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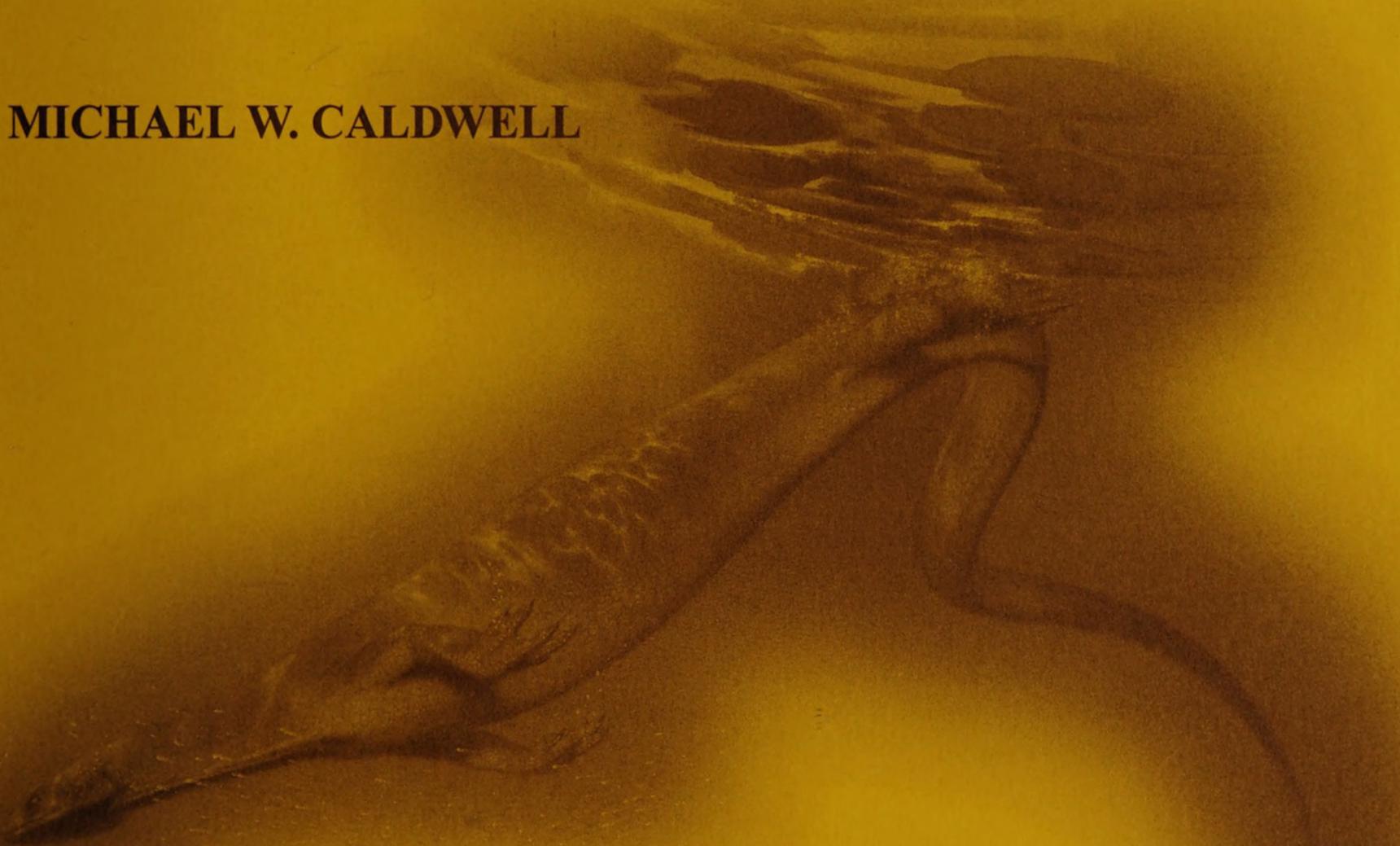
# MEMORIE

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MICHAEL W. CALDWELL



A NEW SPECIES OF  
*PONTOSAURUS* (SQUAMATA, PYTHONOMORPHA)  
FROM THE UPPER CRETACEOUS OF LEBANON  
AND A PHYLOGENETIC ANALYSIS  
OF PYTHONOMORPHA

MILANO LUGLIO 2006

**Michael W. Caldwell**

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In copertina: *Pontosaurus kornhuberi*. Watercolour by Fabio Fogliazza.

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**A new species of *Pontosaurus* (Squamata, Pythonomorpha)  
from the Upper Cretaceous of Lebanon  
and a phylogenetic analysis of Pythonomorpha**

