A new archosaur from the Upper Triassic Pardonet Formation of British Columbia

Elizabeth L. Nicholls, Donald B. Brinkman, and Xiao-Chun Wu

Abstract: ***Sikannisuchus huskyi***, a new genus and species of archosaur, is described from the Upper Triassic (Norian) Pardonet Formation of northeastern British Columbia. It has a broad, flat skull, and may have reached 4 m in length. It is referred to the Archosauria on the basis of a lateral mandibular fenestra, laterally compressed serrated teeth, elongate transverse processes, neural spine table, osteoderms, and thecodont dentition. It is autapomorphic in that the postfrontal enters the border of both the orbit and the supratemporal fenestra, and it has a large prefrontal that contacts both the nasal and the postfrontal, excluding the frontal from the margin of the orbit. The presence of osteoderms and a well-developed clavicle exclude *Sikannisuchus* from the Ornithodira; however, in the absence of any preserved limb material, we cannot assign it to the Crurotarsi. *Sikannisuchus* is not currently referable to any known taxon of archosaur and is left as Archosauria incertae sedis.

Résumé : Un nouveau genre et nouvelle espèce d'archosaure, ***Sikannisuchus huskyi***, est décrit en provenance de la Formation de Pardonet, du Trias supérieur (Norien), dans le nord-est de la Colombie-Britannique. Son crâne est plat et large, et l'animal peut atteindre jusqu'à 4 m de long. L'assignation aux Archosauria est fondée sur la fenêtre mandibulaire latérale, les dents crénelées et comprimées latéralement, les apohyses transversales allongées, la table des neurépines, les ostéodermes et la dentition thécodonte. Il est considéré autapomorphique en raison du postfrontal qui pénètre la bordure de l'orbite d'une part, et la fenêtre du supratemporal d'autre part; le crâne exhibe un préfrontal large en contact avec le nasal et le postfrontal, mais excluant le frontal de la marge de l'orbite. La présence d'ostéodermes et d'une clavicule bien développée proscrit toute appartenance de *Sikannisuchus* aux Ornithodirés; cependant, vu l'absence depréservation de matériel des membres, il ne peut être assigné aux Crurotarsi. Il est impossible actuellement de référer *Sikannisuchus* à un quelconque taxon connu d'archosaures, et il demeure un Archosauria incertae sedis.

[Traduit par la Rédaction]

Introduction

Since 1992, field parties from the Royal Tyrrell Museum have been collecting fossil marine reptiles from the Upper Triassic Pardonet Formation in northeastern British Columbia. The work has been concentrated along the Sikanni Chief River, north of Pink Mountain (Fig. 1). The Pardonet Formation is a transgressive, deep-water limestone (Gibson and Edwards 1990; Edwards et al. 1994), and most of the fossils are shastasaurid ichthyosaurs. Some of the specimens, however, belong to an unusual new archosaur, which is described below. While its relationships within the Archosauria are uncertain, the new form differs enough from other known archosaurs to warrant description. Specimens have been collected over a 3 year period, and some have been acid-prepared. All specimens are housed at the Royal Tyrrell Museum (TMP).

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E.L. Nicholls.[1] Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, AB T0J 0Y0, Canada.
D.B. Brinkman. Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, AB T0J 0Y0, Canada, and Department of Biological Sciences, University of Calgary, Calgary, AB T2N 1N4, Canada.
X.-C. Wu. Department of Biological Sciences, University of Calgary, Calgary, AB T2N 1N4, Canada, and Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, P.O. Box 643, Beijing 100044, People's Republic of China.

[1]Corresponding author (e-mail: Bnicholls@mcd.gov.ab.ca).

Systematic palaeontology

Archosauromorpha Huene, 1946, emended Gauthier et al. 1988

Archosauriformes Gauthier et al. 1988

Archosauria Cope, 1869, emended Gauthier et al. 1988

Sikannisuchus huskyi gen. et sp. nov. (Figs. 2–8)

