINKMAN 1993).

There are a number of well-known, but as yet undescribed fossil crocodilians also considered to bear on the origin of eusuchians. The most notable of these comes from the Aptian-Albian Glen Rose and Cloverly Formations of central Texas and Montana respectively (LANGSTON 1974). Although initially considered to be a new type of atoposaurid (JOFFE 1967, LANGSTON 1974), subsequent accounts of the Glen Rose crocodilian have tentatively classified it as an 'advanced neosuchian' (NORELL & CLARK 1990, CLARK & NORELL 1992, BROCHU 1997a, b, 1999). Most recently, BUSCALIONI et al. (2001) considered it a eusuchian. BUSCALIONI (1991), ORTEGA & BUSCALIONI (1995) and BUSCALIONI et al. (2001) have also provided preliminary accounts of what is referred to as either an indeterminate atoposaurid (BUSCALIONI 1991, ORTEGA & BUSCALIONI 1995) or a neosuchian from the Lower Cretaceous Las Hoyas Formation, near Cuenca, Spain. More recently, MOLNAR & WILLIS (1996) referred an unnamed crocodilian from the Cenomanian Winton Formation of western Queensland, Australia to Neosuchia.

The characteristics used to diagnose neosuchians (and thus metamesosuchians) are discussed in the works of BUFFETAUT (1982), CLARK (1986, 1994), NORELL & CLARK (1990), BUSCALIONI & SANZ (1990), CLARK & NORELL (1992), WU & BRINKMAN (1993), WU et al. (1994, 1996a, b, c, 1997, 2001), ORTEGA & BUSCALIONI (1995), BROCHU (1997b), RUSSELL & WU (1997–1998) and BUSCALIONI et al. (2001). In relation to *S. anatoceps*, these characteristics include the following: reduction or loss of a fenestra antorbitalis (antorbital fenestra); two or less fenestrae quadratica (quadratic fenestrae); confluent nares; condylus mandibularis of the os quadratum level with the condylus occipitalis in occipital aspect; and amphicoelous vertebrae. In addition to 'advanced neosuchians', *S. anatoceps* also displays a miscellany of characters normally associated with Eusuchia, the taxon that includes all extant crocodilian species. These include more than four sagittal rows of dermostea dorsi (FREY 1988b, BUSCALIONI & SANZ 1990, ORTEGA & BUSCALIONI 1995), absence of a processus articularis on the lateral-most dermostea from each transverse row of the scutum dorsi (ROSS & MAYER 1983, FREY 1988b, ORTEGA & BUSCALIONI 1995), and a narrowing of the scutum dorsi in the regio cervicoprothoracica (ROSS & MAYER 1983, FREY 1988b, ORTEGA & BUSCALIONI 1995).

In light of these similarities, in addition to the skeletonised remains of all species of extant crocodilians and other fossil crocodilians from the Lower Cretaceous Araripe Basin of Brazil (*Araripesuchus gomesii* and *Itasuchus camposi*[1]), *S. anatoceps* was compared with material of *Bernissartia fagesii* from the Hauterivian-Barremian of Bernissart, Belgium (IRSNB R46 and IRSNB R1538) and Valanginian Hastings Beds of southern England (BMNH 37712); *Brillanceausuchus babouriensis* from the Lower Cretaceous Babouri-Figuil Basin of northern

[1] The current whereabouts of the holotype of *I. camposi* are unknown (E. BUFFETAUT, pers. comm. 1997). Our comparisons were thus based on the description and photographs of two complete skeletons in BUFFETAUT (1991).

Cameroon (IPMNHP BBR201, IPMNHP BBR296, IPMNHP BBR298, IPMNHP BBR330, IPMNHP BBR331, IPMNHP BBR268, IPMNHP BBR216 and IPMNHP BBR295); *Dyrosaurus minor* and *Dyrosaurus* sp. from the Eocene of Wurno, northern Nigeria (BMNH R177 and BMNH R5617, BMNH R5620, BMNH R5642 and BMNH R5635); *Dyrosaurus* sp. from the Eocene of Samik, Mali (BMNH R10148); *Dyrosaurus* sp. from the Eocene of In Farghas, Mali (BMNH R11056); *Hylaeochampsa vectiania* from the Lower Barremian of the Isle of Wight, UK (BMNH R177); *Theriosuchus pusillus* from the Berriasian of Dorset, UK (BMNH 48216 and BMNH 48330); the Glen Rose crocodilian from the Albian-Aptian of central Texas, USA (TMM 406644-1, USNM 29039, USNM 427794 and MXZ 4453); the Las Hoyas crocodilian from the Lower Cretaceous of Cuenca, Spain (MCLH Las Hoyas 1 and MCLH Las Hoyas 2); and the Winton crocodilian from the Cenomanian of western Queensland, Australia (QM F36211, QM F34642).

Comparisons with other taxa, including dyrosaurs (Troxell 1925, Piveteau 1935, Swinton 1950, Buffetaut 1982, Storrs 1986, Langston 1995, Denton et al. 1997), *Dolichochampsa minima* (Gasparini & Buffetaut 1980, Buffetaut 1987, Gasparini 1996), *Stomatosuchus inermis* (Stromer 1925), *Shamosuchus* (Efimov 1988, Benton & Clark 1988, Norell 1989, Norell & Clark 1990), *Gilchristosuchus palatinus* (Wu & Brinkman 1993) and *Allodaposuchus precedens* (Buscalioni et al. 2001) were made using illustrations and descriptions provided in the literature.

Diagnostic osteological features

Following comparisons with the above material, the following osteological features were found to be unique to *S. anatoceps*:

1) The costae sacrales of *S. anatoceps* differ from those of other crocodilians in that their minimum width in a craniocaudal direction exceeds the maximum width of any of the processus transversi. The condition observed in other crocodilians is such that the minimum width of these costae is either equivalent to or slightly less than that of the processus transversi of the vertebrae thoracicae et lumbicales,

2) Within the columna vertebralis of the cauda, the postzygapophyses of vertebrae caudales VI – XI (the vertebrae terminal to vertebra caudalis XI are not preserved) of *S. anatoceps* unite medially to form a flat, horizontally aligned shelf, which extends terminally over the foramen vertebrale. In all other crocodilians that we have examined, the postzygapophyses of these vertebrae are not united medially,

3) Notable differences between *S. anatoceps* and other crocodilians are observed in the ulna. The extremitas proximalis of this bone is normally considerably larger that the extremitas distalis, which is reduced to a mediolaterally flattened knob that is of an equivalent thickness to the corpus. In *S. anatoceps*, however, the maximum width of the extremitas proximalis is equivalent to that of the extremitas distalis, and slightly less than twice the minimum thickness of the corpus. This is similar to the condition seen in *Theriosuchus pusillus* (BMNH 48216). A tuberculum craniale is also absent on the extremitas proximalis of the ulna of *S. anatoceps*, though this may be related to the ontogenetic stage of the specimen (discussed above). In extant crocodilians, the tuberculum craniale on the extremitas proximalis of the ulna is most likely associated with the attachment of the ligamentum radioulnare (radioulnar ligament). The development of this tuberculum during ontogeny is not known, but as is the case with other tubercula on the ossa membra thoracica et pelvica, it may not be evident during early stages (Brochu 1992),

4) The manus of *S. anatoceps* is unusual in that only digiti manus I et II posses a phalanx unguis. In all extant crocodilian taxa, phalanges unguales are present on digiti manus I – III. This is also the case in the majority of fossil crocodilians where the manus is preserved in entirety, though some taxa such as *Steneosaurus bollensis* and *Dibothrosuchus elaphros* (Wu & Chatterjee 1993) also possess a phalanx unguis on digitus manus IV.