**Abstract** - A new fossil marine squamate from the Upper Cretaceous (Cenomanian) of Lebanon is described and its phylogenetic relationships analyzed. The taxon represents a new species of *Pontosaurus*, previously known from only the type species and only one specimen, designated *Pontosaurus lesinensis* (Kornhuber, 1873). The new taxon is very well preserved including the squamation and a complete tail numbering 163 caudal vertebrae. New and important features of the braincase of pontosaurs are highlighted: 1) the supraoccipital position and its overlap of the parietal; 2) the alar process of prootics elongate contact with parietal; 3) the reduction of the paroccipital process. A phylogenetic analysis of pythonomorphs, utilizing these new characters in a data matrix of 77 characters and 10 terminal taxa, finds nine shortest trees with a tree length of 119 steps (C.I. = 0.773; HI = 0.226). The nine shortest trees vary only in the sistergroup relationships of *Aphanizocnemus libanensis* within non-mosasauroid pythonomorphs, and the ingroup relationships of ophidian pythonomorphs. For example, cladogram one presents the following sistergroup structure: ((Aigialosauridae, Mosasauridae) (Dolichosauridae (*Aphanizocnemus libanensis* ((*Pontosaurus lesinensis*, *Pontosaurus kornhuberi*) (*Adriosaurus suessi* (*Pachyophis woodwardi* (*Pachyrhachis problematicus*, Serpentes)))))). In the context of the hypothesized phylogeny presented in this study, the functional morphology of pontosaurs is discussed, highlighting tail and limb function in relationship to locomotory capability.

**Key words** - Squamates, pythonomorphs, marine lizards, Cretaceous, Lebanon, phylogeny.

**Riassunto** - Una nuova specie di *Pontosaurus* (Squamata, Pythonomorpha) dal Cretacico superiore del Libano e una analisi filogenetica dei Pythonomorpha.

Viene descritto un nuovo squamato fossile marino e ne vengono analizzate le relazioni filogenetiche. Il taxon rappresenta una nuova specie di *Pontosaurus*, genere di cui era precedentemente nota solamente la specie tipo, con un singolo esemplare, denominata *Pontosaurus lesinensis* (Kornhuber, 1873). Il nuovo esemplare qui descritto è molto ben conservato: la coda di 163 vertebre è completa e sono presenti resti delle squame. Vengono messe in luce nuove e importanti caratteristiche della scatola cranica: 1) la posizione del sopraoccipitale e la sua sovrapposizione al parietale; 2) l'esteso contatto del processo alare dei prootici con il parietale; 3) la riduzione del processo paraoccipitale. Una analisi filogenetica dei pitonomorfi che utilizza questi nuovi caratteri in una matrice di 77 caratteri e 10 taxa terminali produce nove alberi con una lunghezza di 119 steps (CI = 0.773; HI = 0.226). Questi nove alberi variano unicamente nelle relazioni filogenetiche di *Aphanizocnemus libanensis* entro i pitonomorfi non-mosasauroidi, e nelle relazioni filogenetiche interne dei pitonomorfi ofidi. Ad esempio il primo cladogramma presenta la seguente articolazione dei successivi sistergroups: ((Aigialosauridae, Mosasauridae) (Dolichosauridae (*Aphanizocnemus libanensis* ((*Pontosaurus lesinensis*, *Pontosaurus kornhuberi*) (*Adriosaurus suessi* (*Pachyophis woodwardi* (*Pachyrhachis problematicus*, Serpentes)))))). La morfologia funzionale dei pontosauri viene discussa nel contesto della filogenesi ipotizzata, evidenziando l'importante funzione locomotoria della coda e degli arti.

**Parole chiave** - Squamati, pitonomorfi, rettili marini, Cretacico, Libano, filogenesi.

## INTRODUCTION

Over the course of their known history, encompassing more than 130 million years, squamate reptiles evolved a wide and surprising array of anatomies as the various clades radiated and adapted into both terrestrial and aquatic environments. For example, limb reduction to complete limblessness, usually associated with extreme increases in body length, is observed in almost all lineages of living squamates (Greer, 1991; Caldwell, 2003) and certainly characterizes the nearly 3,000 species of snakes, which are arboreal, terrestrial, fossorial, cryptic, and aquatic. Modern squamates also show an amazing range in size from the incredibly large komodo dragons to the smallest known living amniotes *Sphaerodactylus ariasae*, a Caribbean gecko, which is only 16 millimeters long (Hedges & Thomas, 2001).

The list of modern squamate adaptations and anatomical innovations allowing them to colonize varied environments is extensive with but two exceptions - the air and the sea. Among more than 7,000 species of living squamates, none have evolved powered flight though some do glide, and only 59 species have evolved and adapted to life in aquatic marine environments: one species of iguana, 50 species of true sea snakes, 5 species of sea kraits, and 3 species of file snakes.

Interestingly, while these living squamates show remarkable adaptations to life in marine environments, the true acme of squamate evolution in marine environments is not found among modern species, but rather among fossil squamates. It is the extinct pythonomorphs, i.e., the dolichosaurs, pontosaurs, aigialosaurs, mosasaurs, and

early snakes, which truly became “aquatic” in every sense nearly 100 million years ago. This aspect of squamate evolution and evolutionary history is very poorly detailed in the literature purporting to evaluate aspects of squamate evolution. For example, the recent and excellent treatise on lizard diversity and evolution by Pianka & Vitt (2003: 260) only uses the word “mosasaur” once in more than three hundred pages, and never even mentions the existence of aigialosaurs, dolichosaurs, pontosaurs, adriosaurus or coniasaurus. As a result, there is also no discussion of the extent of pythonomorph evolution and adaptation to marine environments. This knowledge vacuum can only be rectified by the presentation of synthetic works, fusing phylogeny, function, and anatomy, that detail these missing pieces of squamate evolutionary history.