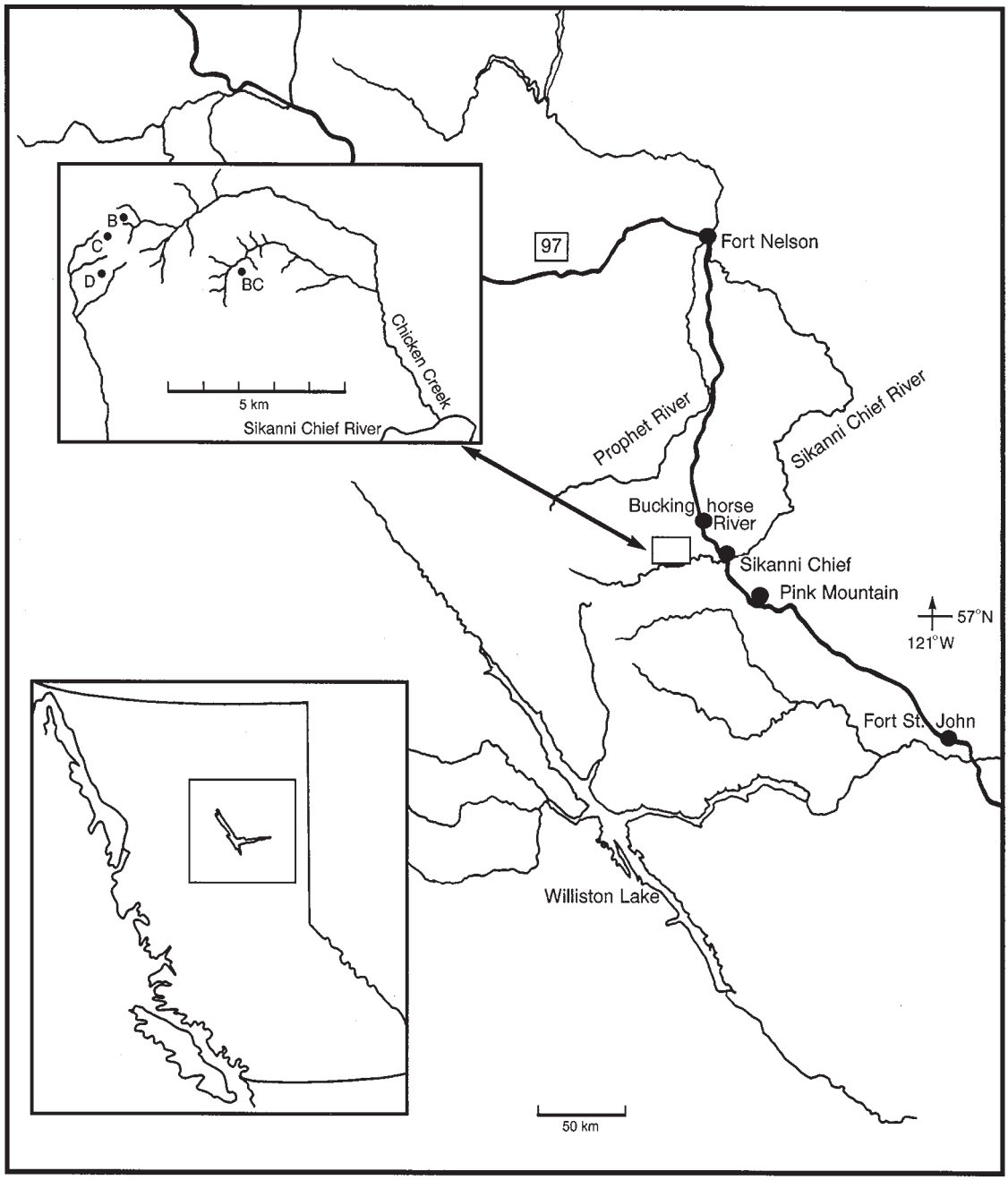
Etymology

Sikanni, in reference to the Sikanni Chief River, in the area where the specimens were found, and *suchus*, from the Greek *souchos*, the Egyptian crocodile-headed god. The species is named after Husky Oil, in appreciation for the extensive helicopter support given to the Royal Tyrrell Museum in the summer of 1996.

Holotype

TMP 94.382.3. Posterior portion of skull roof (Fig. 2). From locality D.

Fig. 1. Map showing location of Chicken Creek, and localities from which specimens were collected.



Paratype

TMP 94.381.1. Disarticulated mandibular and cranial elements, teeth, clavicles, isolated vertebrae and ribs, osteoderms (Figs. 3, 4). From locality C.

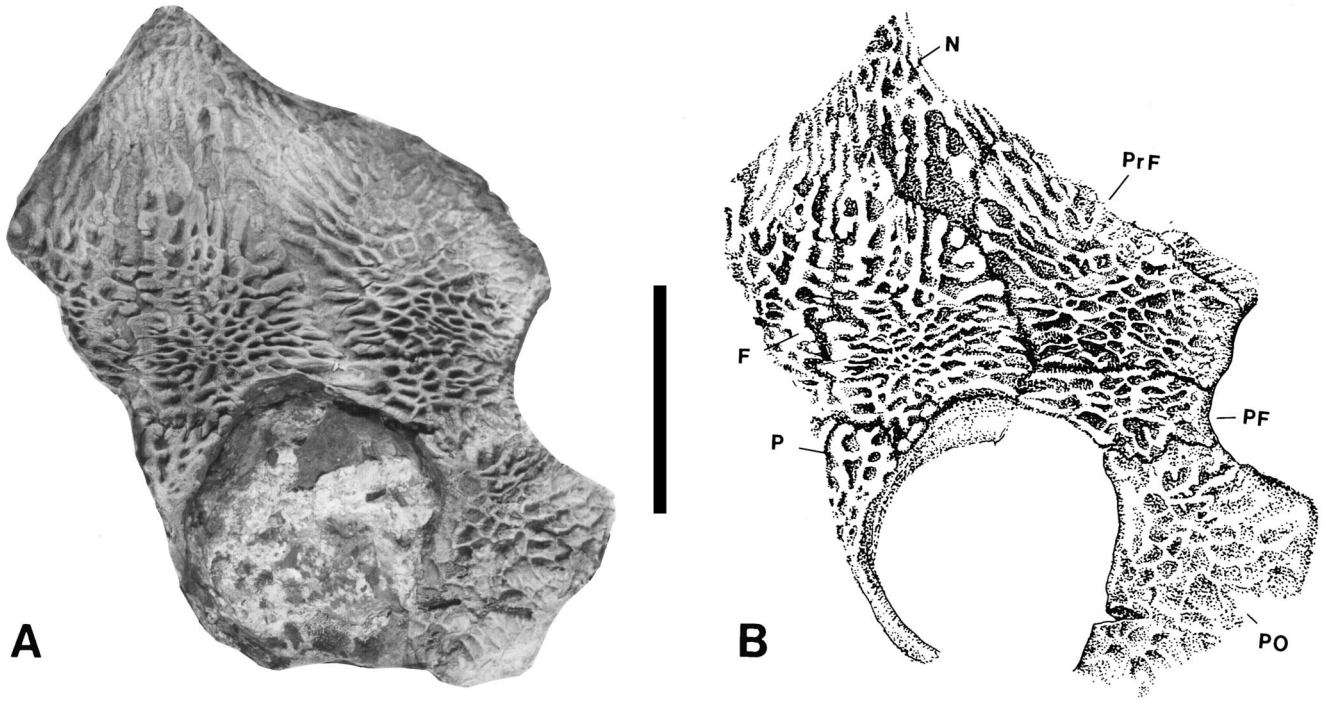
There is no overlap of material with the type specimen. However, we feel justified in referring this material to *Sikannisuchus*, as we consider it unlikely that there would be more than one archosaur with heavy dermal ornamentation in the fauna.