Although seen in a number of other crocodilians, in combination with those mentioned above, the following osteological features are also considered to be diagnostic of *S. anatoceps*. These include the presence of a caudal process of the os maxillare between the ossa lacrimale et prefrontale, separating the former bone from os nasale (also seen in *Alligator mississippiensis*, *Crocodylus megarhinus*, *Stangerochampsa mccabei*, *Brachychampsa montana* and the Glen Rose crocodilian; Norell et al. 1994, Wu et al. 1996b, Brochu 1997a). A condition similar to this is also seen in *Bernissartia fagesii*, but the os lacrimale still appears to be in contact with the os nasale (Buscalioni & Sanz 1990, Text-fig. 1). The os lacrimale of *S. anatoceps* also extends rostrally beyond the rostral limit of the os prefrontale.

One of the most striking features of *S. anatoceps* is the presence of a tetraserial scutum paravertebrale in combination with amphicoelous vertebrae thoracicae, lumbicales et caudalis. Although the former is characteristic of all eusuchians and perhaps an as yet indeterminate species of the dyrosaur *Rhabdognathus* (LANGSTON 1995, Fig. F32), and the latter the majority on non-eusuchians, together these features have not been documented for any crocodilian.

Taxonomic conclusions

Based on the osteological features listed in the previous section, we consider *S. anatoceps* to be sufficiently distinct from other crocodilian taxa to warrant referral to a new genus and species. Additionally, because of its unique combination of a eusuchian-type scutum dorsi and amphicoelous vertebrae thoracicae, lumbicales et caudales, we further consider *S. anatoceps* to be representative of a distinct family within Mesosuchia: Suchisuchidae.

Taphonomy

The preservation of the holotype of *Susisuchus anatoceps* is highly unusual for a fossil crocodilian. Whereas most of the cranium, the cervix, the cranial half of the regio thoracica and the membra thoracica are articulated and include soft-part preservation, the caudal half of the regio thoracica, the regiones lumbicalis et sacralis and the cauda display a high degree of decay (Text-figs. 2 and 3). In light of these features, we have attempted to reconstruct the taphonomic history of the specimen, taking into account aspects of its preservation, soft-tissue anatomy and the palaeoenvironment of the Crato lagoon.

Taphonomic characteristics of the specimen

Relationship to sediment: The skeleton lies parallel to the bedding, but some elements clearly have components that penetrated into the sediment. The cranium and portions of the ossa membri thoracici show cross-cutting relationships with the laminae. Despite the general lack of geopetal fabrics, there is some evidence to suggest that the specimen is lying with its facies dorsalis lower-most. The reverse side of the slab displays a gentle bulge on the surface of the bedding plane outlining the fossil beneath. This represents a lamina drape over the fossil suggesting that the exposed view of the specimen is the down facing side. Furthermore, the left humerus is inclined down into the limestone slab proximally. This is consistent with the carcass settling on to the substrate with its facies dorsalis facing downwards (ie., the carcass sank upside down).

A number of theoretical considerations also suggest that the specimen is lying upside down. Carcasses of recent crocodilians normally float upside down in water, with the membra thoracica et pelvica at right angles to the body. In deep water, both the cauda and the caput droop slightly, so that the venter pars ventralis (infrapubic part of the belly) and the membra are the only portions of the body exposed above the surface (WEIGELT 1927: plate 27, Text-figs. 2 and 3; plate 30, Text-figs. 1 and 2a). Two factors contribute to a carcass assuming such a position. Firstly, the scutum dorsi is heavier and more extensive than the scutum gastralis. (The influence of the scutum dorsi increases in those crocodilians that lack a scutum gastralis, such as *Crocodylus porosus* and *Gavialis gangeticus*.) Secondly, decomposition gases produced in the ventriculus (stomach) and the jejunum and ilium (intestinal tract) cause the cavitas thoracoabdominalis to become bloated, thereby lightening the ventral part of the truncus. In the final stages of decay, the abdominal gases are released through ruptures in either the dermis or the cloaca, and the carcass subsequently sinks as a whole.

The depth of the skeleton is greater than the thickness of laminae within the rock. As such, it cuts through several laminae, most strikingly demonstrated by the left membrum thoracicum. Thus the carcass must have at least sunk partially into a carbonate ooze.

Bone preservation: The bones are preserved as three-dimensional biomineralised structures with a light brown colouration. Where bone is fractured it appears slightly darker. Surface textures of the bones show them to be smooth or slightly fibrous with roughened areas where muscles, tendons or ligaments attached clearly visible. Some bones, for example, elements of the cranium and membra thoracica, are encrusted with a thin (~ 0.2 mm) layer of goethite, which may represent mineralised soft tissue (Text-figs. 2 and 3; see below). Cavities within the bone are filled with orange-brown goethite and calcite. There are traces of black dendritic manganese on the surface of the right scapula and humerus.

Soft tissue preservation: Dark orange-brown stains on the ossa membri thoracici and cranium and the surfaces of bedding planes surrounding these bones are interpreted as fossilised integument. As the limestone is slightly weathered – the Nova Olinda Member limestones are blue/grey when fresh (see FREY & TISCHLINGER 2000) – the orange-brown colouration is considered to be a goethitic weathering product of early diagenetic pyrite (see below). This soft tissue preservation is restricted to the cranium, cervix, cranial half of the truncus and the membra thoracica. It is possible that some of this material may have been prepared away at an early stage of the preparation. The margins of the colour-stained sediment are sharp, and clearly define an outline of the brachia, cubiti, antebrachia, carpi and manus (Text-figs. 2 and 3). The stained regions are amorphous. No detail of squamation is preserved, neither is there any hint of musculature. This material is therefore interpreted as a weathered by-product of a low-fidelity diagenetic mineralisation of the integument.

Bone associations: The skeleton is incomplete, but the elements present are either in articulation or closely approximate their original life association. There is no evidence that bones have been moved while on the lagoon floor as a result of current activity or benthic scavenging. It appears that what is present is what arrived on the lagoon floor, but the possibility that some elements may have been refloated with the build up of decomposition gases cannot be ruled out.

Missing elements: The presence of soft tissue preservation and the articulated nature of the skeleton is evidence that the crocodilian sank to the bottom of the basin with at least some integument and ligaments holding the skeletal elements together. However, the terminal two thirds of the cauda, ossa coxarum et pubis and the membra pelvica are missing, as are portions of the skeleton dermale and some costae thoracicae. No elements of the skeleton lie short distances from the articulated skeleton, and from this it can be concluded that loss of the missing elements occurred before the carcass sank to the bottom.

Taphonomic considerations

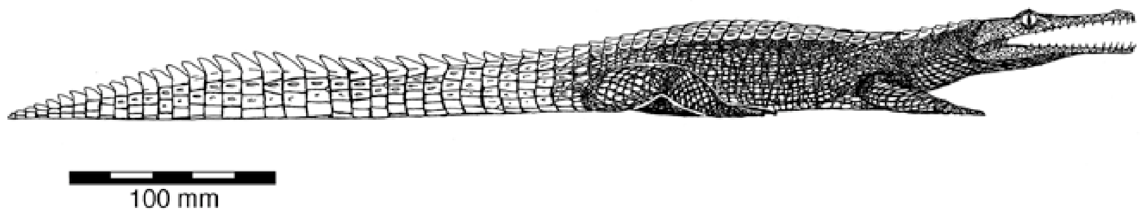
Mode of death: There is no direct evidence for the mode of death of the specimen. Evidence for predation is only circumstantial. The absence of the terminal two thirds of the cauda could be interpreted as the result of a bite, but no dental damage is evident on the terminal-most vertebra preserved on the specimen (vertebra caudalis XI).

