A NEW ALLIGATOR FROM THE UPPER CRETACEOUS OF CANADA AND THE RELATIONSHIPS OF EARLY EUSUCHIANS

by XIAO-CHUN WU, DONALD B. BRINKMAN *and* ANTHONY P. RUSSELL

ABSTRACT. A new alligatorine eusuchian, *Stangerochampsa mccabei* gen. et sp. nov., is described on the basis of a partial skeleton from the Horseshoe Canyon Formation (Early Maastrichtian) of southern Alberta. It is unique in possessing an ectopterygoid/palatine contact, a ventrolateral process of the quadrate, a groove-like recess for nerves and blood vessels in the upper jaw, a rectangular palatine with a lateral process at its midpoint, and a basioccipital with a ventral exposure longer than that of the pterygoid. Several derived characters indicate a close relationship of *S. mccabei* with two Late Cretaceous alligatorines, *Brachychampsa montana* and *Albertochampsa langstoni*. A preliminary phylogenetic analysis, based on 46 characters of selected taxa, leads to the hypothesis that *Leidyosuchus*, rather than *Hylaeochampsa*, is the most primitive eusuchian, supports the monophyly of the Alligatorinae (with the exclusion of *Prodiplocynodon*), and suggests that the Alligatorinae may consist of at least two distinct assemblages.

Two genera of alligatorines have been reported from the Upper Cretaceous of North America, *Albertochampsa langstoni* from the middle Campanian Dinosaur Park Formation (Judith River Group) of southern Alberta (Erickson 1972), and *Brachychampsa montana* from the upper Maastrichtian Hell Creek Formation of Montana (Gilmore 1911; Norell *et al.* 1994). A well-preserved skeleton of an alligatorine recently unearthed from the lower Maastrichtian Horseshoe Canyon Formation, southern Alberta, Canada, here described as *Stangerochampsa mccabei* gen. et sp. nov., represents a third alligatorine genus in the Late Cretaceous and the first crocodylian from these beds to be represented by relatively complete material.

The detailed understanding of the skeleton of *Stangerochampsa mccabei* provides a basis for reconsidering the phylogenetic relationships of early members of the Eusuchia. Recent phylogenetic studies have established the successive sister groups of the Eusuchia (Clark *in* Benton and Clark 1988; Norell 1989; Buscalioni and Sanz 1990; Norell and Clark 1990; Clark and Norell 1992; Willis 1993; Clark 1994), but a number of Mesozoic (Cretaceous) eusuchians, represented by fairly well-preserved specimens, have not been subjected to phylogenetic study. These Mesozoic taxa include *Hylaeochampsa vectiana* (Owen, 1874), *Leidyosuchus* spp., *Brachychampsa montana*, *Prodiplocynodon langi* (Mook, 1941*a*) and *Albertochampsa langstoni*. These taxa are included in the present analysis. A number of Cenozoic alligatorines are also included in order to establish a suite of synapomorphies of the Alligatorinae. Norell *et al.* (1994) recently argued for a close relationship between *B. montana* and *A. langstoni*. The present study further suggests that these two taxa and *S. mccabei* form a monophyletic group of alligatorines from the Upper Cretaceous of western North America.

Institutional abbreviations used in this study are as follows: the American Museum of Natural History, New York (AMNH); the Field Museum of Natural History, Chicago (FMNH); the Royal Ontario Museum, Toronto (ROM); the Royal Tyrrell Museum of Palaeontology, Drumheller (RTMP); the Museum of Paleontology, University of California, Berkeley (UCMP); National Museum of Natural History, Smithsonian Institution, Washington D.C., (USNM); and the Peabody Museum of Yale University, New Haven, (YPM).

[Palaeontology, Vol. 39, Part 2, 1996, pp. 351–375, 3 pls]

SYSTEMATIC PALAEONTOLOGY

CROCODYLOMORPHA Walker, 1970
CROCODYLIFORMES Clark *in* Benton and Clark, 1988
EUSUCHIA Huxley, 1875
CROCODYLIA Gmelin, 1788
CROCODYLIDAE Cuvier, 1808
ALLIGATORINAE Kälin, 1955

Genus STANGEROCHAMPSA gen. nov.

Type species. Stangerochampsa mccabei.

Derivation of name. Refers to the Stanger family, owners of the ranch from which the type specimen was collected.

Diagnosis. As for type and only known species.

Stangerochampsa mccabei sp. nov.

(Plates 1–3; Text-figures 1–3)

Holotype. RTMP.86.61.1, a skeleton including an almost complete skull with mandibles lacking articulars and coronoids, partial postcranium, and many osteoderms.

Locality and Horizon. Quarry L1524 (NE1/4 LD11 S3 T30 R21W 04), about 8 km north-west of the Royal Tyrrell Museum of Palaeontology at Drumheller, southern Alberta, Canada; from the lower half of the Upper Cretaceous Horseshoe Canyon Formation (lower Maastrichtian), 7 m below coal seam number nine.

Derivation of name. A patronym erected in honour of Mr James Ross McCabe who found, collected, and prepared the specimen.

Diagnosis. A small to medium-sized alligatorine distinguished from all other alligatorines in having the following unique derived characters: an enlarged, groove-shaped recess for blood vessels and nerves in upper jaw; a distinctly laterally directed process of quadrate above condyle on ventral surface; palatine of rectangular outline and with a lateral process at its midlength; ectopterygoid contacting palatine along anterior border of suborbital fenestra; ventral exposure of basioccipital longer than that of pterygoid; and suborbital fenestra with a straight anterolateral border formed entirely by ectopterygoid.

This species shares with *Brachychampsa montana* a strongly curved quadratojugal/quadrate suture; with *Albertochampsa langstoni* a palatine with its anterior portion equal in length to its interfenestral portion; and with *B. montana* and *A. langstoni* a lacrimal having an elongate posteroventral process reaching the midpoint of the ventral border of orbit, a skull table strongly rounded anterolaterally, a large incisive foramen, and a maxilla with a broad lateral portion lateral to tooth row.

Additionally, two characters may be unique to *Stangerochampsa mccabei*, but their respective character-states are undetermined in other alligatorines: palatal process of maxilla forming a step-like structure posteromedial to tooth row; and a shallow but distinct groove present on the lateral surface of the anteromedial portion of the laterosphenoid.

DESCRIPTION

Skull

The skull, largely uncrushed and missing only the articular condyle of the left quadrate (Text-fig. 1), has strongly developed sinusoidal curves along the ventral, lateral and dorsal sides of the dental margin. The snout is short, triangular, and wider than long and is slightly longer than the postorbital region of the skull (measured from the anterior borders of the orbits to the posterior margin of the skull table). The large, undivided naris is longer than wide and wider anteriorly than posteriorly. The orbit and supratemporal fenestra are similar in shape, although the latter is about three-fifths of the former in both length and width. The supratemporal passage penetrates only the anterolateral portion of the supratemporal fossa. The relatively small skull table is shorter in length than the orbit, and its anterolateral border is strongly rounded. The infratemporal fenestra is triangular, with the three sides of subequal length, and is larger than the supratemporal fenestra. No distinct marginal ridge is formed around the naris, orbit, or temporal fenestrae. In occipital view, the posttemporal fenestra is closed and the foramen magnum is wider than high.

In ventral view, the skull is unique in that foramina for blood vessels and nerves anterior and posterior to the maxilla/jugal suture are greatly enlarged and connected with one another to form a deep, elongate, groove-shaped recess posterolateral to the tooth row (Text-fig. 1B–C). This recess resembles a common alveolar groove for the posteriormost maxillary teeth. The incisive foramen is large and oval in shape with a slightly smaller posterior end enclosed by the maxillae. The suborbital fenestra is of moderate size and is diagonally oriented with a straight anterolateral border formed entirely by the ectopterygoid. Lines drawn through the long axes of the two suborbital fenestrae cross at the median exit of the eustachian tube. The length of the long axis is about equal to the distance from the posteromedial edge of the suborbital fenestra to the posterolateral corner of the transverse flange of the pterygoid, as well as to the distance from the posteromedial edge of the suborbital fenestra to the centre of the median exit of the eustachian tube. The choana is wider than long, divided by a very thin lamina, and much smaller in size than the incisive foramen. The choana is positioned along the posterior half of the pterygoid and is surrounded posteroventrally by a strongly developed, V-shaped crest, as in many later alligatorines. Two pairs of large fossae for the large caniniform dentary teeth (fourth, and thirteenth or fourteenth) are present, one at the premaxilla/maxilla sutures and one at a position medial to the eighth (right side) or seventh (left side) maxillary tooth, respectively.

The outer surface of the skull is strongly sculpted. The sculpting is characterized by short grooves and ridges in the anterior half of the skull and pits in the posterior half, a pattern common in alligatorines.

Dorsal skull roof. The premaxilla (Text-fig. 1A–C) is elevated around the periphery of the external naris. Anterior to the naris, the premaxilla is very narrow and does not form a roof-like structure overhanging the nasal capsule. The posterodorsal process is sharply pointed, extending posteriorly beyond the level of the fourth maxillary teeth, and reaching the middle of the snout. In ventral view, the premaxillae are widely separated from one another and end at the level of the posterior margin of the large incisive foramen.

The nasal (Text-fig. 1A) is relatively broad. The sutures with the premaxilla, maxilla and prefrontal do not form a straight line. The nasal/premaxillary suture is almost as long as the nasal/maxillary suture. The anterior end of the nasal is much narrower than the posterior end. The two nasals form a W-shaped posterior margin.

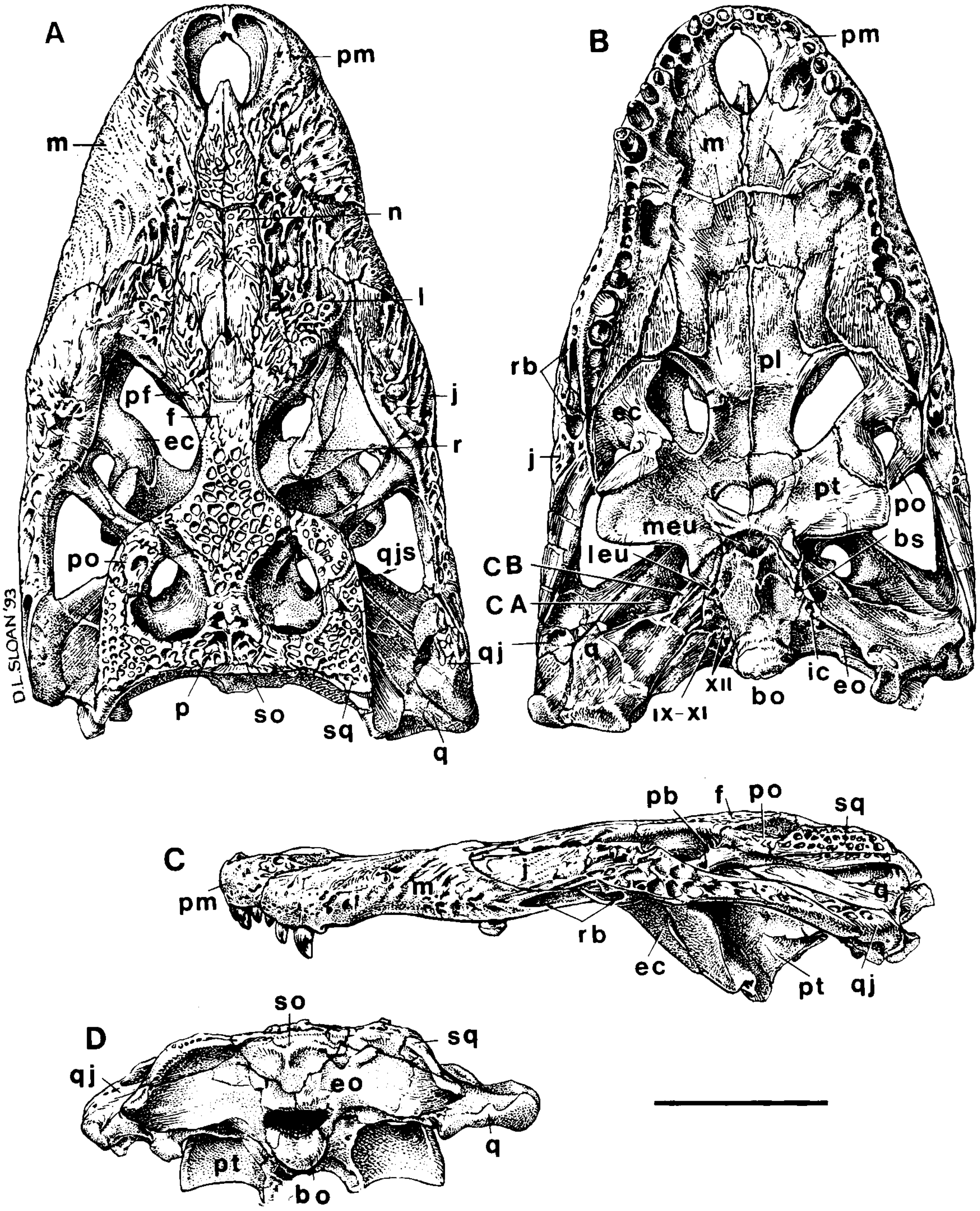
The maxilla (Text-fig. 1A–C) contacts the premaxilla, nasal, lacrimal, jugal and prefrontal. In dorsal view each maxilla is much broader than the maximum width of the nasals. In ventral view the maxilla has a broad portion lateral to the tooth row. The ventral surface of the broad palatal process forms a distinct, step-like structure medial to the last four massive crushing teeth. The elevated lateral portion of the step-like structure is heavily ornamented by fine striae.