Localities and horizon

Four localities (B, C, D, BC) at the headwaters of Chicken Creek, 32 km northwest of the community of Sikanni Chief, British Columbia (Fig. 1). Localities are dispersed throughout an area contained within a 5 km radius. Exact coordinates are available on request from the Royal Tyrrell Museum.

At all localities, specimens were collected from the basal limestone member of the Pardonet Formation, and are associated with remains of shastasaurid ichthyosaurs. Conodont analyses were made by M.J. Orchard of the Geological Survey of Canada (GSC), on matrix samples from specimens collected at localities B, C, and D. He assigned them to the *triangularis* Zone of the early Norian (Report MJO-1995-3. GSC locs. C-302182, C-302183, C-302184). Samples from localities C and D (GSC locs. C-302183, C-302184) contain

Fig. 2. TMP 94.382.3, *Sikannisuchus huskyi*, holotype.Dorsal skull roof, illustrating pattern of dermal sculpturing, and sutures. (A) Photograph. (B) Line drawing. F, frontal; N, nasal; P, parietal; PF, postfrontal; PO, postorbital; PrF, prefrontal. Scale bar = 10 cm.



the conodont *Epigondolella quadrata* and may therefore be slightly older than those from locality B.

Referred specimens

Locality B: TMP 94.380.4, TMP 94.380.8, TMP 96.65.1, TMP 96.65.2, TMP 96.65.4, isolated teeth; TMP 96.65.3, neural arch and spine.

Locality C: TMP 94.381.2, two teeth and a fragment of dermal bone; TMP 94.381.11, caudal centrum; TMP 96.63.1, neural arch and spine (Fig. 6); TMP 96.63.2, three articulated caudal vertebrae; TMP 96.63.7, fragment of skull roof (Fig. 5); TMP 94.381.10, TMP 96.63.3, TMP 96.63.4, TMP 96.63.5, TMP 97.72.4, isolated teeth.

Locality D: TMP 94.382.8, TMP 96.64.2, isolated teeth.

Locality BC: TMP 96.67.4, TMP 96.67.6, TMP 96.67.7, TMP 96.67.8 (Fig. 7), isolated teeth.

Diagnosis

Archosaur with a broad, flat skull. Postfrontal rectangular and enters the border of both the supratemporal fenestra and the orbit. Large prefrontal contacting both the nasal and postfrontal, excluding frontal from orbital margin. Frontal small and enters the border of the supratemporal fenestra. Dermal bone with strongly developed sculpture of pits and radiating ridges. Mediolaterally compressed, recurved teeth, with serrations on both anterior and posterior carinae. Dermal armour present.

Description

Holotype

TMP 94.382.3 (Fig. 2) consists of the right portion of the posterior part of the skull roof. The area preserved includes the supratemporal fenestra, orbit, and the surrounding bones. The bone has been split in the frontal plane, so that while the original external surface of the bone is preserved, the internal, endocranial surface is not. Sutures are well preserved, however, and are visible on both internal and external sides of the specimen. The external surface of the bone has a strongly developed sculpture, consisting of deep pits that radiate outward into ridges and grooves. The supratemporal fenestra is very large and almost circular. Its anterior border is formed by the frontal and postfrontal. The postfrontal is rectangular and enters the border of both the orbit and the supratemporal fenestra. The prefrontal is also large, being approximately equal in size to the frontal. It contacts both the nasal and the postfrontal, excluding the frontal from the orbital margin.