Macro-scavenging: Loss of some skeletal elements could be attributed scavenging. Removal of the membra pelvica and ossa coxarum et pubis from a fresh carcass would have resulted in disruption of the columna vertebralis in or around the regio sacralis (sacral region). Scavenging of a partially decomposed carcass, however, might have allowed removal of the membra pelvica and ossa coxarum et pubis without disrupting the columna vertebralis. Any macro-scavenging must have taken place prior to sinking of the carcass as the benthic environment during deposition of the Nova Olinda Member was inhospitable for macro-benthos.

Postmortem drifting and decay: The Nova Olinda Member fossil assemblage mainly comprises allochthonous species (MARTILL 1998). The rarity of crocodilians in this deposit, the absence of benthos and the restriction of fish to a single common species suggests to us that crocodilians probably only occurred very rarely as live animals within the basin. We therefore consider that the specimen must have drifted to its present position from a river or shoreline. The shoreline of the lagoon was in close proximity to some of the fossiliferous localities at Tatajuba (MARTILL & FREY 1996), but localities yielding fossils in the region of Santana do Cariri are approximately fifteen kilometres from the nearest shoreline.

Further evidence that the carcass was partly decayed when it sank is suggested by the presence of an articulated portion of the scutum dorsi being partly detached from the columna vertebralis. Between the regiones prothoracica et basis caudae of extant crocodilians, the median portion of each median dermosteum paravertebrale is fixed tightly to the cartilago apicalis of the processus spinosi (FREY 1988a). While the latter cartilaginous articulations must have broken down, the dermostea comprising this portion of the scutum dorsi in *Susisuchus anatoceps* were held together by the connective tissue of the integument. The dermostea in the caudal half of the truncus and the preserved part of the cauda of *Susisuchus anatoceps* could only have been lost if the integrity of the epaxial musculature had been destroyed.

The complete nature of the ossa membri thoracici and the surrounding halo of soft tissue demonstrates the



Text-fig. 7. *Susisuchus anatoceps* gen. et sp. nov.; life restoration in right lateral aspect.

intact nature of the integument, at least in this region of the body. The sharp outline of the preserved soft tissue of the proximal and distal parts of the membra thoracica, including the digiti manus, shows that the integument must have still been present during burial. There is no hint of the integument being present in the regiones lumbicalis et sacralis and the cranial half of the cauda. However, the columna vertebralis could only have remained articulated in the absence of the scutum paravertebrale if the ligamenta intervertebralia, the septum transversum and the septum interspinale remained viable prior to embedding. Articulation would have additionally been facilitated through the persistence of the tendons of the m. multifidus. These tendons lie adjacent to the facies laterales of the processus spinosi.

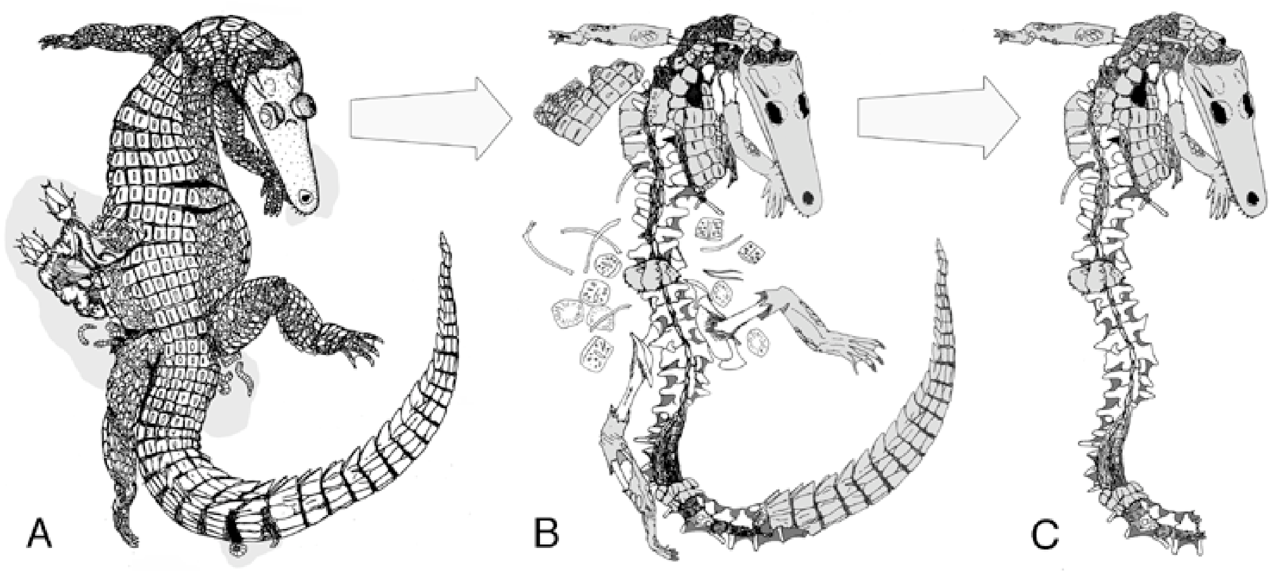
In recent crocodilians, the terminal extent of the m. multifindus occurs in the terminal half of the regio crista caudae pars singularis (portion of the tail that includes the single tail crest), or point at which the costae caudales end (FREY 1988a, SALISBURY 2001). Based on the gradual decrease in length of the costae caudales of *Susisuchus anatoceps*, at least four or five more costae or processus costales (costal processes) can be assumed to have occurred terminal to vertebra caudalis XI. The crista caudae pars duplicata can be reconstructed as extending terminally to at least vertebra caudalis XV or XVI (Text-fig. 7). The cauda of *Susisuchus anatoceps* has thus broken off just cranial to the transition between the regiones crista caudae duplicata et crista caudae singularis, and the terminal extent of the m. multifindus. The terminal two thirds of the columna vertebralis would thus have been held together primarily by the dermis, which could easily have broken down during floating.

In light of these observations, any period of post-mortem drifting must have been short, and any decay that occurred during drifting was minimal. In this respect, the drifting carcass may have been desiccated.

Decay after sinking: Because the skeleton is associated with preserved soft tissues of the integument, it is clear that the carcass sank with parts of the integument associated with at least the membra thoracica and truncus and with ligaments associated with the columna vertebralis still in place. The presence of dermostea demonstrates that some integument of the cervix and truncus was also present. Many of the dermostea nuchae et dorsi show their in situ relationships, but an agglomeration of three dermostea dorsi in the regio lumbicalis and four or five dermostea caudae are disrupted. The disrupted dermostea are, however, in intimate association with the vertebrae indicating that this position was established prior to sinking and burial. Decomposition of soft tissues after sinking, but prior to total burial, clearly must have occurred as there are elements that have disarticulated, but remain in close association, having moved due to geopetal collapse. This is particularly apparent in the cauda, where the arcus haemales have become detached from their corpora vertebrarum and fallen geopetally on to either their facies craniales or their facies terminales (Text-figs. 2 and 3). Other small movements between closely associated elements, especially in the cervix, might be attributed to shrinkage of desiccated integument. The preservation of soft tissues associated with the membra thoracica indicates that this material was still present on the carcass after burial. However, it is probably the case that this soft tissue was intruded into the sediment by sinking into it, as the left humerus clearly penetrates through some of the fine laminae (see above). Thus, preservation of this soft tissue is a result of being intruded into the sediment, rather than rapid burial by a high rate of sedimentation.