This study presents a description and phylogenetic analysis of a new species of ancient marine squamate, assigned to the genus *Pontosaurus*, that was found in 95 million year old rocks (Upper Cretaceous) in Lebanon. This new specimen is remarkably complete, including the preservation of soft tissues, and thus permits a unusual degree of “biological” interpretation (Pl. 1). The genus *Pontosaurus* was previously based on only one specimen, GBA 1873/4/2 (GBA, Austrian Geological Survey, Wien, Austria), the type species, *Pontosaurus lesinensis* (Kornhuber, 1873). *Pontosaurus lesinensis* was found in rocks outcropping on the island of Hvar, Croatia (Pierce

& Caldwell, 2004) that are considered to be chronoequivalents of those in Lebanon that produced the new species described here.

The new specimen was collected from a quarry in the Valley of Al Gabour near Al Nammoura, 10 km southeast of Hadjula, Lebanon (Dal Sasso & Pinna, 1997; Dal Sasso & Renesto, 1999). Previous to this work, Dal Sasso & Pinna (1997) had described the first known lizard from the marine sediments of Lebanon, *Aphanizocnemus libanensis*, which is considered to be Middle Cenomanian in age and was collected at a third quarry near Hakel, Lebanon. The specimen described here is therefore the second known lizard from the platy limestones of Lebanon and is a very different animal compared to *A. libanensis*.

Recent work by Caldwell & Dal Sasso (2004) described the remarkably well-preserved squamation of the new lizard, a feature not usually preserved in vertebrate fossils and certainly not for squamates. In this study the squamation will be reviewed as part of the overall description of the specimen, but the focus will be on the osteology. Characters obtained from this study will be added to a modified version of the character matrix of Pierce & Caldwell (2004) for the purpose of constructing a phylogenetic hypothesis of all pythonomorphs.

## PONTOSAURS, DOLICHOSAURS AND BASAL PYTHONOMORPHS: AN OVERVIEW

In 1873, Kornhuber described a new genus and species of Cretaceous lizard from two separate specimens preserved on platy limestone slabs that had come from quarries outcropping on the island of Hvar, Croatia, known in Italian as Isola di Lesina. Kornhuber’s plate “A” preserved the posterior portion of the skeleton of a small reptile; this plate made its way to Vienna, Austria, by 1869. Kornhuber’s second specimen, plate “B”, arrived in Vienna in 1870 and preserved the anterior portion, including the head, neck and forelimbs, of a second small reptile. Kornhuber’s comparison of the two specimens led him to conclude they were the same thing, if not the same individual, and he therefore assigned them to the same species, *Hydrosaurus lesinensis*; the genus *Hydrosaurus* (Wagler, 1830) is now recognized as the junior synonym of the extant monitor lizard genus, *Varanus* (Merrem, 1820).

In 1892, Gorjanovic-Kramberger renamed *Hydrosaurus lesinensis* as *Pontosaurus lesinensis* (Kramberger, 1892) based on his assessment that it was not similar enough to the extant *Varanus* (= *Hydrosaurus*) to warrant assignment to that genus. In the act of recognizing yet another fossil Adriatic lizard, including *Aigialosaurus dalmaticus* (Kramberger, 1892), *Adriosaurus suessi* (Seeley, 1881), and *Acteosaurus tomassinii* (Meyer, 1860), Kramberger created the Family Aigialosauridae to include all the fossil forms.

Nopcsa (1903) reevaluated the systematic position of *P. lesinensis* in a study that included all of Kramberger’s (1892) taxa, as well as *Dolichosaurus longicollis* (Owen, 1850),

*Opetiosaurus buccichi* (Kornhuber, 1901), *Carsosaurus marchesetti* (Kornhuber, 1893), and *Mesoleptos zendrinii* (Cornalia, 1851). Nopcsa (1903) identified common features shared by *Pontosaurus*, *Acteosaurus*, *Adriosaurus* and *Dolichosaurus*, and assigned them all to the family Dolichosauridae (Gervais, 1852), while *Aigialosaurus*, *Opetiosaurus*, *Carsosaurus*, and *Mesoleptos* were assigned to the family Aigialosauridae.

Since Nopcsa (1903), except for brief mentions in comparative studies (Nopcsa, 1908, 1923; Calligaris, 1987/1988; Rieppel, 1988; Dal Sasso & Pinna, 1997; Dal Sasso & Renesto, 1999), *Pontosaurus* had never been reexamined in any detail until the study of Pierce & Caldwell (2004). The latter study attempted to assess Nopcsa’s (1903) assignment of *Pontosaurus* to the Dolichosauridae based primarily on recent analyses of existing specimens of *Adriosaurus*, *Acteosaurus*, *Dolichosaurus* and *Coniasaurus* (Caldwell, 1999a, 1999b; Caldwell, 2000; Caldwell & Cooper, 1999; Lee & Caldwell, 2000; Caldwell & Lee, 2004).