The frontal (Text-fig. 1A) is relatively long, exceeding one-third of the skull length. The strongly convex posterior margin of the frontal contacts the postfrontal and parietal and forms a small part of the border of the supratemporal fossa. Its narrow anterior portion has a nearly straight suture with the prefrontal. The forked anterior end of the frontal extends slightly beyond the orbits. The narrow interorbital region of the frontal is about half the maximum width of the bone. The ventral surface of the frontal is not exposed, but its orbital portion, which forms the dorsomedial wall of the orbit, is less strongly concave than that of the extant species of *Alligator*.

The unpaired parietal is wider posteriorly than anteriorly (Text-fig. 1A). Both anterior and posterior margins of the parietal curve inwards. The parietal meets the postorbital posterolateral to the frontal, as in most eusuchians. Its sculpted interfenestral region is intermediate in width between that of *Albertochampsa langstoni* and *Brachychampsa montana* (Table 1).

The prefrontal is elongate and triangular in dorsal view (Text-fig. 1A). Its long, slightly convex medial side contacts the nasal and frontal. Its almost straight lateral border sutures mainly with the lacrimal and its anterior end abuts the maxilla. The prefrontal pillar is well-developed. The pillar contacts the palatine and pterygoid ventrally and meets its fellow of the opposite side, behind the space for the olfactory bulbs, by way of a median process.

The lacrimal is a more or less rectangular bone in dorsal view, with a convex anterior margin and a sharply



TEXT-FIG. 1. Skull of *Stangerochampsa mccabei* gen. et sp. nov. in dorsal (A), ventral (B), lateral (C), and occipital (D) views; RTMP.86.61.1, holotype. Abbreviations: bo, basioccipital; bs, basisphenoid; CA, Crest A; CB, Crest B; ec, ectopterygoid; eo, exoccipital; f, frontal; ic, foramen for internal carotid artery; j, jugal; l, lacrimal; leu, foramen for lateral branch of eustachian tube; m, maxilla; meu, foramen for medial branch of eustachian tube; n, nasal; p, parietal; pf, prefrontal; pb, bump just above postorbital/jugal suture; pl, palatine, pm,

TABLE 1. Measurements (in mm) of the skull of *Stangerochampsa mccabei* gen. et sp. nov.

feature	measurement
Length of skull, from tip of snout to posterior edge of cranial table	195
Length of skull, from tip of snout to posterior end of occipital condyle	200·3
Maximal width of skull, across quadratojugals	130
Length of snout	100
Length of post-snout region of skull, from anterior border of orbit to posterior edge of cranial table	95
Maximal width of snout	114
Maximal length of naris	28
Maximal width of naris	25
Maximal length of right orbit	50
Maximal width of right orbit	40·5
Interorbital width	17
Length of cranial table, through centre of supratemporal fenestrae	45
Width of cranial table, across centres of supratemporal fenestrae	75
Maximal length of supratemporal fenestra	30·2
Maximal width of supratemporal fenestra	20·5
Interfenestral width	11
Length of ventral border of left infratemporal fenestra	30
Length of anterior border of left infratemporal fenestra	26·5
Length of posterior border of left infratemporal fenestra	27
Length of incisive foramen	23
Width of incisive foramen	16·5
Length of long axis of left suborbital fenestra	35
Length of short axis of left suborbital fenestra	15·5
Maximal width of choanae	21·2
Maximal length of choanae	14·5
Interfenestral width of palatines	25
Width across pterygoid flanges	84·2
Length of mandible, from anterior tip of dentary to posterior tip of angular	232
Length of mandible, from anterior tip of dentary to posterior edge of articular fossa	212
Maximal depth of mandible	41
Length of symphysis	36·5
Depth of symphysis	12
Length of splenial in symphysis	3·3
Length of long axis of external mandibular fenestra	28·3
Length of short axis of external mandibular fenestra	13

incurved posterior orbital edge (Text-fig. 1A). It is excluded from the nasal by the maxilla/prefrontal contact. Its elongate posteroventral process reaches the midpoint of the ventral border of the orbit. The lacrimal foramen is situated close to the suture of the lacrimal with the prefrontal.

The jugal (Text-fig. 1A–C) has a relatively broad anterior process and a posterior process that is as long as the anterior one. The jugal/lacrimal suture is almost equal in length to the ventral border of the orbit. The ascending process of the jugal tapers dorsally, and interlocks with the descending process of the postorbital.

The postorbital has a remarkably rounded anterolateral border (Text-fig. 1A). An additional posterodorsal process (posterior descending process; Iordansky 1973) is retained, as is the contact of this process with the anterodorsal process of the quadratojugal along the posterodorsal border of the infratemporal fenestra. A weak, but distinct bump is present just dorsal to the suture of the descending process of the postorbital with the ascending process of the jugal. The descending process extends ventrally to meet the ectopterygoid at the ventral base of the postorbital bar, as in other eusuchians. A foramen for a blood vessel is located at the lateral side of the base of the descending process.

The squamosal has a relatively large posterolateral process (Text-fig. 1A). Medially, the squamosal forms almost the entire posterior border of the temporo-orbital foramen. A longitudinal groove for the attachment

---

premaxilla; po, postorbital; q, quadrate; qj, quadratojugal; qjs, quadratojugal spine; r, rib; rb, recess for blood vessels and nerves; so, supraoccipital; sq, squamosal; IX–XI, XII, foramina for cranial nerves IX–XI, XII. Scale bar represents 50 mm.

of the ear flap is clearly marked along its thickened lateral margin. In occipital view, the bone forms the dorsolateral portion of the occiput.

The quadratojugal (Text-fig. 1A–C) has a strongly curved suture with the quadrate. The quadratojugal is relatively large posterior to the infratemporal fenestra and is exposed as broadly as the quadrate and more broadly than the infratemporal bar in dorsal view. A weak, but distinct process, probably a remnant of the infratemporal spine, is present on the quadratojugal, running along the posterior margin of the infratemporal fenestra. The anterior process of the quadratojugal is elongate in ventral view, with a sharply pointed end wedging into the jugal and extending anteriorly beyond the midpoint of the ventral border of the infratemporal fenestra.

Palate. The quadrate is characterized by a distinct process arising from the lateral edge above the articular condyle on the ventral surface (Text-fig. 1B). Crest B (Iordansky 1973) is extraordinarily strongly developled. Crest A (Iordansky 1973) is weakly developed. It meets Crest B posteriorly and, together, they form a fairly strong ventral stem of a Y-shaped crest system. A depression is present on the ventral surface of the quadrate anterior and posterior to the ventral stem of the crest system. The quadrate body is broadly overlapped by the quadratojugal in dorsal view. Its dorsal process, for secondary contact with the squamosal and paroccipital process, is prominent and elongate. A ridge for the attachment of the tympanum, seen in extant alligators, is not clearly marked, but the dorsal (lateral to the external otic recess) and ventral (below the dorsal process) exits of the siphonal duct are present. On the lateral wall of the braincase the quadrate/laterosphenoid suture is strongly raised just above the trigeminal foramen. Ventral to the trigeminal foramen these two bones also meet one another, separating the pterygoid from the trigeminal foramen.

The palatine is elongate and rectangular in ventral view, with a lateral process projecting from its mid-region (Text-fig. 1B). The interfenestral portion of the palatine is as broad and long as its anterior portion (anterior to the lateral process). The lateral process of the palatine is much more strongly developed than it is in other alligatorines. The palatine/pterygoid suture is located entirely posterior to the suborbital fenestra.

The pterygoid is relatively strongly vertically oriented (Text-fig. 1B–C). Anteriorly it forms half the posterolateral border of the suborbital fenestra. The prechoanal portion of the pterygoid is much longer than the postchoanal portion. The pterygoid/ectopterygoid suture is curved, concave towards the pterygoid. No bulla is formed on the dorsal surface of the pterygoid. Dorsally, the bone is excluded from the ventral border of the lateral aperture of the trigeminal foramen by the quadrate/laterosphenoid contact. In addition, the pterygoid flange is positioned more anteriorly than that of any known alligatorine. This is indicated by the relatively great distance between the posterior edge of the transverse flange and the occipital condyle.