Taphonomic conclusions

The cause of death of the new specimen cannot be determined, but aspects of its pre- and post-burial taphonomic history can. The most striking aspect of the specimen is the contrast between the high degree of articulation and integrity of the skeleton and preservation of soft tissues in some areas combined with the absence

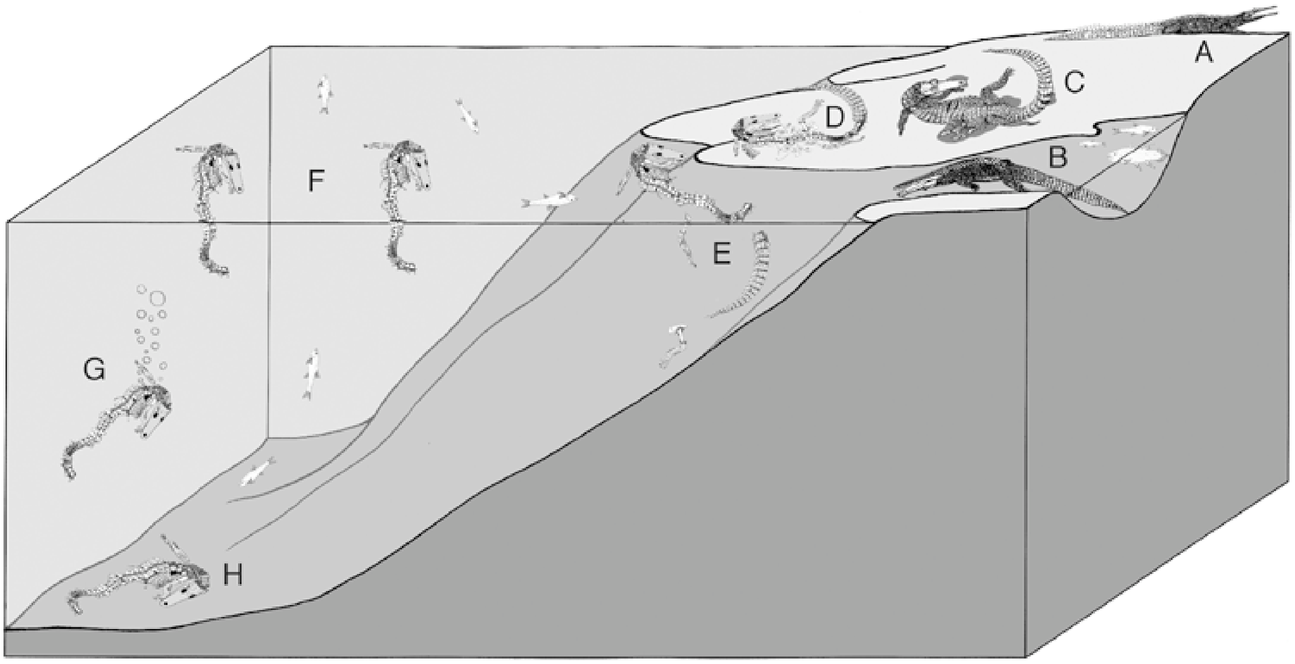


Text-fig. 8. Inferred decay sequence for the *Susisuchus anatoceps* specimen, SMNK 3804 PAL, prior to reaching the bottom of the Crato lagoon. A, following death, decay of the carcass commences out of the water. Bacterial decay and subdermal scavenging are greatest in the abdomen, particularly within and around the cloaca and intestinal tract; B, continued scavenging of the progressively desiccating carcass by insects removes most of its muscle mass, but leaves behind indigestible tendons, ligaments and sheets of connective tissue. The desiccated ligaments hold together portions of the dermis (including the skeleton dermale), columna vertebralis and membra; C, either just prior to or during floating, the ossa coxarum and membra pelvica are lost following separation of the weakened symphyses iliocostales, passively or through macro-scavenging. The terminal two thirds of the cauda are lost in a similar manner, the break occurring just cranial to the transition between the regiones crista caudae duplicata et crista caudae singularis and the terminal extent of the desiccated tendons of m. multifindus.

of the membra pelvica, ossa coxarum et pubis and the terminal two thirds of the cauda. While dismemberment of the carcass may be attributable to predation and/or scavenging, it is difficult to explain how such activity would have removed the membra pelvica and ossa coxarum et pubis from a fresh carcass without rupturing the columna vertebralis in the regio sacralis.

In adult crocodilians, attachment of the os coxae to the costae sacrales is achieved through a strong synchondrosis within the symphysis iliocostalis (in juveniles, this synchondrosis is much weaker). Separation of the symphyses iliocostales, with loss of the ossa coxarum et pubis and the membra pelvica, could only have been achieved on a fresh carcass by predation from an animal with the ability to tear. While this cannot be ruled out, such an animal would most likely have caused further damage to the carcass. An alternate, more plausible explanation, would be that the ossa coxarum and membra pelvica were lost after partial decay of the carcass (Text-figs. 8A and 8B). The close proximity of the bacteria-rich cloaca and intestinal tract to the pelvis may have enhanced local decay.

A number of factors lead us to the consideration that decay of the carcass occurred out of water. Martill (1993) has demonstrated the allochthonous nature of the Nova Olinda Member fossil assemblage. Thus, rather than inhabiting the basin in which the Nova Olinda Member was deposited, the crocodilian probably lived in a local river system. Desiccation of a small carcass at tropical latitudes – the Araripe Basin being approximately 14 degrees South during the Aptian – would have been rapid. We would expect desiccation of soft tissues to be rapid where the soft tissue surface area to volume ratio is high, such as the cover of the membra and the integument covering the cranium, skeleton dermale and perhaps the cervix. We also would expect this to occur in only a few days (our own observations of carcasses while working in the tropics support this). Accelerated decomposition of the viscera under warm conditions would have allowed the membra pelvica and ossa coxarum to have become separated from the truncus via the weak symphysis iliocostalis, perhaps passively, but also perhaps by scavenging. Continued scavenging of the progressively desiccating carcass by insects – Blattodea and Diptera are abundant in the Crato Formation (Grimaldi 1990) – would have liberated the carcass of most of its muscle mass, but left



Text-fig. 9. Post mortem events that befell the *Susisuchus anatoceps* specimen SMNK 3804 PAL as reconstructed from aspects of its preservation, soft-tissue anatomy and the palaeoenvironmental characteristics of the Crato lagoon. A, life in and around one of the small streams that feed into the Crato lagoon; B, death in one of the small streams that feed into the Crato lagoon; C, the carcass is washed ashore where it begins to decay; D, decay continues out of water, with the carcass becoming desiccated; E, the desiccated carcass is refloated and transported into the Crato lagoon. During either stage D or stage E the terminal two thirds of the cauda, the ossa coxae and the membra pelvica are lost; F, the desiccated carcass floats out into the centre of the Crato lagoon; G, gas escapes from the carcass and it begins to sink; H, the carcass settles on the bottom of the lagoon where it begins to get covered in fine sediment.

behind indigestible tendons, ligaments and sheets of connective tissue (Text-fig. 8B). The desiccated ligaments would have held together portions of the skeleton dermale, columna vertebralis and membra thoracica. In a desiccated condition, the carcass would have survived considerably heavy transport in water.