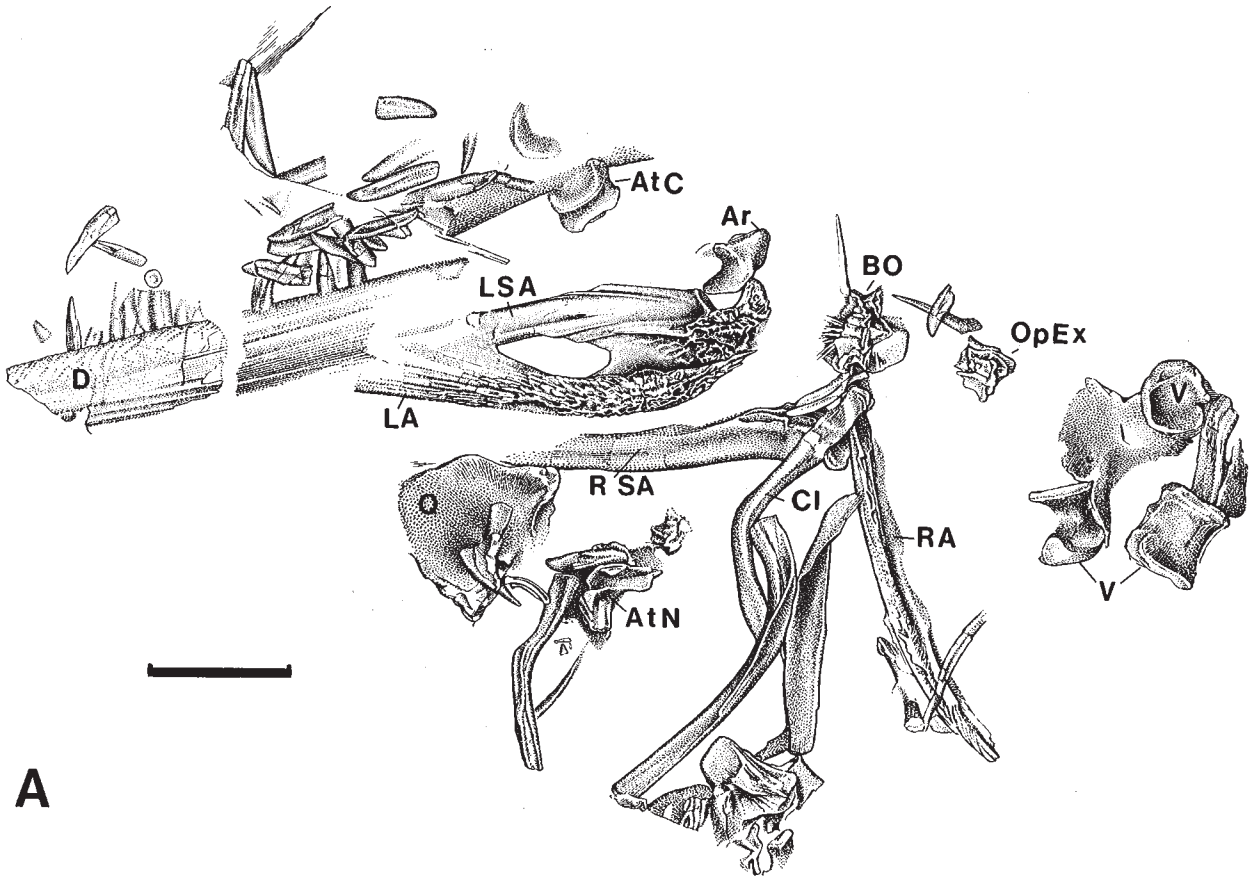
Paratype

TMP 94.381.1 is preserved as three slabs (blocks A, B, C). Two of these (blocks A and B, Figs. 3A and 3B, respectively) are a slab/counter-slab. Consequently, after acid preparation, medial and lateral views of many elements are present in different blocks. Preserved elements include most of the left mandibular ramus, right angular, right surangular, left quadrate, left opisthotic-exoccipital, basioccipital, both clavicles, scattered vertebrae, ribs, scutes, and teeth.

The left mandibular ramus, best seen in lateral view (Fig. 3A), is missing sections of the dentary. Some of this is preserved as impressions in the matrix. What is preserved of the mandibular ramus is 53 cm long, and the complete mandible is estimated to have been 65–70 cm in length.

There is a large lateral mandibular fenestra, which is enclosed primarily by the surangular and angular. The dentary contributes to only a small part of the anteroventral edge of the fenestra. The angular and the posterior part of the surangular are very heavily sculptured. On the dentary, orna-

Fig. 3. TMP 94.381.1, *Sikannisuchus huskyi*, paratype; slab and counter slab. (A) Block A. (B) Block B. A, angular; Ar, articular; AtC, atlas centrum; AtN, atlas neural arch; BO, basioccipital; Cl, clavicle; D, dentary; L, left; OpEx, opisthotic-exoccipital; Ost, osteoderm; PrA, prearticular; Q, quadrate; R, right; SA, surangular; V, vertebra. Scale bar = 10 cm.



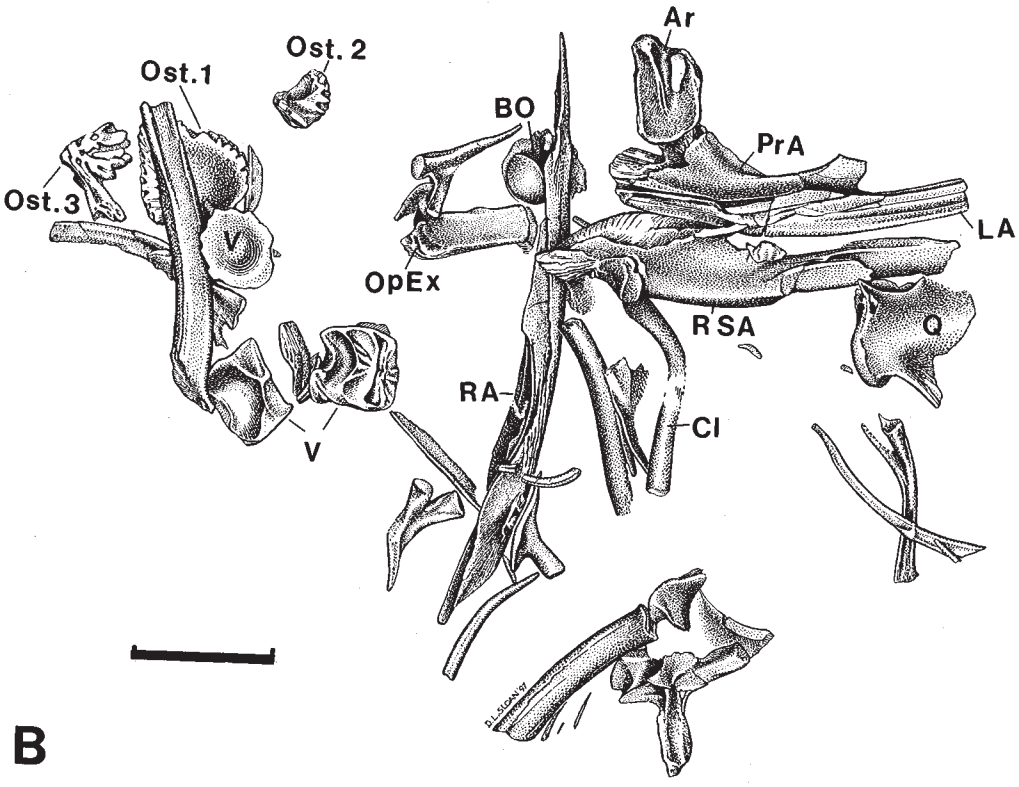


Fig. 4. TMP 94.381.1, Block C. Osteoderm. Scale bar = 1 cm.