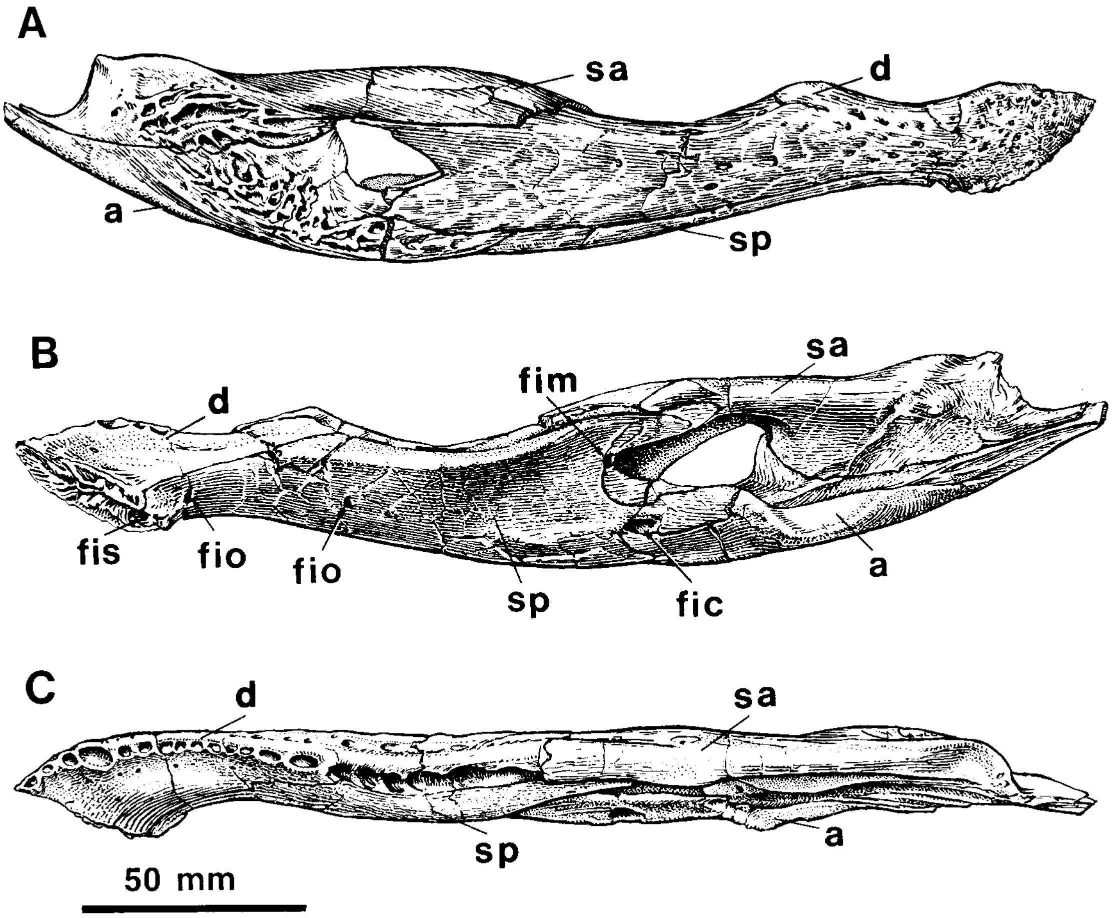
The ectopterygoid is unique in that its anterolateral process extends anteromedially along the anterior border of the suborbital fenestra and meets the lateral process of the palatine, separating the maxilla from the suborbital fenestra (Text-fig. 1B). The posterolateral process of the ectopterygoid turns medially and slightly dorsally. Its distal portion is overlapped by the descending process of the postorbital on the ventral surface of the postorbital bar. The ectopterygoid lacks a posterior jugal process, as defined by Norell (1989). Laterally, this bone does not contribute to the borders of the alveolar groove or the enlarged recess for the blood vessels and nerves. The medial process of the ectopterygoid is short but massive. It overlaps the anterodorsal half of the lateral margin of the pterygoid flange.

Braincase. The basioccipital is characterized by its extensive exposure on the ventral surface of the braincase, which results from the more horizontal orientation of the fan-shaped ventral plate (Text-fig. 1B, D). The ventral exposure of the bone is even longer than the central region of the pterygoid. The W-shaped ridge along the margin and midline of the fan-shaped ventral plate is well-developed. The occipital condyle is formed almost exclusively by the basioccipital. Two lateral and one median exits of the eustachian tube are clearly marked at the suture of this bone with the basisphenoid.

The exoccipital has a large upper portion that forms the major part of the occiput (Text-fig. 1B, D) and a lower portion that is relatively small and faces mainly ventrally. Thus, the four foramina for cranial nerves and the internal carotid artery are not visible in occipital view. The ridge between the upper and lower portions of the exoccipital becomes very strongly expressed laterally, just dorsal to the occipital extension of the cranio-quadrate canal. The median process, formed by the two exoccipitals dorsal to the foramen magnum, is strongly pronounced.

The supraoccipital is exposed on the skull roof (Text-fig. 1A, D). It is triangular in occipital view. A median ridge is weakly developed and does not run along the entire depth of the bone.

The laterosphenoid is well-exposed on both sides of the braincase. It possesses a shallow but distinct groove on the lateral surface of its anteromedial portion. This groove is anterodorsally-posteroventrally oriented,



TEXT-FIG. 2. Right mandible of *Stangerochampsa mccabei* gen. et sp. nov. in lateral (A), medial (B), and dorsal (C) views; RTMP.86.61.1, holotype. Abbreviations: a, angular; d, dentary; fic, foramen intermandibularis caudalis; fim, foramen intermandibularis medius; fio, foramen intermandibularis oralis; fis, foramen for ramus intermandibularis oralis of trigeminal nerve within symphysis; sa, surangular; sp, splenial.

extending from the dorsal condylar process to the trigeminal foramen. Such a groove in the laterosphenoid has not been reported in any other crocodyliforms. In other features, the bone shows no important differences from that of other eusuchians.

The prootic is only visible through the lateral aperture of the trigeminal foramen.

Mandible. The mandible (Text-fig. 2) is relatively straight, lacking a distinct ventral curve of its ventral margin. The anterior portion of the mandible is quite deep. The symphysis is relatively long, reaching posteriorly to the level of dentary tooth 9. The external mandibular fenestra is small, triangular in outline, and is enclosed only by the dentary and angular.

The dentary is, at most, 68 per cent. of the length of the mandible and has a strongly festooned dorsal margin (Text-fig. 2). Laterally, the anterior portion bears small, but deep, sculpted pits, in contrast to the very shallow grooves on the posterior portion. The dentaries form the major portion of the symphysis. The dorsal process of the forked posterior end of the dentary is longer than the ventral process. It meets the angular at the posterodorsal corner of the external mandibular fenestra, as indicated by the sutural mark on the medial surface of the surangular. The ventral process overlaps the angular extensively.

The splenial is half the length of the mandible (Text-fig. 2B). Its narrow anterior portion turns inward and contributes a small part to the symphysis. Two foramina for the ramus intermandibularis oralis of the trigeminal nerve are present on the lingual surface of the splenial. One is located in the middle region and the other is situated anteriorly, close to the symphysis. Within the symphysis, an additional foramen for the branch of the trigeminal nerve is present between the splenial and dentary. Dorsally, the splenial forms the medial wall of the alveolar groove and the individual sockets posterior to the fourteenth tooth on the right side and the thirteenth tooth on the left side. In the region of the massive crushing teeth (the last four), the dorsal surface of the splenial is extremely broadened, being as broad as that of the dentary. Thus, this region greatly overhangs the ventral portion of the bone, as it does in most alligatorines. Anterior to this region, the lingual surface of the bone is convex. Ventrally, the splenial forms the entire ventral border of the mandible anterior to the foramen intermandibularis caudalis.

The surangular lacks both extremities, but would have been about as long as the splenial (Text-fig. 2). It has a distinct convex-concave dorsal margin. A knob-like process along the dorsomedial margin opposes the pterygoid flange when the jaws are closed. Anteriorly, the surangular overlaps the dentary and ends just posterior to the tooth row. The thin posterodorsal portion lateral to the articular fossa of the articular rises upwards. The long, sharp posterior process ends near the posterior tip of the retroarticular process. The lateral suture of the bone curves anterodorsally. Posterior to the external mandibular fenestra, the bone is overlapped extensively by the angular.

The angular is slightly longer than the surangular, attaining 54 per cent. of the mandibular length (Text-fig. 2A). When in articulation, a pronounced dorsal process is present just posterior to the external mandibular fenestra in both lateral and medial views. This process forms the entire posterior border of the external mandibular fenestra. The dorsal contact of the process with the dentary separates the surangular from the border of the external mandibular fenestra. Anteriorly the angular is extensively wedged between the dentary and splenial. Anteromedially it, together with the splenial, encloses the foramen for the ramus intermandibularis caudalis of the trigeminal nerve. Posterior to the foramen, the buttress-like process for the pterygoid flange is strongly developed. The elongate posterior process is stronger than that of the surangular, and together with the latter, covers the lateral surface of the retroarticular process of the articular.

The coronoid is most probably a semicircular ring-like bone, as indicated by the articular facet on the lingual surface of the splenial, angular, and surangular (Text-fig. 2B). A foramen for the ramus intermandibularis medius of the trigeminal nerve is present between the coronoid and splenial.

The articular, as indicated by the pattern of articular faces on the medial surfaces of the surangular and angular (Text-fig. 2B), probably differs little from that of other alligatorines.

Dentition. Teeth of the upper and lower jaws are heterodont, with conical teeth anteriorly and four massive crushing teeth posteriorly. The teeth of the middle region of the upper jaw are similar to the unworn posterior teeth in having a strongly necked crown and a more or less round upper portion. All teeth have fine, radiating striae on their crowns.

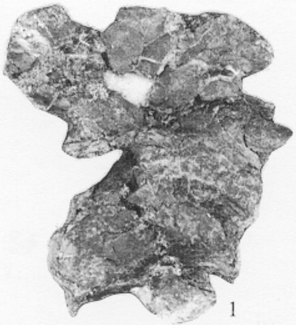
The left premaxillary dentition is complete, consisting of five teeth (Text-fig. 1B). The fourth premaxillary tooth is the largest; the others are all about the same size.

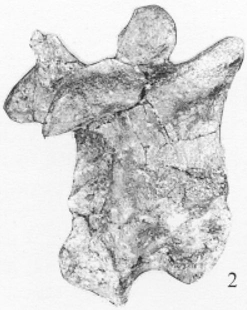
The maxillary dentition has 14 teeth (counting nine unoccupied tooth sockets) on the left side, but 15 teeth on the right (including six unoccupied tooth sockets). The fourth maxillary tooth is the largest and the third is slightly smaller (Text-fig. 1B). There are seven (right) or six (left) small teeth between the fourth tooth and the first crushing tooth. These teeth become larger posteriorly. The four crushing teeth are implanted in a common alveolar groove. One (right) or two (left) more anterior teeth are incorporated in the common groove. From the right side, it appears that only two of the four crushing teeth were functional in life, as suggested by their broad, worn surface. The entire upper dentition has 20 (right) or 19 (left) teeth, with the last one-and-a-half teeth located posterior to the anterior border of the suborbital fenestra.

EXPLANATION OF PLATE 1

Figs 1–9. Vertebrae of *Stangerochampsa mccabei* gen. et sp. nov.; RTMP.86.61.1, holotype. 1, axis in right lateral view; 2–3, cervical 3 in right lateral and ventral views, respectively; 4, cervical 4 in right lateral view; 5, an anterior dorsal in right lateral view; 6, a posterior dorsal in right lateral view; 7, a posterior dorsal in dorsal view; 8–9, sacral 1 in dorsal and ventral views. All × 0·95.