The loss of the terminal two thirds of the cauda could have occurred out of water (passively or by scavenging), but may also have occurred in the water after the soft-tissue holding this portion of the columna vertebralis together had deteriorated.

The small, desiccated carcass must have been refloated, perhaps during seasonal flooding, and was transported into the Crato lagoon (Text-fig. 9). It then sank to the floor of lagoon with its facies dorsalis facing down. There was slight penetration of the carcass into the soft carbonate sediment (Text-fig. 9). Burial of the carcass was followed by partial decomposition of the desiccated integument by sulphate reducing bacteria with resultant precipitation of iron sulphides, most likely pyrite, which has been recorded from unweathered parts of the Nova Olinda Member (Martill 1993). Restriction of this activity to the integument resulted in only localised elevated concentrations of pyrite, producing low-fidelity preservation of the soft tissues. This might have been in part by bacterial autolithification (sensu Wuttke 1983), which has previously been reported for Nova Olinda fossil soft tissues (Martill & Frey 1995).

Continued sedimentation buried the carcass. Compaction of the sediment occurred before diagenetic infilling, and as a result large void spaces, such as those within the cranium, were flattened, resulting in cracking. Bones with small void spaces that were not crushed became filled with calcite.

Discussion

Susisuchus anatoceps is one of the oldest crocodilians with an eusuchian-type scutum dorsi; that is, one comprising a tetraserial scutum paravertebrale and a minimum of one sagittal row of dermostea accessoria (FREY 1988b, ORTEGA & BUSCALIONI 1995, SALISBURY 2001, SALISBURY & FREY 2001). The only other crocodilians of a comparable age that share this feature are an as yet undescribed form from the Albian-Aptian Glen Rose Formation of north-central Texas, USA (LANGSTON 1974, BROCHU 1997b), and a second undescribed form from the Cenomanian Winton Formation of western Queensland, Australia (MOLNAR & WILLIS 1996). Some notosuchids, including *Gobiosuchus kielanae* (OSMÓLSKA et al. 1997) and *Simosuchus clarki* (BUCKLEY et al. 2000, pers comm. 2001) have a scutum dorsi comprising transverse rows of up to 14 dermostea. However, not having seen either of these crocodilians first-hand, we are unsure of the precise nature of the scutum paravertebrale, and are thus cautious about comparing it to that of eusuchians and *S. anatoceps.*

Pending a detailed description by W. LANGSTON Jr., most aspects of the postcranial osteology of the Glen Rose crocodilian cannot be commented on. Similar to eusuchians and *S. anatoceps,* the Glen Rose crocodilian has a tetraserial scutum paravertebrale and at least one sagittal row of dermostea accessoria (cf. BROCHU 1997a, b, 1999). The most complete specimen of the Glen Rose crocodilian, USNM 42 7794, a partial skeleton, includes three vertebrae thoracicae. Unlike the condition seen in *S. anatoceps,* the corpora of all these vertebrae are procoelous (CLARK 1986, NORELL & CLARK 1990, CLARK & NORELL 1992, BROCHU 1997a, b, 1999). Isolated procoelous vertebrae from the Cenomanian Woodbine Formation, Rush Creek Member, Tarrant County, Texas (SMU locality 245) have also been referred to the Glen Rose crocodilian (LEE 1997), having been found in association with a dermosteum paravertebrale (SMU 74639) that is similar to those associated with TMM 406644-1, USNM 42 7794 and MCZ 4453. In light of these observations, the postcranium of the Glen Rose crocodilian is propably eusuchian in nature.

To date, the most detailed account of the Winton crocodilian is that of MOLNAR & WILLIS (1996). MOLNAR & WILLIS (1996) described the scutum dorsi of the Winton crocodilian as being similar to that of *Bernissartia fagesii* (see BUFFETAUT 1975, Pl. III). However, after examining the material (QM F36211, QM F34642), we (SWS and EF) are of the opinion that the scutum dorsi is of a comparable configuration to that seen in *S. anatoceps,* comprising four sagittal rows of singularly-keeled dermostea and, lateral to these, one sagittal row of dermostea accessoria on the left and right sides of the body. A second sagittal row of dermostea accessoria may also be present. The nature of the vertebrae in the Winton crocodilian is not yet known, though preliminary preparation indicates that they may be amphicoelous.

The presence of a eusuchian-type scutum dorsi and amphicoelous vertebrae in the Winton crocodilian suggest it may be referrable to Susisuchidae. Biogeographically, the presence of susisuchid mesosuchians in Australia during the latter part of the Lower Cretaceous would not be surprising. At the beginning of the Cretaceous, Australia was still part of Gondwana, broadly connected to South America via Antarctica (FRAKES et al. 1987). This situation persisted throughout the Lower Cretaceous and lower part of the Upper Cretaceous. By the Maastrichtian and lowest Palaeocene, however, any type of faunal corridor between Australia and South America was probably limited to a chain of islands linking the current Antarctic Peninsula with Cape Horn (VEEVERS 1991, LAWVER et al. 1992, SHEN 1995, LIVERMORE & HUNT 1996). Prior to the Cenomanian, susisuchids could have dispersed easily between South America and Australia, either through inland fluvial systems or along the Atlantic coastline of Antarctica. Such a distribution necessitates the assumption that these crocodilians were present on all the intervening landmasses between South America and Australia during (and perhaps beyond) the upper Lower Cretaceous, including Antarctica, the Indian subcontinent, Madagascar and maybe Africa.

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Appendix of Anatomical Terms

Key to symbols and abbreviations

*	new term
(f)	found in fossil animals only
[hom]	homonym
(pl)	plural
(sing)	singular
[syn]	synonym

Format

Terms are listed in alphabetical order in the following format:

abbreviation **term** (pl: plural, where applicable) [hom: homonym(s). syn: synonym(s)]; English equivalent (where applicable). Annotation (where appropriate).

A

al scap	**ala scapulae** (pl: alae scapulae) [syn: lamina scapulae (ROSSMANN 2000)]; scapular wing.
alv	**alveolus** (pl: alvioli).
alv pmx	**alveolus premaxillaris** (pl: alveoli premaxillares); premaxillary alveoli.
ang	**os angulare** (pl: ossa angularia); angular bone.
antbrach	**antebrachium** (pl: antebrachia); forearm.
ap rost	**apertura rostralis** (pl: aperturae rostrales); rostral aperture.
arc neur	**arcus neuralis** (pl: arcus neurales) [hom: arcus vertebralis]; neural arch.
arc at	**arcus atlantis**; neural arch of the atlas.
arc ax	**arcus axis**; axial neural arch.
arc haem	**arcus haemalis** (pl: arcus haemales) (FREY 1988a) [hom: processus haemalis; haemaphysis]; chevron bone or haemal arch/process.
art	**os articulare** (pl: ossa articularia); articular bone.
at	**atlas**.
ax	**axis** [hom: vertebra cervicalis II].

B

bas	**basis** (pl: bases); base. The base of a bone or part.
brach	**brachium** (pl: brachia); upper arm.
bul occ	**bulla occipitalis** (pl: bullae occipitales); occipital bulla.