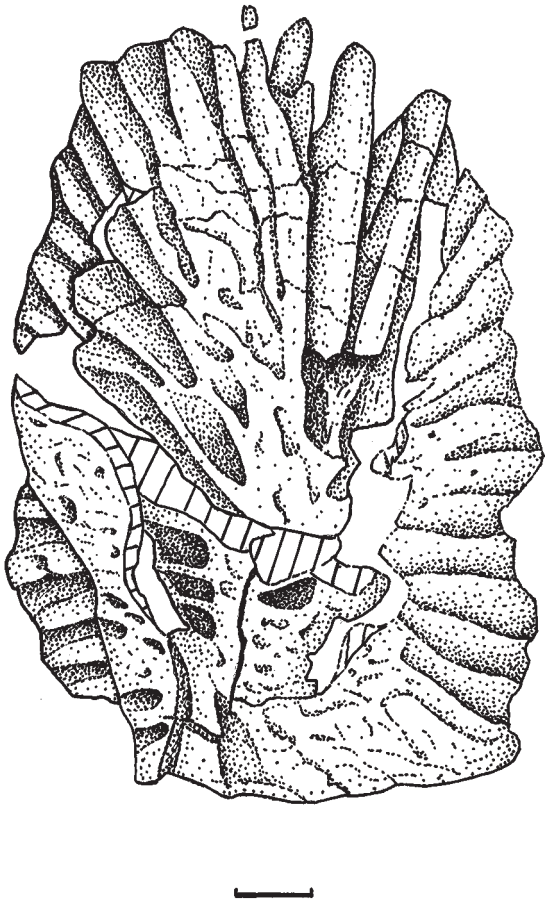
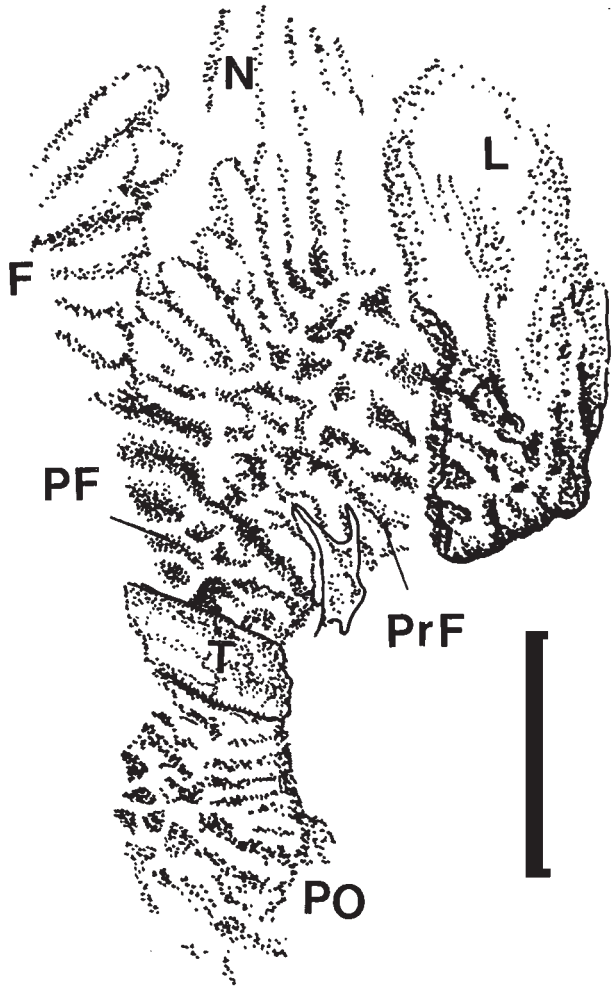


Fig. 5. TMP 96.63.7. Referred specimen, posterior right-hand side of skull. F, frontal; L, lacrimal; N, nasal; PF, postfrontal; PO, postorbital; PrF, prefrontal; T, tooth. Scale bar = 5 cm.



mentation is much more subdued, consisting of faint, longitudinal striations. The symphysial tip of the dentary is heavily pitted.

The surangular forms most of the posterolateral side of the mandibular ramus. It extends posteriorly along the side of the retroarticular process and its dorsal border is deeply notched for the attachment of the articular bone. There is no coronoid process.

The angular is elongate and very slender. It forms much of the ventral border of the ramus, extending along the ventral edge of the dentary to the end of the retroarticular process. The isolated right angular is 44 cm long and trough shaped in cross section.

The left articular is exposed in ventral view (block B, Fig. 3B), slightly dislodged from its articulation with the surangular. It is rectangular and forms a long retroarticular process. Its ventral surface has an elongate ridge for articulation with the surangular.

The medial surface of the mandibular ramus is best seen in block B (Fig. 3B). The prearticular forms the entire ventral border of the adductor fossa and lies in a groove within the angular trough.

Twenty seven teeth are associated with the specimen. Some of these are in place, but many have come out of their sockets and are scattered around the dentary. While most of the teeth are complete, some are preserved as impressions in the matrix.

The teeth have very long roots, which exceed the length of the crown. One of the larger teeth has a total length of 83 mm. The crown makes up 32 mm of this length, while the root makes up the remaining 51 mm. The crowns are mediolaterally compressed, recurved blades, with serrations on both anterior and posterior carinae. There are 3–5 serrations/mm. The size of the serrations varies with the curvature of the tooth, with the larger serrations being found near the middle of the carina.

The left quadrate is split in two (Fig. 3, Q). Its dorsal half forms an expanded wing seen in block A. Its ventral half, in block B, has an hourglass-shaped articular condyle. The ventrolateral edge of the quadrate has an elongate socket for the articulation of the quadratojugal.

The opisthotic-exoccipital is a single element (Fig. 3, OpEx). It forms the lateral wall and part of the floor of the foramen magnum. Dorsally, there is an extensive sutural area for the supraoccipital. The paroccipital process of the opisthotic extends posterolaterally, and is slightly tapered at its distal end.