Owen (1850) described two monotypic genera of marine lizards, *Dolichosaurus longicollis* and *Coniasaurus crassidens*, based on a number of specimens collected from the Lower Chalk (Cenomanian; Upper Cretaceous) of southeast England. *Dolichosaurus* was diagnosed by a uniquely high number of cervical and dorsal vertebrae while unique tooth characters diagnosed *Coniasaurus*; Owen did not identify any characters linking these two taxa. Nopcsa (1908) restudied Owen’s specimens and added several new specimens to the list of known con-

asaurs and dolichosaurs. Unfortunately for *Coniasaurus*, Owen (1850) had misidentified the tooth-bearing element of the type specimen (a maxilla) as a dentary leaving Nopcsa (1908) to build on this error by first, not finding the true type, and second, by identifying a pair of well-preserved dentaries as Owen's type specimen (see Caldwell & Cooper [1999] for the venue of the holotype and a redescription of the type material). Caldwell's (1999a) description of *Coniasaurus gracilodens* highlighted several notable differences with *C. crassidens* such as tooth shape, maxillary tooth number, and robustness of the maxilla (the maxilla of *C. crassidens* is much more elongate than that of *C. gracilodens*). Interestingly, all species assigned to *Coniasaurus* are known only from disarticulated skulls and isolated vertebral elements. In contrast, the type and referred specimens of *Dolichosaurus longicollis* are articulated postcranial skeletons with only one very fragmentary skull and no preserved teeth (Caldwell, 2000). Without consideration of pontosaurs, adriosaur, or acteosaurs, coniasaur and dolichosaur have been thought to be nested within basal mosasauroids (mosasaur and aigialosaur) since Nopcsa, (1908), or recently, since Caldwell's (1999b) hypothesis that they are the sistergroup to mosasauroids. The difficulty in resolving the *Coniasaurus* - *Dolichosaurus* problem is that both taxa are represented by non-comparable data: *Dolichosaurus* is known from complete postcrania with little or no skull material, while both species of *Coniasaurus* are known from skulls and only a small number of disarticulated vertebrae.

Nopcsa's (1903) suggestion that pontosaurs, adriosaur,

acteosaurs, coniasaur, and dolichosaur might all be assigned to the Dolichosauridae, in association with recent studies proposing a sistergroup relationship between all these taxa and the mosasauroids (Caldwell, 1999b; Lee & Caldwell, 2000), highlight the phylogenetic importance of these animals in understanding the evolution of Mesozoic marine squamates. Recent work by Caldwell & Lee (1997), Lee & Caldwell (1998, 2000), and Caldwell (1999b), all of which examined the larger problem of squamate phylogeny, found Serpentes to be nested within a squamate clade including dolichosaurids and mosasauroids, a group referred to as the Pythonomorpha (see Cope's [1869] original diagnosis of this group as contrasted with Lee & Caldwell's [2000] slightly modified definition).

To date, the one hundred and fifty-five years of investigation on Cenomanian marine squamates has achieved the consensus view that the fossil forms (i.e., pontosaur, adriosaur, acteosaur, coniasaur, and dolichosaur) are closely related to each other; there is also a reasonable degree of consensus that these squamates share a common ancestor with mosasaurids and aigialosaurids. However, as to the phylogenetic position of this larger group within squamates, and of snakes with any one group of squamates, there is no common agreement. For the purposes of this study, I will consider pontosaurs, adriosaur, acteosaur, coniasaur, and dolichosaur as informal generic groupings assigned to the Pythonomorpha; the Dolichosauridae, the conventional taxon for all these taxa, will be treated as including only *Dolichosaurus* and *Coniasaurus*.

## SYSTEMATIC PALAEOLOGY

Reptilia Linnaeus, 1758

Squamata Opper, 1811

Pythonomorpha Cope, 1869

Genus *Pontosaurus* Kramberger, 1892

Type Species: *Hydrosaurus lesinensis*

Kornhuber, 1873

*Pontosaurus lesinensis* (Kornhuber, 1873)

Holotypus: GBA 1873/4/2 (GBA, Austrian Geological Survey, Wien, Austria): articulated cranial and postcranial remains of one individual; postcranium includes 12 articulated cervical vertebrae, 28 dorsal vertebrae, shoulder girdles, forelimbs, fragments of femur, and pelvic girdle.

Locus typicum: Hvar Island (= Isola di Lesina), 43°10'N, 16°30'E, Croatia; upper Cenomanian-upper Turonian (Upper Cretaceous).

Generic Diagnosis: Long, slender lizard possessing unique supraoccipital-parietal articulation, with supraoccipital resting on top of and forming w-shaped suture with parietal; elongation of all postdentary bones; 10-12 cervical vertebrae; hypapophyses with large, unfused peduncles on C2-C10; 26-28 dorsal vertebrae; fused scapulocoracoid with primary coracoid emargination.

*Pontosaurus kornhuberi* sp. nov.

(Figs. 1, 2, 3 A-B, 4-18)

Synonymy: cf. *Pontosaurus* sp. Caldwell & Dal Sasso, 2004.

Derivatio nominis: named in honour of Prof. A. Kornhuber in recognition of his contributions to the study of pythonomorph squamates.

Holotypus: MSNM V3662: complete, articulated skeleton of one individual (1,037 mm in length), including trachea, bronchi and squamation, preserved on platy limestone slab, housed in the Museo di Storia Naturale di Milano.