C

can	**canalis** (pl: canales); canal.
can ptp	**canalis posttemporalis** (pl: canales posttemporales); posttemporal canal.
cap	**caput** (pl: capitis); head.
cap hu	**caput humeri** (pl: capitis humeri) [syn: caput articulare humeri (FÜRBRINGER 1888)]; humeral head.
cap rad	**caput radii** (pl: capitis radii); radial head. The head of the proximal extremity of the radius, specifically its articular surface.
cap ul	**caput ulnae** (pl: capitis ulnae); ulnar head. The proximal head of the ulna, specifically its articular surface.
capm	**capitulum** (pl: capitula).
capm cost	**capitulum costae** (pl: capitula costarum) (FREY 1988a); costal capitulum.
car	**carina** (pl: carinae); keel.
car dermost	**carina dermostealis** (pl: carinae dermosteales) (SALISBURY & FREY 2001); osteodermal keel.
carp	**carpus** (pl: carpi); wrist.
carpi	**ossa carpi** [hom: ossa carpalia]; bones of the wrist.
cart apic	**cartilago apicalis** (FREY 1988a); apical cartilage.
cauda	**cauda**; tail.
caud	**caudalis** [hom: posterior]; caudal.
cav n	**cavitas nasalis**; nasal cavity.
cav tymp	**cavum tympanicum** [hom: cavitas tympanica] (tympanic cavity)
cerv	**cervicalis**; cervical.
cerv	**cervix**; neck.
cing mem thor	**cingulum membrum thoracicum**; pectoral girdle.
circ art	**circumferentia articularis** (pl: circumferentia articulares); wheel-like articular surface.
cloac	**cloaca**.
col po	**columna postorbitalis** (pl: columnae postorbitales); postorbital bar.
cond lat	**condylus lateralis** (pl: condylus laterales); lateral condyle.
cond mand	**condylus mandibularis** (pl: condylus mandibulares); mandibular condyle.
cond med	**condylus medialis** (pl: condylus mediales); medial condyle.
cond occ	**condylus occipitalis**; occipital condyle.

cond lat **condylus lateralis** (condylus laterales); lateral condyle.
cor **coracoideum** (pl: coracoidea) [hom: os coracoideum]; coracoid.
corp **corpus** (pl: corpora); body or main shaft of a bone.
corp ax **corpus axis**; axial body.
corp cost **corpus costae** (pl: corpora costarum); costal body. The main shaft of the rib.
corp hu **corpus humeri** (pl: corpora humeri); humeral shaft.
corp rad **corpus radii** (pl: corpora radii); radial shaft. The main shaft (diaphysis) of the radius.
corp scap **corpus scapulae** (pl: corpora scapulae) [hom: collum scapulae]; scapular neck.
corp ul **corpus ulnae** (pl: corpora ulnae); ulnar shaft. The main shaft (diaphysis) of the ulna.
corp vert **corpus vertebrae** (pl: corpora vertebrarum); vertebral centrum/body.
cost **costa** (pl: costae); rib.
cost caud **costa caudalis** (pl: costae caudales); caudal ribs.
cost cerv **costa cervicalis** (pl: costae cervicales); cervical rib.
cost sac **costa sacralis** (pl: costae sacrales); sacral ribs.
cost thor **costa thoracica** (pl: costae thoracicae); thoracic rib.
cox os **coxae** (ossa coxarum); hip bone.
cr **crista** (pl: cristae); crest or ridge.
cr caud **crista caudae** (pl: cristae caudae) (Salisbury & Frey 2001); tail crest. Crest of the tail that is formed by scales.
cr caud dup **crista caudae pars duplicata** (Salisbury & Frey 2001); double tail crest.
cr caud sing **crista caudae pars singularis** (Salisbury & Frey 2001); single tail crest. Unpaired portion of the tail crest.
cr sorb **crista supraorbitalis** (pl: cristae supraorbitales); supraorbital ridge.
cranm **cranium**; skull.
cub **cubitus** (pl: cubiti); elbow.

D

d os **dentale** (pl: ossa dentalia); dentary bone.
den **dens** (pl: dentes); tooth.
den max **dens maxillaris** (dentes maxillares); maxillary teeth.
den pmx **dens premaxillaris** (dentes premaxillares); premaxillary teeth.
derm **dermis**; the skin.
dermost **dermosteum** (pl: dermostea) (Salisbury & Frey 2001); osteoderm.
dermost acc **dermosteum accessorium** [syn: 'accessory osteoderm' (Frey 1988a)] (pl: dermostea accessoria) (Salisbury & Frey 2001); accessory osteoderm.
dermost caud **dermosteum caudae** (pl: dermostea caudae) (Salisbury & Frey 2001); caudal osteoderm.
dermost dors **dermosteum dorsale** (pl: dermostea dorsalia) (Salisbury & Frey 2001); dorsal osteoderm.
dermost nuch **dermosteum nuchale** (pl: dermostea nuchalia) (Salisbury & Frey 2001); nape osteoderm.
dermost paravert **dermosteum paravertebrale** (pl: dermostea paravertebralia) (Salisbury & Frey 2001); paravertebral osteoderm.
diap **diapophysis** (pl: diapophyses).
dig man **digitus manus** (pl: digiti manus); finger.
digm man **ossa digitorum manus**; bones of the fingers.
dermost gast **dermosteum gastrale** (pl: dermostea gastralia) (Salisbury & Frey 2001); breast or belly osteoderm.
dex **dexter**; right.
dist **distalis**; distal.
dors **dorsalis**; dorsal. Pertaining to, or in the direction of, the upper side of the head, neck, trunk and tail.

E

ect os **ectopterygoideum** (pl: ossa ectopterygoidea); ectopterygoid bone
ex os **exoccipitale** (pl: ossa exoccipitalia); exoccipital bone.
ext **externus**; external.
extr **extremitas** (pl: extremitates); extremity.
extr dist **extremitas distalis** (extremitates distales); distal extremity.
ext om cor **extremitas omalis coracoidei** (pl: extremitates omales coracoidei) [syn: corpus ossis coracoideum (Rossmann 2000)]; coracoidal head. The shoulder or ventral end of the coracoid (omis, Gk. shoulder).
ext om scap **extremitas omalis scapulae** (pl: extremitates omales scapulae); scapular head. The shoulder or ventral end of the scapula (omis, Gk. shoulder).
extr prox **extremitas proximalis** (pl: extremitates proximales); proximal extremity.