Four vertebrae are associated with TMP 94.381.1. The atlas centrum is visible in ventral view (Fig. 3A, AtC). It is much shorter than wide and has articular facets both anteri-

Fig. 6. TMP 96.63.1. Referred specimen. Neural arch of dorsal vertebra (posterior view) showing spine table and elongate transverse processes indicating well-developed epaxial musculature. Scale bar = 5 cm.

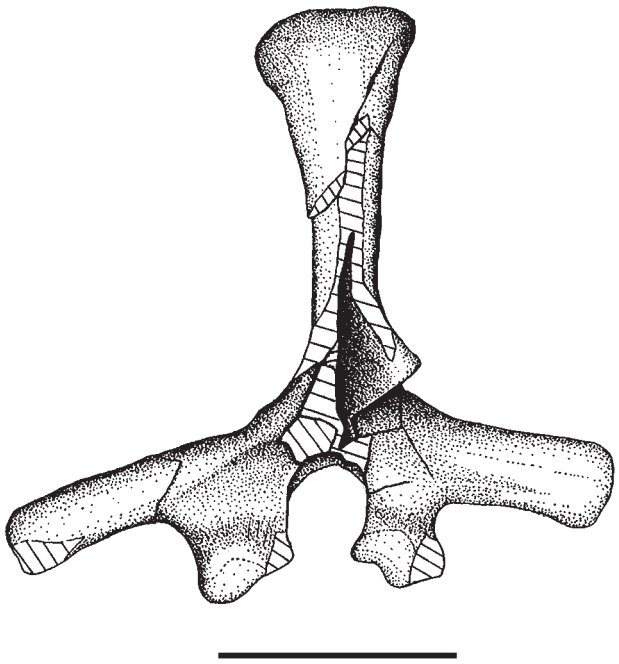
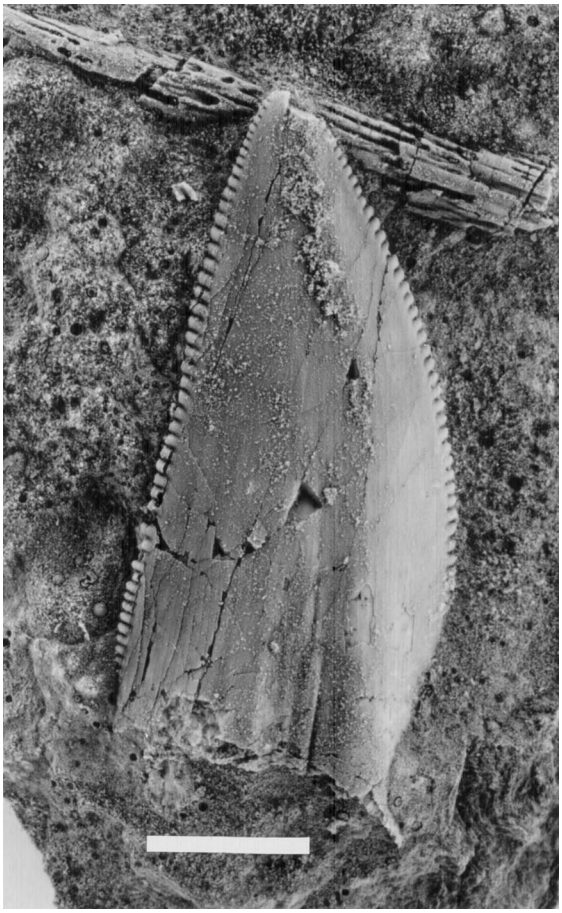


Fig. 7. TMP 96.67.8. Tooth of referred specimen. Scale bar = 5 cm.



orly and posteriorly for the first and second intercentra. The right atlas neural arch has separated from the centrum and is seen in medial view (Fig. 3A, AtN). It has a long posterior extension enclosing a very clearly defined neural canal. The atlas centrum and neural arch closely resemble those of *Ticinosuchus* (Krebs 1965, Fig. 17). The remaining three centra are amphicoelous, more elongate and laterally compressed. Their length slightly exceeds the height/width of the articular face. A single, round parapophysis is visible on one of them. It is high on the centrum and continuous with the anterior rim of the centrum. These are probably cervicals. The cervical ribs are double headed and have a pronounced anterior process.

Both clavicles are preserved, one in blocks A and B (Fig.3), and one in block C. They are long, compressed rods, curved at right angles about one third of the way along their length. The shorter, medial segment has an overhanging lip along its edge, presumably for the attachment of the interclavicle. The longer segment, which would have attached to the scapula and coracoid, is flattened.

Parts of four osteoderms are preserved. One is complete, but visible only on its smooth, concave inner surface (Fig. 3B,Ost.1). It is pear shaped in outline, bilaterally symmetrical, and not unlike the anterior cervical scute in *Ticinosuchus* (Krebs 1965, Fig. 61). The margins are fluted and wrinkled, however, indicating the presence of a pronounced sculpturing on the outer surface of the scute.