PLATE 1


1


2

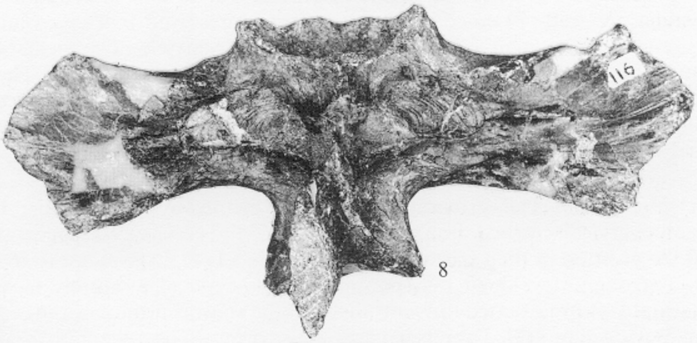

3

4

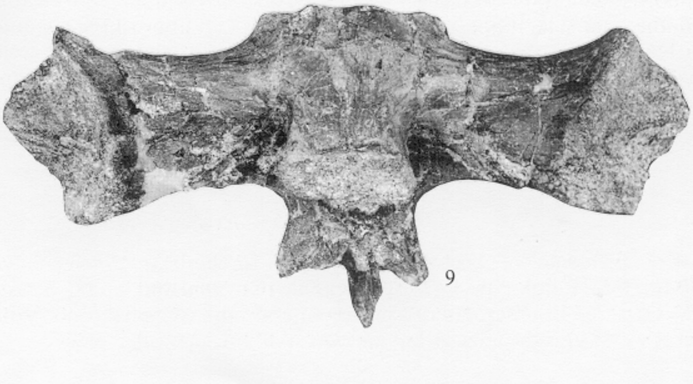

5


6

7



8


9

WU *et al.*, *Stangerochampsa mccabei*

TABLE 2. Measurements (in mm) of girdle and limb elements of *Stangerochampsa mccabei* gen. et sp. nov.

feature	measurement	feature	measurement
Maximal length of preserved portion of right scapula	74	Length of left ulna	83
		Length of right radius	70
Maximal width of preserved portion of right scapula	40·5	Length of left radius	70
		Length of metacarpal IV	26·9
Maximal length of preserved portion of left scapula	74·5	Maximal depth of left ilium	46·6
		Maximal length of right pubis	70
Maximal width of preserved portion of left scapula	35·5	Maximal width of ventral expansion of right pubis	41
Length of preserved portion of interclavicle	91·6	Length of left femur	142
		Length of right metatarsal II	59·5
Estimated length of interclavicle	97	Length of right metatarsal III	69
Length of right humerus	107	Length of right metatarsal IV	59
Length of right ulna	80		

No dentary teeth are preserved (Text-fig. 2c). The dentary dentition consisted probably, as suggested by tooth sockets, of 20 teeth on the right side and 19 on the left. Tooth sockets indicate that dentary teeth 4, and 13 (left) or 14 (right) were much larger than the others. Eight (left) or nine (right) small tooth sockets are present between dentary teeth 4, and 13 or 14, respectively. The last tooth of the small set is distinctly larger than the others. Teeth between dentary tooth 13 or 14 and the first crushing tooth become gradually larger and, together with the crushing teeth, are implanted in a common alveolar groove on both sides.

Postcranial Skeleton

The postcranial skeleton was largely disarticulated. Seventeen vertebrae are almost complete. Ten ribs and 12 gastralia are well-preserved. The one chevron preserved lacks its ventral portion. The pectoral girdles are respresented by a pair of scapulae and the interclavicle. The elements of the forelimbs include the right humerus, two radii, two ulnae, one metacarpal and one phalanx. The pelvic girdle lacks both ischia. The hindlimb is represented by the left femur, left calcaneum, three right metatarsals, and one phalanx. More than 100 dorsal osteoderms and ten ventral osteoderms are preserved. Measurements of postcranial elements are listed in Table 2.

Vertebral column. The vertebral column is represented by five cervicals, six dorsals, one sacral, and five caudals. The five cervicals include the axis, cervicals 3–5, and cervical 9, recognizable by the configuration of their spines and the position of their parapophyses (Pl. 1, figs 1–4). In contrast to that of any known alligatorines, the axis has a strongly developed hypapophysis, while cervical 3 entirely lacks a hypapophysis. In cervical 3, the parapophyses are situated far ventrally, and the ventral surface of the centrum is smoothly concave rather than convex, ridged or keeled as it is in other alligatorines. The hypapophyses on cervicals 4, 5 and 9 are very strong.

The presence of a strong hypapophysis indicates that one of the six dorsals is from the anterior section (Pl. 1, fig. 5). The remaining dorsals are from the posterior section as suggested by the morphology and position of the articular facets for ribs (Pl. 1, figs 6–7). These posterior dorsals are more massive than the anterior dorsal and cervicals, and their centra have a smooth ventral surface. The sacral vertebra is determined to be the first,

---

EXPLANATION OF PLATE 2

Figs 1–9. Elements of pectoral girdle and forelimb of *Stangerochampsa mccabei* gen. et sp. nov.; RTMP.86.61.1, holotype. 1–2, right scapula in medial and lateral views; 3, interclavicle in lateral view; 4–7, right humerus in anterolateral, posterolateral, anteromedial, and posteromedial views; 8, right radius in lateral view; 9, right ulna in lateral view. All × 1.


1


2


3


4


5


6


7


8


9

WU *et al.*, *Stangerochampsa mccabei*

on the basis of its articulation with the sacral rib (Pl. 1, figs 8–9). It is amphicoelous, and its centrum has a flat ventral surface. Its neural spine is broad and low and is taller posteriorly than anteriorly.

The five caudals all have well-developed transverse processes. One, probably from the anterior region of the tail, is relatively massive and short and has a weak, but distinct, median ridge along its ventral midline. The remaining four caudals, probably from the middle section, have a longitudinal groove on the ventral surface. This groove is deeper posteriorly than anteriorly in each caudal, and is relatively deeper in the most posterior caudals.

Ribs and chevron. Of the preserved ribs, seven are from the cervical region. These include the first pair, four from pairs 3–5, and one from pair 9. The first cervical rib is similar to that of extant alligatorines, differing only in that the lateral surface is more convex anteriorly and more concave posteriorly. This rib extends posteroventrally and ends at the middle of the fourth cervical vertebra. Cervical rib 9 resembles the anterior dorsal ribs, differing only in that its shaft is shorter and its dorsal ridge is much stronger. The five dorsal ribs come probably from the first five dorsal vertebrae, judging from differences in the position of the parapophyses and configuration of the dorsal ridges. The first sacral rib is still articulated with the sacral vertebra (Pl. 1, figs 8–9), and is very similar to that of later alligatorines. The preserved chevron is represented by its dorsal portion. The foramen for the blood vessel is transversely narrow but dorsoventrally deep.

Gastralia. Among the preserved gastralia, the last pair are massive and have a characteristic spatula-shaped end. The remaining gastralia are very slender, but also have an expanded end.

Pectoral girdle and forelimbs. The scapula (Pl. 2, figs 1–2) is longer than the radius. The broadened dorsal border is about three times as wide as the narrowest region of the shaft of the bone. The acromial crest on the ventrolateral surface is very strong. The scapula expands anteriorly beyond the acromial crest. A pronounced knob-like process for the attachment of the *caput scapulae* of the *M. triceps brachii* is present. Ventral to the process and acromial crest, the lateral surface of the scapula is deeply concave. In addition, a bump situated at the midpoint of the posteromedial margin of the bone probably marks the insertion of the scapular branch of the *caput coracoideum* of the *M. triceps brachii.*

The interclavicle (Pl. 2, fig. 3) lacks only its anterior tip. Its anterior end and middle region are relatively broad so the anterior portion of the shaft is strongly necked.

The right humerus is complete (Pl. 2, figs 4–7). The bone is relatively short, being about 76 per cent. of the length of the femur. The ridge-like scar of the *M. teres major*, extending from the head onto the shaft along the anterolateral margin of the bone, is strongly developed.

The radius and ulna (Pl. 2, figs 8–9) show no obvious differences from those of fossil or extant alligatorines.

The foot is represented by a single metacarpal, probably the fourth, and a single, probably penultimate, phalanx.

Pelvic girdle and hindlimbs. The right ilium is almost complete (Pl. 3, figs 1–2). The posterior process of the ilium is relatively broad and the anterior process is pronounced. Dorsally, the iliac blade turns medially so that its medial surface is strongly concave.

The complete right pubis (Pl. 3, fig. 3) differs from that of later alligatorines in that its shaft is relatively much shorter, and its broad distal portion extends more proximally.

The femur (Pl. 3, figs 4–6) resembles that of later alligatorines but is proportionally longer, when compared with the radius, than in the extant species of *Alligator.* On the dorsolateral surface the scars of the *M. puboischiofemoralis internus*, *M. iliofemoralis*, and *M. ischiotrochantericus* are strongly developed.

The left calcaneum (Pl. 3, figs 8–9) is almost identical to that of the extant species of *Alligator.* Two foramina (one small) are seen on the bottom of the socket for the astragalus, and three small foramina are present on the lateral surface.

EXPLANATION OF PLATE 3

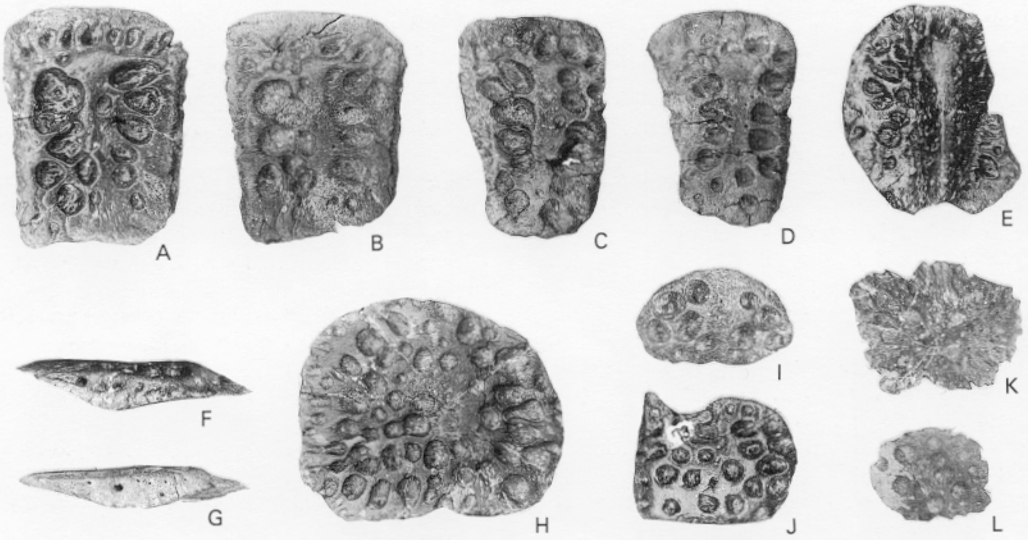
Figs 1–9. Elements of pelvic girdle and hindlimbs of *Stangerochampsa mccabei* gen. et sp. nov.; RTMP.86.61.1, holotype. 1–2, right ilium in lateral and medial views; 3, right pubis in lateral view; 4–6, left femur in lateral, medial and posterior views; 7, right metatarsal II in dorsal view; 8–9, left calcaneum in dorsal and ventral views. All × 1.

PLATE 3

WU *et al.*, *Stangerochampsa mccabei*

The three metatarsals (II–IV) are from the right foot, on the basis of the overlapping facet on the dorsomedial surface. Metatarsal II (Pl. 3, fig. 7) is the longest and most massive. The preserved phalanx is short but very massive when compared with these metatarsals. It is probably the first phalanx of the first digit.

Osteoderms. Of the preserved dorsal osteoderms, 98 are almost complete. Osteoderms from the medial rows of the trunk and anterior portion of the tail are rectangular in outline, with a slightly narrowed posterior border and a very weak dorsomedian ridge (Text-fig. 3A–B). A sutural facet is present on both lateral and medial sides and an overlapping facet is present along the anterodorsal margin. As in other early eusuchians, and unlike the situation in most non-eusuchian crocodyliforms, the overlapping facet of the dorsal osteoderms does not rise to form an elevated anterodorsal margin, but is very thin and grades smoothly into the sculpted posterior portion (Text-fig. 3F–G). Osteoderms from the more lateral rows of the trunk and anterior portion of the tail are much longer than wide and usually broader anteriorly than posteriorly (Text-fig. 3C–D). These osteoderms have a stronger median ridge, a sutural facet on both sides, and an overlapping facet anterodorsally. Osteoderms from the flank row of the trunk and tail are more or less triangular in outline or have a round lateral border. A sutural facet is present only on the medial side and most do not have an overlapping facet along the anterodorsal margin. An osteoderm, probably from the first transverse row of the trunk, is strongly keeled, but lacks a sutural facet on both sides and an overlapping facet anterodorsally (Text-fig. 3E).