F

f os **frontale** (pl: ossa frontalia); frontal bone.
fac **facies** (pl: facies); surface.
fac art **facies articularis** (pl: facies articulares); articular surface.
fac art carp **facies articularis carpalis** (pl; facies articulares carpales); carpal articular surface.
fac art cor **facies articularis coracoidea** (pl: facies articulares coracoidea); coracoidal articular surface.
fac art dens **facies articularis dentalis** (facies articulares dentales); dental articular surface.
fac art ext **facies articularis externa** (pl: facies articulares externae) (Salisbury & Frey 2001); external articular surface.
fac art hu **facies articularis humeralis** (pl: facies articulares humerales); humeral articular surface. The part of the coracoidal head that articulates with the humerus.
fac art int **facies articularis interna** (pl: facies articulares internae) (Salisbury & Frey 2001); internal articular surface.
fac art mc **facies articularis metacarpalis** (pl: facies articulares metacarpales); metacarpal articular surface.
fac art scap **facies articularis scapularis** (pl: facies articulares scapulares); scapular articular surface. The surface

of the coracoidal head that articulates with the scapula.

fac ext — **facies externa** (pl: facies externae); external surface.

fac int — **facies interna** (pl: facies internae); internal surface.

fac/marg dors — **facies/margo dorsalis** (pl: facies/margines dorsales); dorsal surface/margin.

fac/marg vent — **facies/margo ventralis** (pl: facies/margines ventrales); ventral surface/margin.

fac/marg lat — **facies/margo lateralis** (pl: facies/margines laterales); lateral surface/margin.

fac/marg med — **facies/margo medialis** (pl: facies/margines mediales); medial surface/margin.

fac/mar cran — **facies/margo cranialis** (pl: facies/margines craniales); cranial surface/margin.

fac/marg caud — **facies/margo caudalis** (pl: facies/margines caudales); caudal surface/margin.

fac/marg rost — **facies/margo rostralis** (pl: facies/margines rostrales); rostral surface/margin.

fac pal — **facies palatina**; palatal surface.

fac sut — **facies sutura** (pl: facies suturae); sutural surface.

fac sym il — **facies symphysialis ilii*** (pl: facies symphysiales ilii) (Salisbury & Frey 2001); iliac symphysial surface. The surface of the sacral rib that contributes to the iliocostal symphysis.

fen — **fenestra** (pl: fenestrae).

fen inftemp — **fenestra infratemporalis** (pl: fenestrae infratemporales); infratemporal fenestra.

fen mand ext — **fenestra mandibularis externa** (pl: fenestrae mandibulares externae); external mandibular fenestra.

fen pmx — **fenestra premaxillaris** (pl: fenestrae premaxillares) [syn: foramen incisivum]; premaxillary fenestra.

fen suborb — **fenestra suborbitalis** (pl: fenestra suborbitales) [hom: fenestra palatina]; suborbital fenestra.

for — **foramen** (pl: foramina).

for aë — **foramen aërium** (pl: foramina aëria).

for cor — **foramen coracoideum*** (pl; foramina coracoidea) [syn: foramen supracoracoideum (Wettstein 1937–54); 'coracoid foramen' (Brochu 1992)]; coracoidal foramen.

for duct — **foramen ductus** (foramina ducti).

for l — **foramen lacrimale** (pl: foramina lacrimalia); lacrimal foramen.

for mag — **foramen magnum.**

for nut — **foramen nutricium** (pl: foramina nutricia) [hom: foramen nutriens]; nutrient foramen.

for stp — **foramen supratemporale** (pl: foramina supratemporalia) [syn: fenestra supratemporalis]; supratemporal foramen.

for vert — **foramen vertebrale** (foramina vertebralia); vertebral foramen.

fos — **fossa** (pl: fossae).

fos art mand — **fossa articularis quadratica** (pl: fossae articulares quadraticae); articular fossa for the quadrate, or mandibular fossa.

fos art q — **fossa articularis quadratica** (pl: fossae articulares quadraticae); articular fossa of the mandible.

fos retart — **fossa retroarticularis** (pl: fossae retroarticulares); retroarticular fossa.

fos vert — **fossa vertebralis** (pl: fossae vertebrales); vertebral fossa.

fos vert cran/caud/term — **fossa vertebralis cranialis/caudalis/terminalis** (pl: fossa vertebrales craniales/caudales/terminales) (Salisbury & Frey 2001) (f); cranial/caudal/terminal vertebral fossa.

G

gast — **gastralis** (Salisbury & Frey 2001); gastral.

H

hu — **humerus** (pl: humeri).

I

inc — **incisura** (pl: incisurae); notch or cavity.

inc arc haem — **incisura arcus haemalis*** (pl: incisurae arcus haemales); haemal concavity. The concave internal arch formed by the articular process of each haemal arch. If the articular processes have fused to form a single articular surface, then this arch is closed and has to be termed a foramen.

inc pmxm — **incisura premaxillomaxillaris*** (pl: incisurae premaxillomaxillares); premaxillomaxillary notch.

J

j — os **jugale** (pl: ossa jugalia); jugal bone.

L

l — os **lacrimale** (pl: ossa lacrimalia); lacrimal bone.

lam arc neur — **lamina arcus neuralis** (pl: laminae arcus neurales) [hom: lamina dorsalis arcus]. The dorsal part of the neural arch that forms the base of the neural spine.

lat caud — **latus caudae**; lateral surface of the tail.

ls — os **laterosphenoidale** (pl: ossa laterosphenoidalia); laterosphenoid bone.

M

man — **manus** (pl: manus); the hand, including the middle of the hand and all the fingers.

mand — **mandibula**; mandible or lower jaw.

marg — **margo** (pl: margines); margin.

marg suporb — **margo supraorbitalis** (pl: margines supraorbitales); supraorbital region.

max — os **maxillare** (pl: ossa maxillaria); maxillary bone.

mc — **metacarpus** (pl: metacarpi); middle of the hand.

mem thor — **membrum thoracicum** (pl: membra thoracica); forelimb.

mem pelv — **membrum pelvicum** (pl: membra pelvica); hind limb.

mes cran — **mesa cranii** (Salisbury & Frey 2001); skull table.

mt — ossa **metacarpi** (sing: os metacarpale) [hom: ossa metacarpalia]; bones of the middle hand.

N

n — os **nasale** (pl: ossa nasalia); nasal bone.

naris — **naris** (pl: nares); nostril or external nasal aperture.

ncrm — **neurocranium.**

nuc — **nucha**; nape of the neck or nuchal region.

sq	**os squamosum** (pl: ossa squamosa) [syn: squamosum]; squamosal bone.
spin itp	**spina infratemporalis** (pl: spinae infratemporales); infratemporal spine.
sulc	**sulcus** (pl: sulci).
sulc intcond	**sulcus intercondylaris** (pl: sulci intercondylares); intercondylar sulcus.
sulc pf	**sulcus prefrontalis** (pl; sulci prefrontales); prefrontal suture.
sut	**sutura** (pl: suturae); suture.
sut angd	**sutura angulodentalis** (pl: suturae angulodentales); angulodental suture.
sut angsupang	**sutura angulosupraangularis** (pl: suturae angulosupraangulares); angulosupraangularis suture.
sut fpf	**sutura frontoprefrontalis** (pl: suturae frontoprefrontales; frontoprefontal suture.
sut lj	**sutura lacrimojugalis** (pl: suturae lacrimojugales); lacriomojugal suture.
sut med	**sutura mediana** (pl: suturae medianae); median suture.
sut neurcent	**sutura neurocentralis** (pl: suturae neurocentrales) (Frey 1988a); neurocentral suture.
sut centcost	**sutura centrocostalis** (pl: suturae costocostales); costocentral suture. The suture between a caudal rib and the centrum of a caudal vertebra.
sut fpf	**sutura frontoprefrontalis** (pl; suturae frontoprefrontales); frontoparietal suture.
sut lpf	**sutura lacrimoprefrontalis** (pl: suturae lacrimoprefrontales); lacrimoprefrontal suture.
sut lsp	**sutura laterosphenoidoparietalis** (suturae laterosphenoidoparietales); laterosphenoidoparietal suture.
sut pls	**sutura parietolaterosphenoidalis** (pl: suturae parietolaterosphenoidales; parietolaterosphenoid suture.
sut qex	**sutura quadratoexoccipitalis** (pl: suturae quadratoexoccipitales); quadratoexoccipital suture.
sut qls	sutura quadratolaterosphenoidalis (pl: suturae quadratolaterosphenoidales); quadratolaterosphenoidal suture.
sut qqj	**sutura quadratoquadratojugalis** (pl: suturae quadratoquadratojugales); quadratoquadratojugal suture.
sut sqp	**sutura squamosoparietalis** (pl: suturae squamosoparietales); squamosoparietal suture.