Diagnosis: Maxilla with large medially inflected premaxillary process; jugal with distinct posteroventral tuberosity; parietal with broad flat, medially expanded dorsal table extending onto parietal rami; frontal margin emarginated with no distinct nasal processes; 10-11 cervical vertebrae; 26 dorsal vertebrae; 2 pygal vertebrae; 163 caudal vertebrae; non-imbricated scales on cheek, imbricated scales on remainder of body.

Locus typicum: Quarry in the Valley of Al Gabour near Al Nammoura, 10 km southeast of Hadjula, Lebanon (Dal Sasso & Pinna, 1997; Dal Sasso & Renesto, 1999).

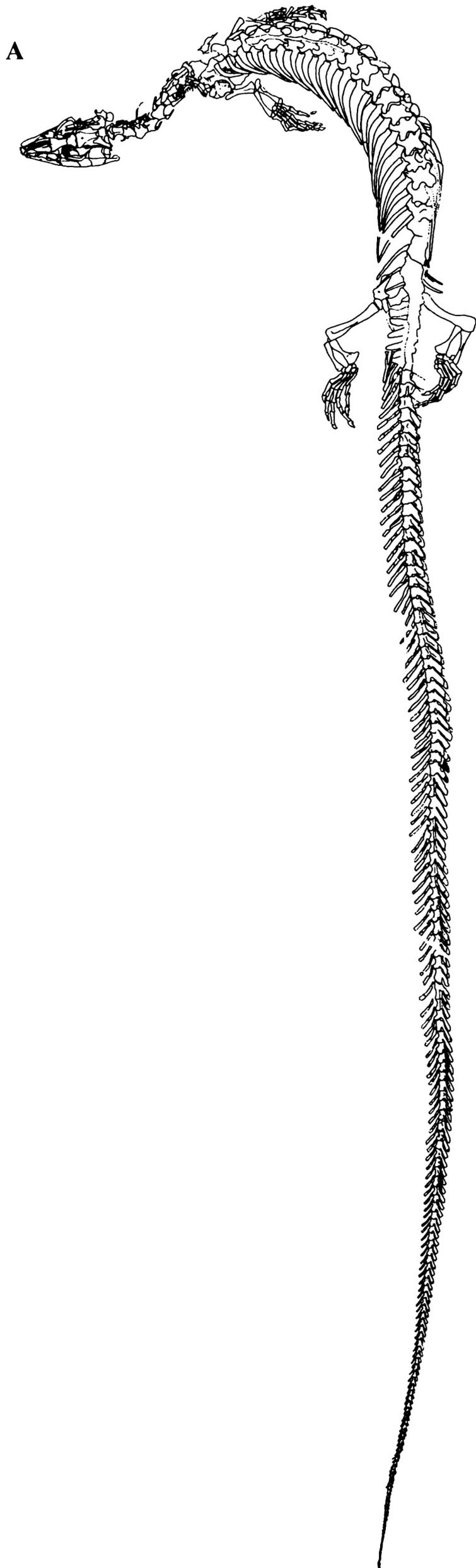


Fig. 1 - Holotype, *Pontosaurus kornhuberi*, MSNM V3662. A) Interpretative drawing; B) photo. Scale bar = 10 cm.

## OSTEOLOGICAL DESCRIPTION

### State of preservation

MSNM V3662 possesses a long (46 mm long), thin skull (18.6 mm wide) with large orbits (Figs. 1, 2, 3 A-B) and an elongated postorbital region. The skull is flattened and preserved in dorsal view, but was clearly compressed from the left as the left mandible is exposed in lateral view while the right has rotated medially underneath the dermatocranium; only the medial aspect of the right mandible is visible to the right of the parietal. Likewise, the left maxilla has shifted into lateral view, and is broken away; the right maxilla is preserved in dorsal view, but is crushed downwards so that the ascending process is compressed onto the maxillary shelf. The neck bears at least 10 and probably 11 cervical vertebrae with ribs, and a trachea extending to the third dorsal rib. The limbs are well developed, and the fore-

are both well preserved and in articulation. There are 26 pachyostotic trunk vertebrae and ribs; pachyostosis is not evident in the sacral or caudal skeleton. The tail is exceptionally long (680 mm) and possesses 163 caudal vertebrae; the number of caudals is reduced by two from the 165 as reported by Caldwell & Dal Sasso (2004) due to the recognition in this study of two probable pygal vertebrae. The haemal spines are almost twice as long as the neural spines and articulate with distinct haemapophyses; transverse processes disappear at the 8<sup>th</sup> caudal vertebra. Detailed preservation in this fine-grained limestone has preserved the squamation both as molds, casts, and in many places, the original material included tonal variation.

### Skull

The skull is represented by the premaxilla, right maxilla and partial left maxilla, fragments of the septomaxillae, vomers, and possibly nasals, partial right and left prefrontals, complete right and left jugals, the left postorbital, postfrontal, and squamosal, and fragments of the right-side series of the same, a well preserved frontal, and parietal, the supraoccipital, a well-preserved left exoccipital-opisthotic and fragments of the right, probable left and right prootics, a left quadrate with fragments of the right, a well preserved left dentary with teeth, a well preserved left surangular with a poorly exposed right surangular, left and right articulars (Figs. 2, and 3 A-B), and perhaps the quadrate ramus of the right pterygoid.