TEXT-FIG. 3. Osteoderms of *Stangerochampsa mccabei* gen. et sp. nov.; RTMP.86.61.1, holotype. A–B, dorsal trunk osteoderms from medial rows in dorsal view; C–D, dorsal trunk osteoderms from lateral rows in dorsal view; E, a dorsal trunk osteoderm from the first transverse row in dorsal view; F–G, dorsal trunk osteoderms in side views (anterior to right); H, a large dorsal neck osteoderm from right side in dorsal view; I, small dorsal neck osteoderm in dorsal view; J, dorsal neck osteoderm from right side in dorsal view; K–L, two ventral osteoderms in lateral views. All × 1.

Eight osteoderms from the neck region are present. They are distinctive in being wider than long and in having no distinct dorsomedian ridge and no overlapping facet along the anterodorsal margin (Text-fig. 3H–J). They are either laterally, or both laterally and posteriorly, rounded. A sutural facet is present only on the medial side, which indicates that two longitudinal rows of osteoderms were present in the neck region, as in other alligatorines. Two of the eight cervical osteoderms are very small, elliptical in outline, and may be from

TABLE 3. List of taxa considered in the present analysis. * indicates that original specimens were studied directly.

Goniopholis: *G. lucasii*, *AMNH 5782, Upper Jurassic Morrison Formation, Colorado, North America (*Amphicotylus lucasii* Mook, 1942*a*).
Sunosuchus: *S.* sp., *IVPP 10606–611, Upper Jurassic Qigu Formation, Xinjiang, China (Wu *et al.* in press); *S. miaoi*, Middle Jurassic (previously Upper Jurassic, Sun *et al.* 1992) Xiangtung Formation, Gansu, China (Young 1948; Buffetaut 1986).
Shamosuchus: *S. djadochtaensis*, *AMNH 6412, Upper Cretaceous Djadochta Formation, Mongolia (Mook 1924); *Shamosuchus* spp. (Efimov, 1988).
Bernissartia: *B. fagesii*, Lower Cretaceous Bernissart Clay (Wealden Formation), Belgium (Norell and Clark 1990); Upper Cretaceous, Barremian, Galve, Spain (Buscalioni and Sanz 1990).
Leidyosuchus: *L. canadensis*, *ROM 1903 (Lambe 1908) and *L. gilmorei*, *AMNH 5352, Upper Cretaceous Judith River Group, Alberta, Canada (Mook 1942*b*); *Leidyosuchus* sp., *RTMP 86.221.1, Upper Cretaceous Judith River Group, Alberta, Canada; *L. formidabilis*, Paleocene Tongue River Formation, North Dakota, North America (Erickson 1976).
Crocodylinae: *Crocodilus americanus*, *AMNH 7121; *C. niloticus*, *AMNH 10081; *C. affinis*, *YPM 1345, Middle Eocene Bridger Beds, Wyoming (Marsh 1871); *Brachyuranochampsa eversolei*, *AMNH 4993, Eocene Middle Washakie, Wyoming (Zangerl 1944); (Iordansky 1973; Mook 1921*b*, 1921*c*).
Prodiplocynodon: *P. langi*, *AMNH 108 (cast), Upper Cretaceous Lance Formation, Wyoming, North America (Mook 1941*a*).
Brachychampsa: *B. montana*, *AMNH 5032 (Gilmore 1911); *UCMP V133901, Upper Cretaceous Hell Creek Formation, Montana, North America (Norell *et al.* 1994); Upper Cretaceous Hell Creek Formation, South Dakota, North America (Carpenter and Lindsey 1980).
Albertochampsa: *A. langstoni*, *RTMP 81.46.1 (cast), Upper Cretaceous Dinosaur Park Formation, Alberta, Canada (Erickson 1972).
Hylaeochampsa: *H. vectiana*, Lower Cretaceous Wealden Formation, Isle of Wight (Clark and Norell 1992).
Wannaganosuchus: *W. brachymanus*, Upper Paleocene Tongue River Formation, North Dakota, North America (Erickson 1982).
Allognathosuchus: *A. mooki*, *AMNH 6780, Eocene Puerco Formation, New Mexico, North America (Simpson 1930); *Allognathosuchus* sp. *YPM: PU 17111, 7472, 3964, 8383. *A. polyodon*, Eocene Wasatch Beds, North America (Mook 1921*a*).
Ceratosuchus: *C. burdoshi*, *FMNH 15576, Upper Paleocene Plateau Valley Beds, Colorado, North America (Schmidt 1938).
Alligator prenasalis: Lower Oligocene, South Dakota, North America (Mook 1932).
Procaimanoidea: *P. utahensis*, *USNM 15997, Upper Eocene Uinta Formation, Utah, North America (Gilmore 1946). *P. kayi*, Middle Eocene, Bridger Beds, Wyoming, North America (*Hassiacosuchus kayi* Mook 1941*b*).
Alligator mcgrewi: Lower Miocene Marseland Formation, Nebraska (Schmidt 1941); *AMNH 8700, Lower Miocene Marseland Formation, Nebraska, North America.
Alligator thomsoni: Middle Miocene Snake Formation, Nebraska, North America (Mook 1923).
Alligator mefferdi: Middle Pliocene Ash Hollow Formation, Nebraska, North America (Mook 1946).
Alligator mississippiensis: *RTMP 84.182.2, 84.183.18, 90.7.104.
Alligator spp: *A. luicus*, Middle Miocene Shanwang Formation, Shandong, China (Li and Wang 1987); *A. sinensis* (Cong *et al.* in press).

the anterior portion of the neck (Text-fig. 3I–J). The remaining six, two of which are very large (Text-fig. 3H), are assumed to be from the four continuous transverse rows in the posterior region of the neck.

The ventral osteoderms are irregular in outline and variable in size (Text-fig. 3K–L). They are very thin and bear a sculpting of small and shallow pits. Their sculpted lateral surface is flat, but their medial surface is convex.

TABLE 4. Characters employed in the phylogenetic analysis. 0, primitive state; 1, derived state.

1. Premaxillae longitudinally narrow anterior to naris (0); wide, broadly overhanging nasal capsule (1).
2. Distinct lateral constriction between premaxilla and maxilla present (0); absent (1) (modified from Clark *in* Benton and Clark 1988).
3. Nares undivided or partially divided (0); fully divided (1) (modified from Clark *in* Benton and Clark 1988).
4. Nasal excluded from naris (0); entering into naris (1) (modified from Clark *in* Benton and Clark 1988).
5. Nasal ending posteriorly well before orbit (0); beyond, or at level of anterior borders of orbits (1).
6. Nasal/lacrimal contact present (0); absent (1) (Clark *in* Benton and Clark 1988).
7. Nasal/premaxillary suture shorter than nasal/maxillary suture (0); almost as long as the latter (1).
8. Two nasals narrower than each maxilla in dorsal view (0); broader than each maxilla (1).
9. Snout longer than wide (0); wider than long (1).
10. Snout longer than postorbital region (0), shorter than postorbital region (1).
11. Dorsal border of orbit flat (0); ridged (1) (modified from Buscalioni and Sanz 1990).
12. Lacrimal narrow and elongate (0); short and broad (1) (modified from Clark *in* Benton and Clark 1988).
13. Posteroventral process of lacrimal short (0); reaching midway along ventral border of orbit (1).
14. Lacrimal/jugal suture as long as or longer than ventral border of orbit (0); much shorter than ventral border of orbit (1).
15. Anterior and posterior processes of jugal different in length (0); similar (1).
16. Anterior process of quadratojugal absent or very short (0); long, reaching half-way along lower temporal bar (1) (modified from Norell 1989).
17. Quadratojugal spine pronounced (0); knob-like or absent (1) (modified from Norell, 1989).
18. Quadratojugal/quadrate suture slightly curved (0); strongly curved posteroventrally (1).
19. Posterodorsal process of postorbital present (0); absent (1) (Norell 1989).
20. Postorbital not forming supratemporal fossa (0); formaing supratemporal fossa (1).
21. Postorbital/parietal contact posterolateral to frontal absent (0); present (1) (Clark and Norell 1992).
22. Postorbital/ectopterygoid contact absent (0); present (1).
23. Skull table more or less square anterolaterally (0); strongly rounded (1).
24. Incisive foramen small (0); very large (1).
25. Incisive foramen enclosed by premaxillae and maxillae (0); entirely located within premaxillae (1).
26. Palatine/pterygoid suture situated before posterior edge of suborbital fenestra (0); entirely behind suborbital fenestra (1).
27. Portion of palatine anterior to lateral process short (0); as long as interfenestral portion (1).
28. Maxilla very narrow lateral to tooth row in ventral view (0); broad (1).
29. Choana located anteriorly, across level of posterior borders of suborbital fenestrae (0); positioned posteriorly, almost behind suborbital fenestrae (1) (modified from Clark *in* Benton and Clark 1988).
30. Choana situated between palatines and pterygoids (0); entirely within pterygoids (1) (Clark *in* Benton and Clark 1988).
31. Supraoccipital not exposed on skull roof (0); exposed (1).
32. Surangular forming border of external mandibular fenestra (0); excluded from external mandibular fenestra (1).
33. Splenial forming medial walls of a few posterior-most tooth sockets, less than 25 per cent. of length of tooth row (0); largely forming medial walls of posterior 7–9 tooth sockets or groove, more than 40 per cent. of length of tooth row (1).
34. Dorsal surface of splenial portion of medial walls of tooth sockets or groove narrow (0); very wide, as broad as that of lateral walls (1).
35. Three or more teeth present posterior to anterior border of suborbital fenestra (0); two or fewer teeth present posterior to anterior border of suborbital fenestra (1).
36. Posterior four or five massive crushing teeth absent (0); present (1) (modified from Clark *in* Benton and Clark 1988).
37. A few teeth present between dentary tooth 4 and tooth at the second peak of sinusoidal waves (0); eight or nine small teeth between dentary tooth 4 and dentary tooth 13 or 14 at the second peak of sinusoidal waves present (1).

TABLE 4. (*cont.*)

38. The fifth maxillary tooth as large as, or larger than the fourth (0); the fourth tooth largest, the fifth tooth much smaller than the fourth (1).
39. Hypapophysis of cervical vertebrae weak or absent (0); strong (1) (Clark *in* Benton and Clark 1988).
40. Posterior iliac process at same level as anterior iliac process (0); above level of anterior iliac process (1) (Buscalioni and Sanz 1990).
41. Anterior iliac process pronounced or small but distinct (0); knob-like or almost absent (1) (modified from Clark *in* Benton and Clark 1988).
42. Cervical rib 1 without a mid-posterior expansion (0); having a mid-posterior expansion (1).
43. Cervical rib 2 single-headed (0); double-headed (1).
44. Two longitudinal rows of dorsal osteoderms with anterolateral pegs (0); more than two longitudinal rows of osteoderms without anterolateral pegs (1) (modified from Clark *in* Benton and Clark 1988).
45. Dorsal osteoderms of trunk overlapped (0); not overlapped (1) (modified from Clark *in* Benton and Clark 1988).
46. Anterodorsal margin of dorsal trunk osteoderms for overlapping distinctly elevated (0); not elevated but smoothly continuing to sculpted posterior portion (1) (modified from Norell and Clark 1990).