T

trun	**truncus**; trunk.
tubc	**tuberculum** (pl: tubercula); tubercle.
tubc cost	**tuberculum costae** (pl: tubercula costarum) (Frey 1988a); costal tuberculum. Dorsal articular head of the rip.
tubc cran	**tuberculum craniale** (pl: tubercula cranalia); cranial tubercle.

U

ul	**ulna** (pl: ulnae).
uln	**os unlare** (pl: ossa ulnaria) [hom: os carpi ulnare]; ulnare.

V

ven	**venter**; abdomen or belly.
ven vent/lat	**venter pars ventralis**; infrapubic part of the abdomen or belly. This terms refer to the part of the belly that is below the lateral margins of the pubic bones. The infrapubic part of the belly is partially lateral and partial ventral, and extends from the lateral margin of the pubic bone to the last sternal segment of the thoracic ribs and caudal border of the sternum. It also includes the part of the belly comprising gastral ribs.
vert caud	**vertebra caudalis** (pl: vertebrae caudales); caudal vertebra.
vert cerv	**vertebra cervicalis** (pl: vertebrae cervicales); cervical vertebra.
vert lumb	**vertebra lumbicalis** (pl: vertebrae lumbicales); lumbar vertebra.
vert prothor	**vertebra prothoracica** (pl: vertebrae prothoracicae) [hom: vertebrae thoracicae I et II]; prothoracic vertebra.
vert sac	**vertebra sacralis** (pl: vertebrae sacrales); sacral vertebra.
vert thor	**vertebra thoracica** (pl: vertebrae thoracicae); thoracic vertebra.
vest n	**vestibulum nasi**; nasal vestibule.

O

occip — **occiput.**

orb — **orbita** (pl: orbitae); orbit.

P

pal — **os palatinum** (pl: ossa palatina); palatal bone.

pal oss sec — **palatum osseum secundare**; bony secondary palate.

palma — **palma** (pl: palmae); palm of the hand.

par — **os parietale** (pl: ossa parietalia); parietal bone.

pars — **pars** (pl: partes); part.

pars alv max — **partes alveolaris maxillaris**; part of the maxilla that includes the tooth row.

pars alv pmx — **partes alveolaris premaxillaris**; part of the premaxilla that includes the tooth row.

pars sq — pars squamosalis (pl: partes squamosales); squamosal part.

ped arc neur — **pedunculus arcus neuralis** (pl: pedunculi arcus neurales) (Salisbury & Frey 2001) [hom: pediculus arcus; lamina lateralis arcus]; peduncle of the neural arch.

pel — **pelvis.** The pelvis of crocodilians is formed by the consolidation of the two hip bones, four sacral ribs and two sacral vertebrae.

phal man — **phlanx digiti manus** (pl: phlanages digiti manus); digit of the hand.

phal ung — **phalanx unguis** (pl: phalanges unguis); claw or claw phalanx.

pis — **os pisiforme** (pl: ossa pisiformia); pisiform bone.

pmx — **os premaxillare** (pl: ossa premaxillaria); premaxillary bone.

po — **os postorbitale** (pl: ossa postorbitalia); postorbital bone.

postzyg — **postzygapophysis** (pl: postzygapophyses) [hom: zygapophysis caudalis (Baumel & Witmer 1993); processus articularis caudalis (Frey 1988a)].

prezyg — **prezygapophysis** (pl: prezygapophyses) [hom: zygapophysis cranialis (Baumel & Witmer 1993); processus articularis cranialis (Frey 1988a); processus articularis cranialis arcus vertebralis (Rossmann 2000)].

proc — **processus** (pl: processus); process.

proc caud — **processus caudalis** (pl: processus caudales); caudal process.

proc cost — **processus costalis** (pl: processus costales) (Frey 1988a); costal process.

proc cran — **processus cranialis** (pl: processus craniales); cranial process.

proc parocc — **processus paroccipitalis**; paroccipital process.

proc retart — **processus retroarticularis** (pl: processus retroarticulares); retroarticular process.

proc spin — **processus spinosus** (pl: processus spinosi) [hom, processus dorsalis]; neural spine or neural process.

proc trans — **processus transversus** (pl: processus transversi); transverse process.

proc vent — **processus ventralis** (pl: processus ventrales); ventral process.

pty — **os pterygoideum** (pl: ossa pterygoidea); pterygoid bone.

Q

q — **os quadratum** (pl: ossa quadrata); quadrate bone.

qj — **os quadratojugale** (pl: ossa quadratojugalia); quadratojugal bone.

R

rad — **radius** (pl: radia).

radl — **os radiale** (pl: ossa radialia) [hom: os carpi radiale]; radiale.

ram — **ramus** (pl: rami); arm or branch of a bone or part.

ram mand — **ramus mandibulae** (pl: rami mandibulae); mandibular ramus.

rec tymp — **recessus tympanicus** (pl: recessus tympanica); tympanic recess.

reg cr caud sing — **regio crista caudae pars singularis** (Frey & Salisbury 2001). Portion of the tail that includes the single tail crest.

reg cervprothor — **regio cervicoprothoracica** (Salisbury & Frey 2001); cervicoprothoracic region. The area of transition between the neck and trunk, delimited internally by the caudal-most cervical vertebra and first prothoracic vertebra. The cervicoprothoracic region is continuous with the shoulder.

reg itp — **regio infratemporalis** (pl: regiones infratemporales); infratemporal region.

reg om — **regio omalis** [hom: omus]; shoulder. This is the arbitrarily delimited region of junction between the arm and the trunk.

reg sac — **regio sacralis**; sacral region. The portion of the trunk delimited internally by the pelvis.

reg thor — **regio thoracica** [hom: thorax]; thoracic region. The portion of the trunk delimited internally by the thoracic vertebrae, inclusive of the prothoracic vertebrae, thoracic ribs (vertebral, lateral and sternal segments) and sternum.

rost — **rostrum** (pl: rostra). The snout, comprising the bony parts of the upper jaw or maxilla (exclusive of the cheeks) and the lower jaw or mandible.

rost max — **rostrum maxillare**; maxillary rostrum, upper jaw or maxilla.

S

sa — **os supraangulare** (pl: ossa supraangularia); supraangular bone or surangular.

scap — **scapula** (pl: scapulae).

sctm — **scutum** (pl: scuta) (Salisbury & Frey 2001); shield.

sctm gast — **scutum gastrale** (Salisbury & Frey 2001; shield of the breast and belly.

sctm dors — **scutum dorsi**; shield of the back.

sctm nuch — **scutum nuchae**; shield of the nape.

sctm paravert — **scutum paravertebrale**; paravertebral shield.

seg vertcost — **segmentum vertebrocostale** (pl: segmenta vertebrocostalia) (Salisbury & Frey 2001); vertebral segment of a thoracic rib.

seg latcost — **segmentum laterocostale** (pl: segmenta laterocostalia) (Salisbury & Frey 2001); lateral segment of a thoracic rib.

sk axl — **skeleton axiale**; axial skeleton.

sk antbrach — skeleton antibrachium; forearm skeleton.

so — **os supraoccipitale**; supraoccipital bone.