### Premaxilla

The premaxilla is a single bone and is well preserved though broken into small fragments along the length of the premaxillary bar (Fig. 4 A-B). The anterior tooth-bearing portion of the premaxilla (Fig. 4 C-D) is a small median element that flares right and left to support two teeth on each side of the sagittal plane (Figs. 2, 3, and 4). At its anterior tip, it is broad and flat with a small space equivalent to the width of one tooth base separating the right and left pairs of teeth; the anterior extent of the bone is posteriorly deepened just enough to support the alveoli for the four teeth and immediately becomes constricted posterior to this point in order to form a long and thin narial bar similar to that of *Pontosaurus lesinensis* (Fig. 3 C-D) (Pierce & Caldwell, 2004).

The premaxilla and its internarial bar is much better preserved in MSNM V3662 than that of the type of *Pontosaurus lesinensis* (Fig. 3 A-D) and shows an important feature shared in common with *Coniasaurus gracilodens* Caldwell, 1999. On the right side of the premaxilla in MSNM V3662 there is a small, laterally positioned fossa or small platform that lies below the level of the internarial bar and immediately posterior to the tooth bearing portion of the bone (Fig. 4 C-D). Immediately lateral, and still in proximate articulation is a matching,



Fig. 2 - *Pontosaurus kornhuberi*, MSNM V3662, detail of the skull.

limb (65 mm long) is reduced in size relative to the rearlimb (98 mm long); the right forelimb is not well exposed but the left is well preserved and articulated. The rearlimbs