PHYLOGENETIC RELATIONSHIPS

In order to interpret the phylogenetic position of *Stangerochampsa* within the Eusuchia, a phylogenetic analysis of *Stangerochampsa*, six Mesozoic and nine Cenozoic eusuchians has been undertaken (see Tables 3, 5). These taxa were selected because of the availability of original specimens or because good illustrations have been published (Table 3). As in Norell's study (1989), the Crocodylinae is treated as a single taxon. The outgroups used to polarize character-states are *Bernissartia*, *Shamosuchus*, *Goniopholis* and *Sunosuchus*. Most recent studies of *Bernissartia* (Buscalioni and Sanz 1990; Norell and Clark 1990), strongly support Clark's (*in* Benton and Clark 1988) hypothesis that this taxon is one of the closest sister groups of the Eusuchia among the neosuchians that are represented by relatively complete specimens. However, the phylogenetic relationships between *Bernissartia* and *Shamosuchus* are unresolved (Clark *in* Benton and Clark 1988), so both are included as outgroups. *Goniopholis* and *Sunosuchus*, both members of the Goniopholidae (Wu *et al.* in press), are used as more remote outgroups. These four genera are treated separately in scoring characters, in contrast with previous studies (Norell 1989; Willis 1993) in which the relevant taxa were combined to form two outgroups in scoring each character.

The data matrix is based on direct observation of 13 of the 20 included taxa. Published descriptions were relied on for the remaining seven taxa (see Table 3). Some anatomical features have been reinterpreted on the basis of restudy of original material. Gilmore (1911) reconstructed the premaxillae of *Brachychampsa montana* as meeting on the midline posterior to the incisive foramen, and Erickson (1972) followed this reconstruction in his interpretation of the palate of *Albertochampsa langstoni*. However, a new skull of *B. montana* (UCMP V133901) and re-examination of the original type specimen shows that the premaxilla is similar to that of *Stangerochampsa mccabei* in both configuration and relationship to the incisive foramen. We believe that the two premaxillae are most probably separated by the palatal processes of the maxillae posterior to the large incisive foramen in *A. langstoini* as well. Clark and Norell (1992) mentioned in the diagnosis of *Hylaeochampsa vectiana* that the ectopterygoid contacts the palatine anteriorly in that species. However, the relevant portion is incomplete in that taxon and no such contact is indicated in their figures and descriptions.

This analysis is based on 46 characters (Tables 4–5). Three-fifths of the characters are new, the remainder are derived or modified from those used in previous studies (Clark *in* Benton and Clark

TABLE 5. The distribution of 46 characters among the 20 taxa considered in this analysis. Characters are listed numerically to correspond with Table 3. '0', primitive; '1', derived; '?', missing or uncertain; 'N', not applicable. '%', indicates the completeness of the 20 taxa, measured as the percentage of the 45 characters scored for a taxon.

		1	1	2	2	3	3	4	4		
	12345	67890	12345	67890	12345	67890	12345	67890	12345	6	%
Outgroups											
Goniopholis	00000	00000	00000	000?0	00000	00000	00000	00000	0??00	0	93·5
Sunosuchus	00000	10000	00000	0?000	00000	00000	00000	00000	00000	0	97·8
Shamosuchus	00001	00000	00000	0?0?1	0?001	01010	0N000	0000?	?????	?	76·1
Bernissartia	00011	00000	11000	00000	01001	00010	0N000	1?000	0??10	0	91·3
Ingroups											
Hylaeochampsa	????1	1??0?	1110?	??011	110??	00011	1???1	?????	?????	?	43·4
Leidyosuchus	00000	00000	00000	00010	01001	00011	10000	00011	01110	1	100
Prodiplocynodon	00010	00000	00010	0?010	11001	00011	1???0	000??	?????	?	73·9
Albertochampsa	01011	01000	01100	0?0?1	11110	01111	1???1	1?1??	?????	?	69·7
Brachychampsa	01011	11010	01101	11101	11110	10111	10111	110??	?????	?	82·6
Stangerochampsa	01011	11010	01101	11101	11110	11111	11111	11111	01110	1	100
Wannaganosuchus	01011	10011	01010	??0?1	1?001	??011	??111	11111	01110	1	82·6
Allognathosuchus	01010	11011	01011	010?1	11001	00011	11111	111??	???10	1	87·0
Ceratosuchus	010??	?0010	0????	?????	??00?	??011	????1	??1??	?????	?	32·6
Procaimanoidea	01010	10101	01010	010?1	1?001	00011	001?0	111??	?????	?	76·1
Alligator mcgrewi	01010	10111	01010	010?1	11000	10011	01110	111??	?????	?	80·4
A. prenasalis	01011	10000	01010	0?0?1	11001	10011	101?0	11111	1????	?	82·6
A. thomsoni	11010	10000	11010	110?1	11001	?0011	001?0	111??	?????	?	76·1
A. mefferdi	11110	10000	11010	01001	11001	10011	00110	111??	???10	1	89·1
A. mississippiensis	11110	10000	11010	01001	11001	00011	00010	11111	11111	1	100
Crocodylinae	10010	00000	00000	00010	11001	00011	10000	00011	01111	1	100

1988; Norell 1989; Buscalioni and Sanz 1990; Norell and Clark 1990). Many characters in previous studies were modified by changing the character polarity. This is a result of restricting the outgroup comparisons to the four closest sister groups of the Eusuchia rather than using all crocodylomorphs. The genera that are multispecific, such as *Leidyosuchus*, *Allognathosuchus* and *Goniopholis*, are assumed to be monophyletic. Since there is no established phylogeny of the species in these genera, where both primitive and derived characters occur, the primitive character state is scored for the genus. The resulting data matrix was analysed by using PAUP (version 3.1.1; Swofford 1993). A list of characters applying to each node and the terminal taxa can be found in Text-figure 4. However, we emphasize that this is a very preliminary study because (1), it has not been demonstrated that multispecific taxa are monophyletic and (2), some Cenozoic taxa represented by well-preserved material, such as *Diplocynodon*, are not included.

Results and Discussion

The analysis of the present data matrix produces two equally parsimonious cladograms (tree length = 81, consistency index = 0·581, and retention index = 0·781). As shown in the strict consensus cladogram (Text-fig. 4), the two cladograms are congruent in the following points:

1. The monophyly of the Eusuchia is supported. It is defined here by five unequivocal characters; choana situated entirely within pterygoid (Character 30); supraoccipital exposed on skull

roof (character 31); presence of strong hypapophysis on cervical vertebrae (character 39); posterior iliac process above level of anterior iliac process (character 40); and anterodorsal margin of dorsal trunk osteoderms for overlapping not elevated, but smoothly continuing to sculpted posterior portion (character 46). These characters, except for character 31, were also considered to be synapomorphies of the Eusuchia in previous studies (Clark *in* Benton and Clark 1988; Buscalioni and Sanz 1990; Norell and Clark 1990; Wu and Brinkman 1993). Character 31 is included here because the presence of the primitive state in some ingroups is interpreted as a reversal and it is unequivocally primitive in all outgroups. Character 42 (cervical rib 1 with a mid-posterior expansion) and character 43 (cervical rib 2 double-headed) may also be synapomorphies of the Eusuchia, but the respective character-states are determined in only one of the outgroups and five ingroups.

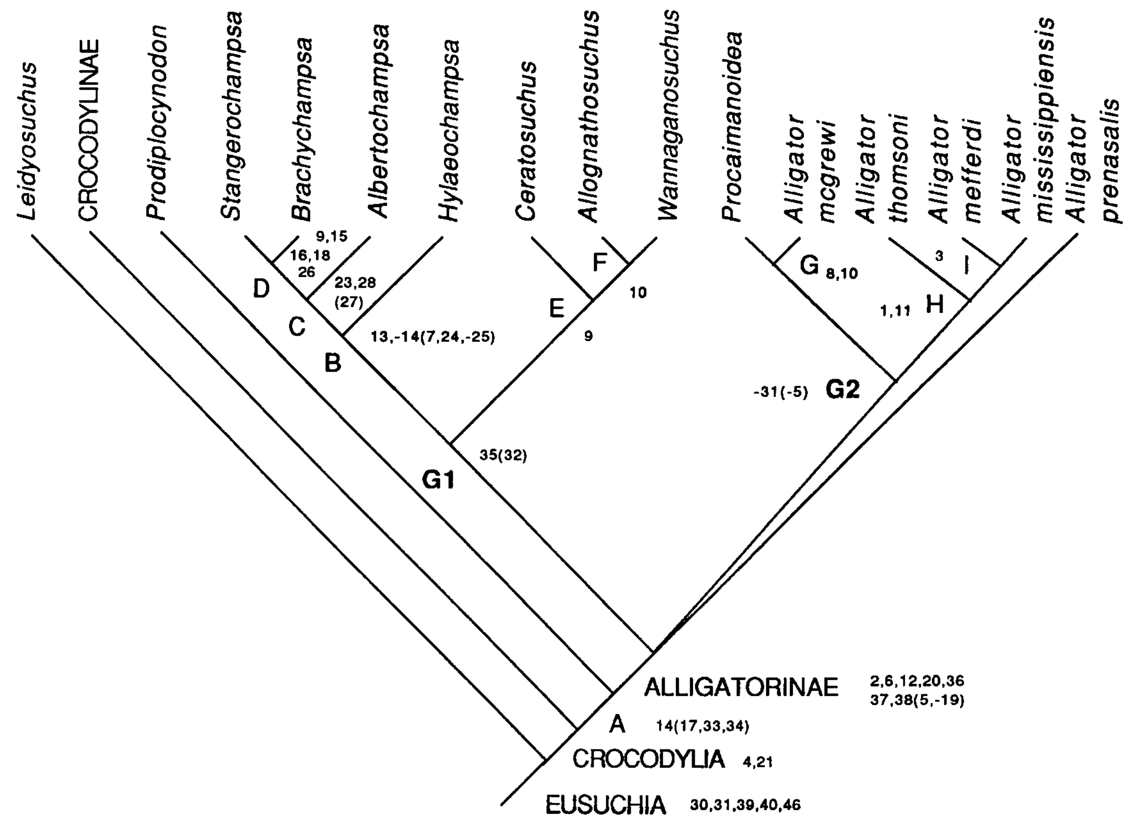
2. Although *Hylaeochampsa* is the oldest eusuchian yet known, it is not the most primitive representative of the Eusuchia. Rather, *Hylaeochampsa* is hypothesized to be a relatively derived alligatorine. This is based on the presence of three of seven newly recognized unequivocal synapomorphies of the Alligatorinae. These are character 6 (nasal/lacrimal contact absent), character 12 (lacrimal short and broad), and character 20 (postorbital forming supratemporal fossa). The states of the remaining four alligatorine synapomorphies are unknown in the genus.

3. In contrast to previous studies, *Leidyosuchus* is recognized to be the most primitive known eusuchian. It is primitive in that the nasals are excluded from the nares (character 4) and the postorbital fails to meet the parietal posterolateral to the frontal (character 21). The primitive state of character 4 is also seen in some members of the Crocodylinae. No other eusuchian exhibits the primitive state of character 21. Thus these characters define a group including all eusuchians except *Leidyosuchus* (Crocodylia; Text-fig. 4). *Leidyosuchus* is unequivocally more primitive than *Hylaeochampsa* in eight characters (characters 5, 6, 11, 12, 13, 20, 21 and 35). No character of *Leidyosuchus* is more derived than in *Hylaeochampsa.*

4. *Prodiplocynodon*, which was previously postulated to be an alligatorine (see Steel 1973; Carroll 1988), is unequivocally excluded from the Alligatorinae because it lacks all seven unequivocal synapomorphies of the latter (discussed below). A sister-group relationship between *Prodiplocynodon* and the Alligatorinae, rather than the Crocodylinae (Group A, Text-fig. 4), is suggested by character 14 (jugal/lacrimal suture much shorter than ventral border of orbit). However, this relationship is only weakly supported because the character is present as a derived feature within the Crocodylinae and is reversed in three ingroups of the Alligatorinae. The analysis recognized three additional characters supporting a close relationship of *Prodiplocynodon* and the Alligatorinae (characters 17, 33 and 34), but this evidence is equivocal because they are all uncertain in *Prodiplocynodon* and some alligatorines. Therefore, the phylogenetic relationship of *Prodiplocynodon* is relatively less strongly supported than are those of the other taxa included.