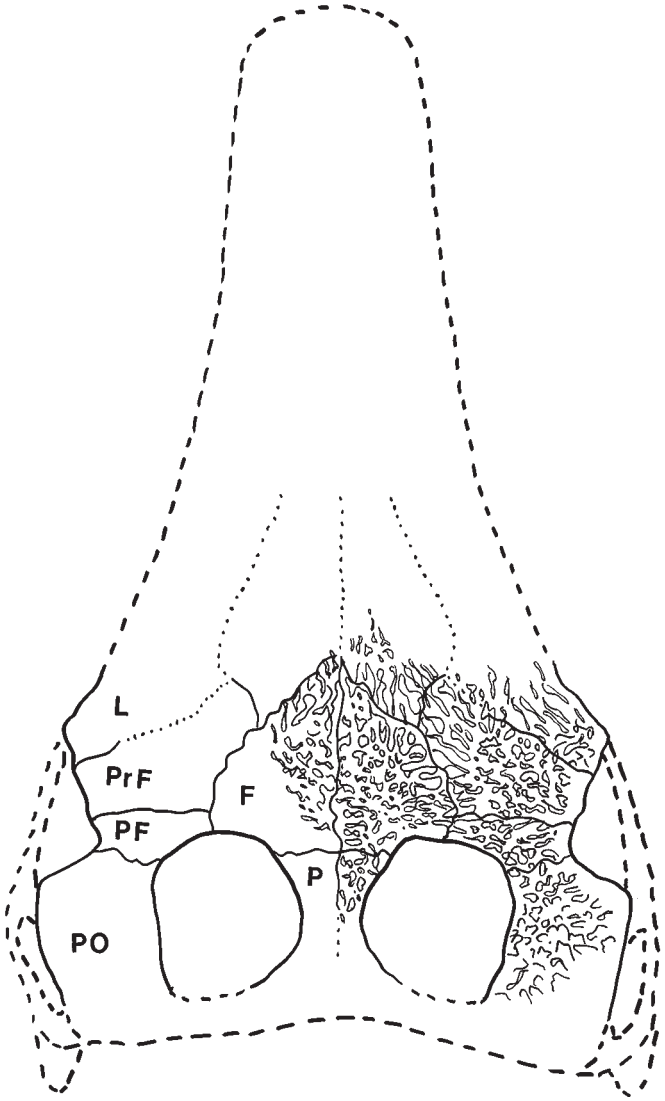
A second broken osteoderm is small, irregular in shape, and heavily sculptured with ridges and wrinkles (Fig. 3B,Ost.2).

The remaining two osteoderms are similar in configuration. One of these is very incomplete (Fig. 3B, Ost.3). The other is complete, but was damaged during preparation (Fig. 4). The anterior edge is convex, the posterior edge is straight. The medial and lateral edges of the osteoderm are gently convex, with no indication of sutural contact with adjoining scutes. The osteoderm is heavily ornamented with a network of coalescing ridges and grooves. The sculpturing radiates from the centre of a low, elongate boss situated on the midline, but slightly posterior to the midpoint of the osteoderm. Anteriorly, the sculpture does not extend to the edge of the osteoderm. However, there is no clearly defined smooth lamina as in *Doswellia* (Weems 1980; Long and Murry 1995). If there was an anteroposterior overlap, it was minimal.

Referred material

TMP 96.63.7 is the right side of the posterior portion of a skull roof (Fig. 5). It is preserved mainly as impressions in the matrix. While most of the bone has broken away, the lacrimal is preserved in place at the anterior edge of the orbit. Consequently, impressions of the external, sculptured surface of the prefrontal and postfrontal are juxtaposed with the smooth, internal surface of the lacrimal. Acid preparation reproduced the external surface of the original specimen (Fig. 5). The suture between the postfrontal and the postorbital is covered by an overlying tooth; the suture between the postfrontal and prefrontal is not visible in the impression. The border of the orbit is clear however, as is

Fig. 8. Reconstruction of posterior skull roof of *Sikannisuchus huskyi*. Shading corresponds to area covered by TMP 94.382.3 and TMP 96.63.3. F, frontal; L, lacrimal; P, parietal; PF, postfrontal; PO, postorbital; PrF, prefrontal.



the lacrimal–prefrontal suture. As this is the same part of the skull that is preserved in the holotype, we considered the possibility that TMP 96.63.7 might be an impression of that specimen, or in some way associated with it. It does, however, appear to represent a second, slightly smaller individual. It may be part of the paratype, but was not found associated with it.

Neural arches and spines are preserved in two specimens (TMP 96.65.3, TMP 96.63.1, Fig. 6). The arches are high, and the transverse processes are elongate, suggesting an enlarged epaxial muscle mass. The neural spine is expanded distally to form a dorsal spine table.

Two of the isolated teeth (TMP 96.65.2, TMP 96.64.2) are not as mediolaterally compressed as the other teeth, and their crowns are somewhat rounded in cross section. These are believed to be either premaxillary, or anterior dentary teeth.

Seven of the isolated teeth (TMP 96.63.5, TMP 96.63.4, TMP 94.380.4, TMP 94.380.8, TMP 94.381.10, TMP 96.67.8, TMP 97.72.4) are either shed teeth or were in the process of being replaced when the animal died. These teeth have no root, and a resorption pit is present in the base of the crown (Fig. 7).

Discussion

A reconstruction of the skull roof, based on TMP 94.382.3 and TMP 96.63.7, is shown in Fig. 8. Our identification of *Sikannisuchus* as an archosauriform is based on presence of the following characters: (1) Lateral mandibular fenestra (Clark et al. 1993), and (2) mediolaterally compressed, serrated teeth (Gauthier 1984). Within the Archosauriformes, it can be assigned to the group including Proterochampsidae and Archosauria on the presence of (3) elongate transverse processes on trunk vertebrae, suggesting enlarged epaxial muscle mass (Gauthier 1984), and (4) osteoderms (Gauthier 1984; Parrish 1993). It is identified as an archosaur on the presence of (5) thecodont dentition (Gauthier 1984), and (6) neural spine table (Gauthier 1984).