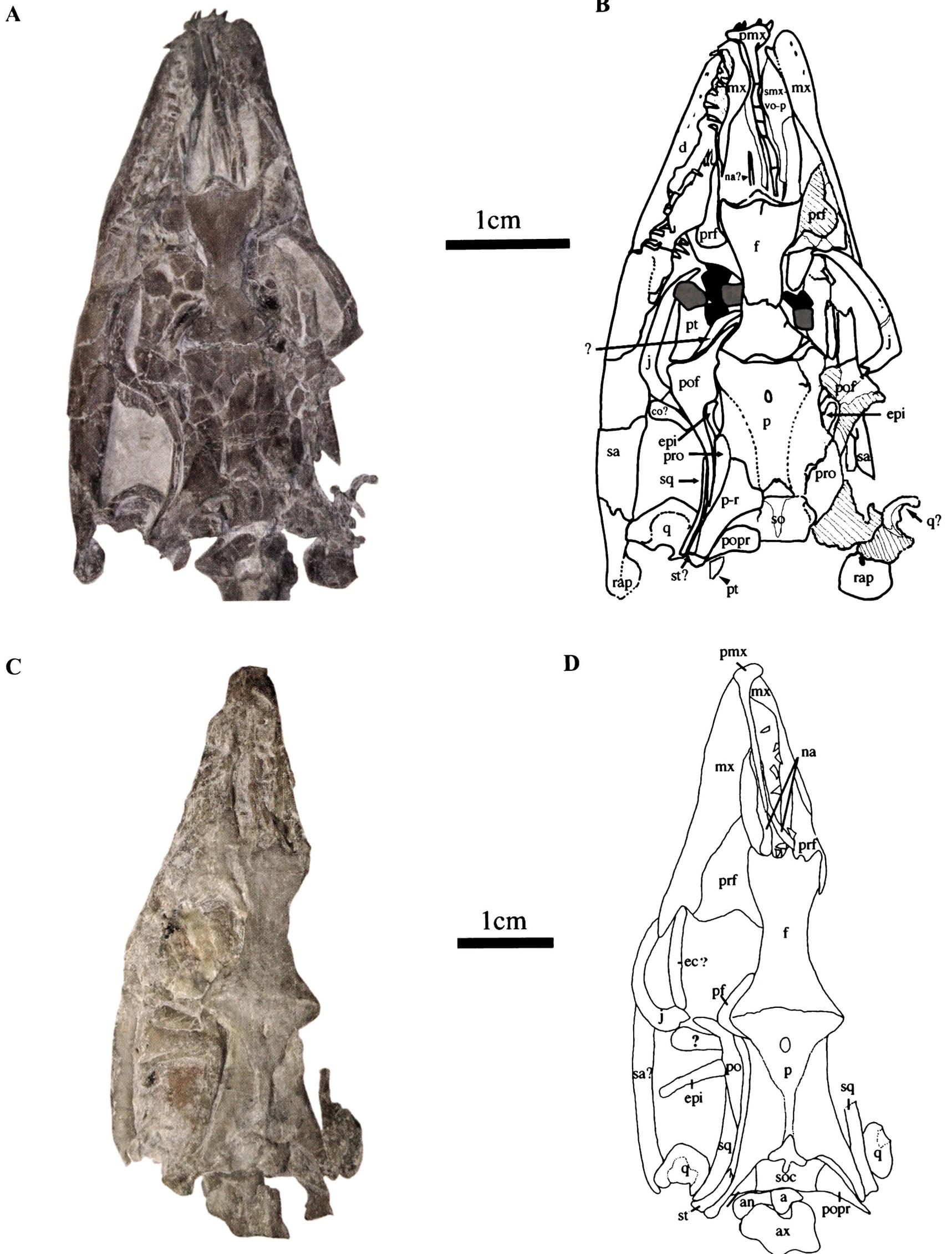


Fig. 3 - Skulls of *Pontosaurus kornhuberi* MSNM V3662 (A-B) and *Pontosaurus lesinensis* GBA 1873/4/2 (C-D). A) Dorsal surface of skull; B) line drawing of same; C) dorsal surface of skull; D) line drawing of same. Abbreviations: a, atlas intercentrum; an, atlas neural arch; ax, axis; co, coronoid; d, dentary; ec, ectopterygoid; epi, epipterygoid; f, frontal; j, jugal; mx, maxilla; na, nasal; p, parietal; p-r, parietal ramus; pf, postfrontal; pmx, premaxilla; pof, postorbitofrontal; po, postorbital; popr, paroccipital process of the exoccipital-opisthotic; prf, prefrontal; pro, prootic; pt, pterygoid; q, quadrate; rap, retroarticular process; smx-vo-p, septomaxilla and vomeropalatine; soc, supraoccipital; sq, squamosal; st, supratemporal; sa, surangular.

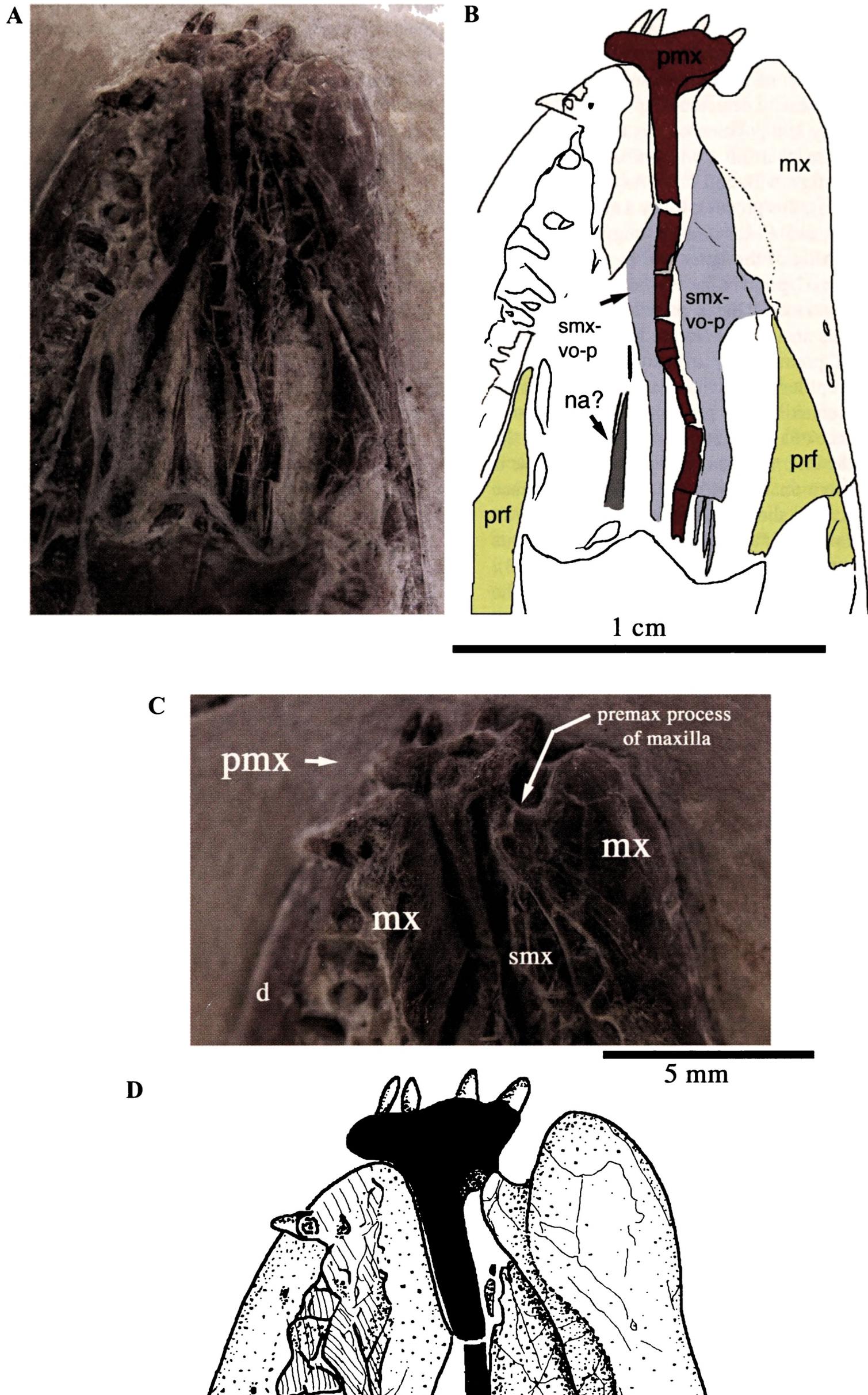


Fig. 4 - Snout of *Pontosaurus kornhuberi*, MSNM V3662. A) Overview of palatal elements viewed through external narial opening; B) line drawing with palatal and snout elements illustrated in color (premaxilla = red; septomaxilla and vomeropalatine = blue; prefrontal = yellow; possible nasal fragment = grey); C) photo detail of premaxilla showing right and left maxillae, premaxillary bar, and well preserved premaxillary process of right maxilla; D) line drawing of same with premaxilla highlighted in red. Abbreviations: see Fig. 3.

anteromedially directed hook-shaped process extending from the maxillary shelf of the right maxilla. The sidewall of the right maxilla is compressed on top of the maxillary shelf but the separation of the transverse shelf and vertical sidewall are still easily detected (Fig. 4 C-D).