The species of *Diplocynodon* that are traditionally referred to the Alligatorinae (Steel 1973; Carroll 1988) are comparable morphologically with *Prodiplocynodon langi*. Like *Prodiplocynodon*, they are probably not alligatorines because, where known (characters 2, 20, 36, 37 and 38), none of the alligatorine synapomorphies are present. A similar phylogenetic position was concluded for *Diplocynodon* (represented by *D. hantoniensis*) in the study of Norell *et al.* (1994).

5. A monophyletic Alligatorinae, excluding *Prodiplocynodon*, is supported by seven unequivocal characters: character 2 (lack of a distinct lateral constriction between premaxilla and maxilla); character 6 (absence of a nasal/lacrimal contact); character 12 (lacrimal short and broad); character 20 (postorbital forming supratemporal fossa); character 36 (presence of four or five posterior massive crushing teeth); character 37 (dentary tooth 4 and dentary tooth 13 or 14 large, and presence of eight or nine small teeth between these large teeth); and character 38 (maxillary tooth 4 the largest and maxillary tooth 5 very small). Of these synapomorphies, characters 2, 37 and 38 are represented by their primitive states in all outgroups. The remaining four, characters 6, 12, 20 and 36 are represented by a derived character state in one of the four outgroups. The primitive states of character 6 (nasal/lacrimal contact present) and character 38 (maxillary tooth 5 largest) occur by reversal in *Albertochampsa* and *Brachychampsa*, respectively.



TEXT-FIG. 4. The consensus tree of two equally parsimonious cladograms generated by the present analysis, depicting relationships within the Eusuchia. In each node, unequivocal characters are followed by equivocal characters in brackets and ' – ' before a character indicates the reversal of the character. Characters of terminal taxa are as follows. *Hylaeochampsa*; 11, (19); *Albertochampsa*: –6; *Brachychampsa*: –38, (–27, –32); *Allognathosuchus*: 7, 15, (–5); *Procaimanoidea*: (–26); *Alligator mcgrewi*: 9, –25, 32; *Alligator thomsoni*: 16; *Alligator mississippiensis*: –33, 45, (–26); Crocodylinae: 1, 45.

6. Within the Alligatorinae two groups are recognized. *Hylaeochampsa, Albertochampsa, Brachychampsa, Stangerochampsa, Allognathosuchus, Wannaganosuchus* and *Ceratosuchus* (Group 1, Text-fig. 4) are linked by one unequivocal character (character 35, two or fewer teeth present posterior to anterior border of suborbital fenestra) and one equivocal character (character 32, surangular excluded from external mandibular fenestra). A second group, including *Procaimanoidea, Alligator mcgrewi, A. thomsoni, A. mefferdi* and *A. mississippiensis* (Group 2, Text-fig. 4), is supported by one unequivocal character, (character 31, no exposure of supraoccipital on skull roof [0 by reversal]) and one equivocal character (character 5, nasal ending posteriorly well before orbit [0 by reversal]).

7. Within Group 1, two monophyletic subgroups are present, Group B and Group E. Group B is supported by two characters (character 13, a long posteroventral process of the lacrimal reaching to the midpoint of the ventral border of the orbit, and character 14 [0 by reversal], the lacrimal/jugal suture being as long as the ventral border of the orbit). In addition, Group B is supported by three equivocal characters (character 7, nasal/premaxillary suture almost as long as nasal/maxillary suture; character 24, incisive foramen very large; and character 25 [0 by reversal], incisive foramen

enclosed by premaxillae and maxillae). These three characters are equivocal because they are unknown in *Hylaeochampsa*, and two of them are shared by one (character 7) or more (character 25) taxa of other groups. Group E is defined only by one unequivocal character (character 9, snout wider than long), although the derived state of this character is also present in a subgroup of Group B and a taxon in Group 2.

8. Within Group B, *Stangerochampsa* and *Brachychampsa* are the most derived taxa. These genera (Group D, Text-fig. 4) share five unequivocal synapomorphies. They are character 9 (snout wider than long), character 15 (anterior and posterior processes of jugal similar in length), character 16 (anterior process of quadratojugal long, reaching half-way along ventral border of infratemporal fenestra), character 18 (quadrate/quadratojugal suture strongly curved) and character 26 (palatine/pterygoid suture lying entirely behind suborbital fenestra). Derived states of characters 15, 16 and 26 are also present in one or two taxa of Group 2.

9. *Stangerochampsa*, *Brachychampsa* and *Albertochampsa* are united in a monophyletic Group C by two characters, character 23 (skull table strongly rounded anterolaterally) and character 28 (maxilla broad lateral to tooth row on ventral surface [Text-fig. 1B]). Character 27 (anterior portion as long as interfenestral portion of palatine) might be an additional synapomorphy of Group C, but it is ambiguous because it is present in the primitive state in *Brachychampsa*, is unknown in two taxa of Group 1, and is also derived in one of the four outgroups.

10. Within Group E, *Allognathosuchus* and *Wannaganosuchus* are more closely related to one another than either of them is to *Ceratosuchus* (Group F, Text-fig. 4). This relationship is supported by one unequivocal character (character 10, snout shorter than postorbital region of skull). The derived state of this character is also present in Group G of Group 2.

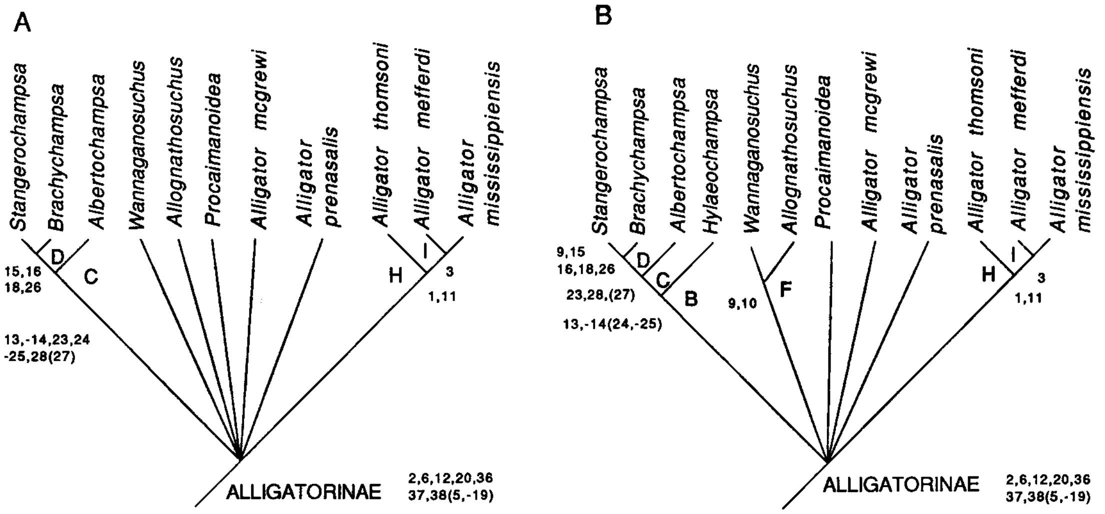
11. Within Group 2, two monophyletic subgroups are recognized. *Alligator mcgrewi* and *Procaimanoidea* form a monophyletic Group G, which is defined unequivocally by character 8 (two nasals broader than each maxilla in dorsal view) and character 10 (snout shorter than postorbital region of skull). Character 8 offers strong support for Group G because it is known in all taxa except *Hylaeochampsa* and is primitive in the taxa outside the group. The derived state of character 10 is also present in Group F of Group 1. *Alligator thomsoni*, *A. mefferdi* and *A. mississippiensis* are included in a monophyletic Group H, which is linked by two unequivocal synapomorphies: character 1 (premaxilla longitudinally wide anterior to naris and broadly overhanging nasal capsule) and character 11 (dorsal border of orbital ridged). Character 1 is unknown in *Hylaeochampsa* and is also derived in the Crocodylinae. Character 11 is also derived in *Hylaeochampsa*. Character 3 (nares fully divided) uniquely supports a close relationship between *A. mefferdi* and *A. mississippiensis* (Group 1, Text-fig. 4).

This analysis further supports a close relationship between *Bernissartia* + *Shamosuchus* and the Eusuchia. They share four unequivocal characters: character 22 (postorbital contacting ectopterygoid), character 25 (incisive foramen enclosed by premaxillae only), character 29 (choana almost entirely behind suborbital fenestra) and character 44 (more than two longitudinal rows of osteoderms without an anterolateral process). Characters 22 and 25 have not been recognized previously as synapomorphies of this clade.

The two most parsimonious cladograms produced by this analysis differ only in the position of *Alligator prenasalis* relative to Group 1 and Group 2. Character 5 (nasal ending posteriorly beyond or at level of anterior border of orbits) suggests unequivocally a close relationship between *A. prenasalis* and Group 1 (early alligatorines), while character 41 (anterior iliac process knob-like or absent) supports unequivocally a close relationship between *A. prenasalis* and Group 2 (late alligatorines). However, *A. prenasalis* is probably more closely related to Group 2 than it is to group 1, since the consistency index of character 41 is much higher than that of character 5.

The low percentage of the characters known for *Ceratosuchus* (32·6 per cent.) and *Hylaeochampsa* (43·4 per cent.) may have affected the phylogenetic relationships postulated. Therefore, further analyses, in which one or both of these genera were eliminated, have been carried out.

With both *Ceratosuchus* and *Hylaeochampsa* excluded, 14 equally parsimonious cladograms result. All of these cladograms support the phylogenetic relationships of the taxa outside the



TEXT-FIG. 5. A, part of the consensus tree of 14 equally parsimonious cladograms produced by eliminating *Hylaeochampsa* and *Ceratosuchus*; B, part of the consensus tree of three equally parsimonious cladograms produced by eliminating only *Ceratosuchus*. Explanations of characters and the letters on each node as in Text-figure 4.

Alligatorinae and retain Group C (the monophyly of which is further supported by four additional synapomorphies) and Group H within the Alligatorinae (Text-fig. 5A). However, relationships among *Wannaganosuchus*, *Allognathosuchus*, *Procaimanoidea*, *Alligator mcgrewi*, *A. prenasalis*, Group C and Group H are unresolved.

If only *Ceratosuchus* is eliminated, the analysis produces three equally parsimonious cladograms. Relationships between the taxa are established slightly better in this analysis than in the previous one (Text-fig. 5B). This analysis supports a close relationship between *Wannaganosuchus* and *Allognathosuchus* and recognizes that *Hylaeochampsa* is the sister-taxon of Group C, as was the case in the first analysis. The relationships of *Procaimanoidea*, *Alligator mcgrewi*, and *A. prenasalis* remain unresolved, as they did in the second analysis.

These analyses demonstrate that the close phylogenetic relationship of the Mesozoic alligatorines is supported strongly and suggest that the genus *Alligator* is not a monophyletic group. These analyses also show that elimination of taxa with a relatively low percentage of known characters is not helpful in establishing a better resolved phylogeny of the taxa retained.