Within the Archosauria, *Sikannisuchus* is autapomorphic in the following combination of characters: (1) rectangular postfrontal that enters the border of both the orbit and the supratemporal fenestra; (2) frontal that has extensive contact with the border of the supratemporal fenestra; (3) very large prefrontal, contacting both the nasal and the postfrontal and excluding the frontal from the orbital margin; (4) strongly developed dermal sculpturing. Some of these characters are present in other primitive archosauromorphs, but not in this combination. In most archosauriforms the postfrontal does not enter the border of the supratemporal fenestra. *Lotosaurus* is an exception, if Parrish's reconstruction is correct (Parrish 1993, Fig. 6C). However, in *Lotosaurus*, the prefrontal and postfrontal do not meet, and the frontal has extensive contact with the orbital margin. In *Postosuchus* the postfrontal enters the supratemporal fenestra, but it does not enter the orbit. The prefrontal and postfrontal meet in *Postosuchus*, excluding the frontal from the orbital margin. However the prefrontal does not contact the nasal and the frontal does not enter the supratemporal fenestra (Chatterjee 1985). In *Prestosuchus*, the prefrontal and postfrontal meet, and the frontal enters the border of the supratemporal fenestra. However, the prefrontal is quite small and does not make contact with the nasal (Parrish 1993). In *Saurosuchus* there is a large prefrontal that contacts the nasal, but the prefrontal and postfrontal do not meet and the frontal forms part of the orbital margin (Sill 1974; Parrish 1993). In none of these forms is there extensive sculpturing of the dermal bone.

Sikannisuchus has a number of derived characters shared with aquatic archosauromorphs including *Doswellia* (Weems 1980), proterochampids (Sill 1967; Romer 1971), and derived crocodylomorphs. In all of these forms there is a broad, flat skull, lacking a parietal crest, and the supratemporal fenestra and arch are horizontal, rather than vertical, in orientation. However, of these taxa, only *Sikannisuchus* has a postfrontal bone.

The dermal sculpturing of *Sikannisuchus* bears some resemblance to that of the primitive Triassic archosauromorph

Doswellia (Weems 1980). *Doswellia*, however, lacks both a lateral mandibular fenestra and a postfrontal bone, and its teeth are small and conical (Weems 1980).

The blade-like serrated teeth of *Sikannisuchus* closely resemble those of the rauisuchians *Ticinosuchus* (Krebs 1965) and *Saurosuchus* (Sill 1974), although this tooth form is widespread among carnivorous archosauriforms.

Although the specimens are incomplete, cranial and mandibular material are clearly associated with teeth and osteoderms in TMP 94.381.1. The isolated vertebrae are referred to this taxon as they are archosauriform and it is unlikely that more than one archosauriform would be present in the fauna.

In spite of its fragmentary condition, we feel the creation of a new taxon is justified. The temporal region of *Sikannisuchus* is highly autapomorphic and easily identifiable. The presence of osteoderms and a well-developed clavicle excludes *Sikannisuchus* from the Ornithodira (Sereno 1991). However, its affinities with the Crurotarsi cannot be confirmed in the absence of any preserved limb elements. As *Sikannisuchus* cannot presently be assigned to any known archosaurian taxon, we are leaving it as Archosauria incertae sedis until more complete material is found.

Habitat and environment of deposition

The Pardonet Formation in British Columbia is a deep-water, carbonaceous–argillaceous limestone representing the final phase of a Late Triassic marine transgression. Deposition is believed to have occurred in a relatively deep water distal shelf setting (Gibson and Barclay 1989; Gibson and Edwards 1990). At all localities, *Sikannisuchus* is associated with the remains of shastasaurid ichthyosaurs, which are fully adapted to the marine environment.

Archosaurs have not commonly inhabited the marine environment. Marine crocodylomorphs from the Jurassic and Cretaceous are one of the few exceptions. Archosaur remains have been reported from Triassic marine strata before. The most complete of these is *Ticinosuchus ferox*, a rauisuchian known from two specimens from the Grenzbitumenzone (Anisian–Ladinian) of Switzerland and Italy (Krebs 1965; Pinna and Arduini 1978). Wiman (1918) reported an isolated archosaur centrum from the Anisian of Spitzbergen, and Huene (1939) described a phytosaur snout from Carnian marine sediments in Austria. However, all of these specimens are believed to be the remains of terrestrial animals washed out to sea.

The habitat of *Sikannisuchus* is controversial, and the authors of this paper hold different opinions. We interpret *Sikannisuchus* as an aquatic animal, due to its broad, flat skull. However, there are two alternate hypotheses for the occurrence of these specimens in the marine environment. The first hypothesis (supported by E.L.N.) is that *Sikannisuchus* inhabited the local river systems, and the specimens at Chicken Creek are the result of carcasses washed out to sea. The four localities at the headwaters of Chicken Creek are in a restricted area encompassing a radius of about 5 km. Most of the specimens are from localities C and D. Specimens from the other two localities consist of nine isolated teeth and a single neural arch. Bloated vertebrate remains can float for weeks at sea, with the jaws and teeth being among the first elements to drop away from the decomposing carcass (Schäfer 1972). This scenario could easily explain the distribution of *Sikannisuchus* specimens. TMP 94.382.3 and TMP 96.63.7 indicate that at least two individuals are present. However, if the animal lived in the local river system, it would not be uncommon for carcasses to wash out to sea. This hypothesis could be falsified by the discovery of additional specimens in more widespread localities.

The second hypothesis (supported by D.B.B. and X.-C.W.) is that these specimens are the remains of a number of individuals, and that the animal was actively living in the marine environment. It should be noted that there is no demonstrated association between the specimens, and it is entirely possible that a number of individuals are represented. This is supported by conodont analyses, which suggest that locality B may be slightly younger than localities C and D. The Recent salt water crocodile, *Crocodylus porosus*, is equally at home in both salt and fresh water, and has been recorded up to 200 km out to sea (Bustard and Choudhury 1980; Doubilet 1996). *Sikannisuchus* may have inhabited a local river system and not infrequently swam far out to sea. This scenario would be supported if in the future additional specimens are found at other localities.

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