CONCLUSIONS

The primary results of this study are: (1), *Stangerochampsa mccabei* was a Late Cretaceous alligatorine with a durophagous feeding behaviour, indicated by the contact of the ectopterygoid with the palatine and crushing teeth at the back of the tooth row; (2), *Leidyosuchus*, rather than *Hylaeochampsa*, is the most primitive known eusuchian, and the latter is an alligatorine; (3), excluding *Prodiplocynodon* (and probably *Diplocynodon*), the monophyly of the Alligatorinae in a cladistic sense is well-established; (4), most of the Mesozoic and Early Cenozoic alligatorines form a monophyletic group while the Late Cenozoic alligatorines are members of a second monophyletic group; differences may reflect different feeding adaptations; (5), the Mesozoic alligatorines of western North America constitute a monophyletic group.

Acknowledgements. We are greatly indebted to Mr J. R. McCabe (the Royal Tyrrell Museum of Palaeontology [RTMP], Drumheller) for finding, collecting and preparing the specimen and for proof-reading the manuscript. We thank Drs M. Norell and J. Clark (American Museum of Natural History [AMNH], New York), Dr H.-D. Sues (Royal Ontario Museum, Toronto), Dr J. Ostrom and Ms M. A. Turner (Peabody Museum of Yale University, New Haven), and Dr N. Hotton III and Mr R. Perdy (National Museum of Natural History, Smithsonian Institution, Washington D.C.) for access to specimens (including those loaned to AMNH from the Field Museum of Natural History, and the Museum of Paleontology, University of California, Berkeley) examined in this study. We are grateful to Drs M. Norell and H. Hutchison for sharing unpublished information. Dr E. Buffetaut reviewed the manuscript carefully and made significant comments and suggestions, leading to its improvement. We acknowledge gratefully the contributions of Ms D. L. Sloan, who made the specimen drawings, and Mr J. R. McCabe and Mr C. Coy of the RTMP, who made the photographs. X.-C. Wu thanks Drs X. Yü, J. Meng, X. Wang, M. Norell and H.-D. Sues for their hospitality during his visits to New Haven, New York, and Toronto. X.-C. Wu was supported by a University of Calgary Postdoctoral Fellowship.

REFERENCES

BENTON, M. J. and CLARK, J. M. 1988. Archosaur phylogeny and the relationships of the Crocodylia. 295–338. *In* BENTON, M. J. (ed.). *The phylogeny and classification of the tetrapods, Volume 1: amphibians, reptiles, birds.* Systematics Association Special Volume 35A, Clarendon Press, Oxford, 377 pp.

BUFFETAUT, E. 1986. Remarks on the anatomy and systematic position of *Sunosuchus miaoi* Young, 1948, a mesosuchian crocodilian from the Mesozoic of Gansu, China. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1986** (11), 641–647.

BUSCALIONI, A. A. and SANZ, J. L. 1990. The small crocodile *Bernissartia fagesii* from the Lower Cretaceous of Galve (Teruel, Spain). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, **60**, 129–150.

CARPENTER, K. and LINDSEY, D. 1980. The dentary of *Brachychampsa montana* Gilmore (Alligatorinae; Crocodylidae), a Late Cretaceous turtle-eating alligator. *Journal of Paleontology*, **54**, 1213–1217.

CARROLL, R. L. 1988. *Vertebrate paleontology and evolution.* Freeman, San Francisco, 698 pp.

CLARK, J. A. 1994. Patterns of evolution in Mesozoic crocodyliforms. 84–97. *In* FRASER, N. C. and SUES, H.-D. (eds). *In the shadow of the dinosaurs: early Mesozoic tetrapods.* Cambridge University Press, Cambridge and New York, 435 pp.

—— and NORELL, M. A. 1992. The Early Cretaceous crocodylomorph *Hylaeochampsa vectiana* from the Wealden of the Isle of Wight. *American Museum Novitates*, **3032**, 1–19.

CONG LINYU, HOU LIANHAI and WU XIAO-CHUN in press [*The gross anatomy of* Alligator sinensis *Fauvel: integument, osteology, and myology.*] Science Press, Chinese Academy of Sciences, Beijing, China. [In Chinese with English Summary].

CUVIER, G. 1808. Sur les ossemens fossiles de crocodiles et particulièrement sur des environs du Havre de Honfleur, accedes remarques sur les squelettes des sauriens de la Thuringie. *Annales du Muséum* (*National*) *d'Histoire Naturelle, Paris*, **12**, 73–110.

EFIMOV, M. B. 1988. [On the fossil crocodiles of Mongolia and USSR.] *Transactions of the Joint Soviet-Mongolian Palaeontological Expedition*, **34**, 81–90. [In Russian].

ERICKSON, B. R. 1972. *Albertochampsa langstoni* gen. et sp. nov., a new alligator from the Cretaceous of Alberta. *Scientific Publications of the Science Museum of Minnesota* (*NS*), **2**, 1–13.

—— 1976. Osteology of the early eusuchian crocodile *Leidyosuchus formidabilis*, sp. nov. *Monograph of the Science Museum of Minnesota* (*Paleontology*), **2**, 1–61.

—— 1982. *Wannaganosuchus brachymanus*, a new alligator from the Paleocene of North America. *Journal of Paleontology*, **56**, 492–506.

GILMORE, C. W. 1911. A new fossil alligator from the Hell Creek Beds of Montana. *Proceedings of the United States National Museum*, **41**, 297–302.

—— 1946. A new crocodilian from the Eocene of Utah. *Journal of Paleontology*, **20**, 62–67.

GMELIN, J. F. 1788. *Systema naturae de Carolus Linnaeus. Editio decema tertia, acuta, reformate, 2*, N.P., Leipzig, 1661 pp.

HUXLEY, T. H. 1875. On *Stagonolepis robertsoni*, and on the evolution of the Crocodilia. *Quarterly Journal of the Geological Society, London*, **31**, 423–438.

IORDANSKY, N. N. 1973. The skull of the Crocodylia. 201–262. *In* GANS, C. and PARSONS, T. S. (eds). *Biology of the Reptilia. Volume 4.* Academic Press, London, 539 pp.

KÄLIN, J. A. 1955. Crocodilia. 695–784. *In* PIVETEAU, J. (ed.). *Traite de paléontologie, 5.* Masson, Paris, 1113 pp.

LAMBE, L. M. 1908. On a new crocodilian genus and species from the Judith River Formation of Alberta. *Transactions of the Royal Society of Canada*, **1**, 219–244.

LI JINLING and WANG BAOZHONG. 1987. [A new species of *Alligator* from Shanwang, Shandong.] *Vertebrata PalAsiatica*, **25**, 199–207. [In Chinese].

MARSH, O. C. 1871. Notice of some new fossil reptiles from the Cretaceous and Tertiary formations. *American Journal of Science (Series 3)*, **6**, 447–459.

MOOK, C. C. 1921*a*. *Allognathosuchus*, a new genus of Eocene crocodilians. *Bulletin of the American Museum of Natural History*, **44**, 105–121.

—— 1921*b*. Skull characters of recent Crocodilia with notes on the affinities of the recent genera. *Bulletin of the American Museum of Natural History*, **44**, 123–268.

—— 1921*c*. Notes on the postcranial skeleton in the Crocodilia. *Bulletin of the American Museum of Natural History*, **44**, 67–103.

—— 1923. A new species of *Alligator* from the Snake Creek Beds. *American Museum Novitates*, **73**, 1–13.

—— 1924. A new crocodilian from Mongolia. *American Museum Novitates*, **117**, 1–5.

—— 1932. A study of the osteology of *Alligator prenasalis* (Loomis). *Bulletin of the Museum of Comparative Zoology*, **74**, 18–41.

—— 1941*a*. A new crocodilian from the Lance formation. *American Museum Novitates*, **1128**, 1–5.

—— 1941*b*. A new crocodilian, *Hassiacosuchus kayi*, from the Bridger Eocene Beds of Wyoming. *Annals of the Carnegie Museum*, **28**, 207–220.

—— 1942*a*. Skull characters of *Amphicotylus lucasii* Cope. *American Museum Novitates*, **1165**, 1–5.

—— 1942*b*. A new crocodilian from the Belly River Beds. *American Museum Novitates*, **1202**, 1–5.

—— 1946. A new Pliocene alligator from Nebraska. *American Museum Novitates*, **1311**, 1–12.

NORELL, M. A. 1989. The higher level relationships of the extant Crocodylia. *Journal of Herpetology*, **23**, 325–335.

—— and CLARK, J. M. 1990. A reanalysis of *Bernissartia fagesii*, with comments on its phylogenetic position and its bearing on the origin and diagnosis of the Eusuchia. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, **60**, 115–128.

—— —— and HUTCHISON, J. H. 1994. The Late Cretaceous alligatoroid *Brachychampsa montana* (Crocodylia): new material and putative relationships. *American Museum Novitates*, **3116**, 1–26.

OWEN, R. 1874. Monograph on the fossil Reptilia of the Wealden and Purbeck Formations. Supplement 6 (*Hylaeochampsa*). *Palaeontographical Society Monograph*, **27** (125), 1–7.

SCHMIDT, K. P. 1938. New crocodilians from the Upper Paleocene of western Colorado. *Geological Series of the Field Museum of Natural History*, **6**, 315–321.

—— 1941. A new fossil alligator from Nebraska. *Geological Series of the Field Museum of Natural History*, **8**, 27–32.

SIMPSON, G. G. 1930. *Allognathosuchus mooki*, a new crocodile from the Puerco Formation. *American Museum Novitates*, **445**, 1–16.

STEEL, R. 1973. *Crocodilia, Handbuch der Paläoherpetologie, 16.* Gustav Fischer Verlag, Stuttgart and Portland, 116 pp.

SUN AILIN, LI JINLING, YE XIANGKUI, DONG ZHIMING and HOU LIANHAI 1992. *The Chinese fossil reptiles and their kins.* Science Press, Beijing and New York, 260 pp.

SWOFFORD, D. 1993. Phylogenetic Analysis Using Parsimony (Version 3.1.1).

WALKER, A. D. 1970. A revision of the Jurassic *Hallopus victor* (Marsh) with remarks on the classification of crocodiles. *Philosophical Transactions of the Royal Society of London, Series B*, **257**, 323–372.

WILLIS, P. M. 1993. *Trilophosuchus rackhami* gen. et sp. nov., a new crocodilian from the Early Miocene limestones of Riverleigh, northwest Queensland. *Journal of Vertebrate Paleontology*, **13**, 90–98.

WU XIAO-CHUN and BRINKMAN, D. B. 1993. A new crocodylomorph of 'mesosuchian' grade from the Late Cretaceous Upper Milk River Formation, southern Alberta. *Journal of Vertebrate Paleontology*, **13**, 153–160.

—— —— and RUSSELL, A. P. in press. *Sunosuchus junggarensis*, sp. nov. (Archosauria: Crocodyliformes) from the Upper Jurassic of Xinjiang, China. *Canadian Journal of Earth Sciences.*

YOUNG, C. C. 1948. Fossil crocodiles in China, with notes on dinosaurian remains associated with the Kansu crocodiles. *Bulletin of the Geological Society of China*, **28**, 225–288.

ZANGERL, R. 1944. *Brachyuranochampsa eversolei* gen. et sp. nov., a new crocodilian from the Washakie Eocene of Wyoming. *Annals of the Carnegie Museum*, **30**, 77–84.

XIAO-CHUN WU

ANTHONY P. RUSSELL

Vertebrate Morphology Research Group
Department of Biological Sciences
The University of Calgary
2500 University Drive N.W., Calgary
Alberta T2N 1N4, Canada
(X.-C.W originally from the
Institute of Vertebrate Paleontology
and Paleoanthropology
Academia Sinica, P.O. Box 643
Beijing 100044
People's Republic of China).

DONALD B. BRINKMAN

Royal Tyrrell Museum of Palaeontology
Box 7500, Drumheller
Alberta T0J 0Y0, Canada

Typescript received 10 June 1994
Revised typescript received 15 May 1995