The morphology and position of this anatomical feature is identical to that of *Coniasaurus gracilodens* (Caldwell, 1999a, figs. 6 B, and 7 B). As was suggested by Caldwell (1999a), this process, likely a synapomorphy of *C. gracilodens* and *P. kornhuberi*, suggests that the very small premaxilla of the latter and by extension the probably equal sized premaxilla of the former, would have been mobile around these paired processes. The morphology of this anatomical feature hints at an unsuspected degree of premaxillary mobility in these small pythonomorph reptiles. The maxilla was not firmly sutured to the premaxilla, the premaxilla was long, and there is no evidence of a firm suture with the frontal at the posterior tip of the internarial bar. Similar snout kinesis is observed in modern snakes with the notable difference being the significantly shorter narial bar (Frazetta, 1970).

The internarial bar of *Pontosaurus kornhuberi* appears to bear a tiny notch at the posteriormost tip (Fig. 4 A-B); presumably, this notch contacted some portion of the internarial process of the frontal. It is not clear how firmly sutured this contact was, but it appears to have been rather loose. In contrast to *P. kornhuberi*, the internarial bar of *P. lesinensis* is sandwiched between a pair of nasal bones situated along its lateral borders that appear to restrict the premaxillary contribution to the external narial opening and seem to prevent its contact with the frontal bone, a scenario consistent with all squamates except mosasauroids (Fig. 3 C-D; Pierce & Caldwell, 2004). If nasals were present in *P. kornhuberi*, they are not well represented in MSNM V3662 by anything more than one possible sliver of bone lying in the left narial opening (Fig. 4 A-B). It is also possible that this fragment is a portion of the palatine and not the nasal. Further support for the absence of nasal bones is the different frontal margin morphology of *P. kornhuberi* as compared to *P. lesinensis* (the former is an effaced “w”-shape while the latter is a “w-w”-shape bearing two small nasal processes parasagittal to the internarial process [Fig. 3 C-D]).

### Maxilla

The left maxilla is very poorly preserved and will not be described here. The right is much better preserved (Figs. 2, 3 A-B, 4) even though it is only visible in dorsal view; an accurate tooth count is therefore problematic. As described previously, the anterior tip of the maxilla is rounded and rises gently into a shallow but vertically oriented lateral wall that frames the margin of the narial opening (Fig. 4 A-B). Medial to the sidewall of the maxilla and near the anterior tip of the bone, is a well-developed premaxillary process that extends medially and anteriorly towards a fossa or recess on the premaxilla; the maxillary shelf, beginning immediately posterior to the premaxillary process, bears a scalloped margin lateral to its contact with the vomers. In dorsal view the anterior two-thirds of the maxilla shows an

identical morphology to the maxilla of *Coniasaurus gracilodens* (Caldwell, 1999a). The difference between the maxillae of *P. kornhuberi* and *C. gracilodens* is the height and extent of the ascending process of the maxilla in the latter taxon. *Pontosaurus kornhuberi* possesses a low ascending process, similar to *P. lesinensis* (Fig. 3 A-D) and a fairly long anteriorly directed prefrontal that blocks any articulation between the frontal and maxilla. In *P. lesinensis* the ascending process is a long, low sloping feature of the maxilla that rises to form only about one half of the lateral margin of the narial opening (Fig. 3 C-D); a similar condition also characterizes *P. kornhuberi* except that the maxillary contribution to the narial opening is less, comprising about two fifths of the margin (Figs. 3 A-B, 4 A-B).

The posterior process of the maxilla extends below the orbit only far enough to contact the anterior tip of the jugal. However, this distance appears to be equal to about one half of the orbit diameter; a similar condition is observed in all mosasauroid pythonomorphs (Russell, 1967). Due to preservation and orientation of the element, it is not possible to determine how far posteriorly, and perhaps how far beneath the orbit, the dentition extended. In *Pontosaurus lesinensis* (Pierce & Caldwell, 2004), *Coniasaurus gracilodens* (Caldwell, 1999a) and *C. crasidens* (Caldwell & Cooper, 1999), the dentition terminates at the anterior margin of the orbit, as it does in other mosasauroids; it seems likely that the same condition exists in *P. kornhuberi*.

Although a maxillary tooth count is not possible, some aspects of the maxillary dentition are preserved on the left side of the skull and are worth describing. Most of the anterior teeth have been crushed and broken but some are well enough preserved so that their general outline can be observed: sharp slightly recurved piercing teeth set within a mass of ossified tissue as in other mosasauroids (Russell, 1967; Carroll & deBraga, 1992; deBraga & Carroll, 1993; Caldwell *et al.*, 2002); fluting similar to that observed in *Pontosaurus lesinensis* is not visible.

### Septomaxilla

The septomaxillae are likely preserved in *Pontosaurus kornhuberi*, but it is not possible to differentiate the morphology of either the left or right element due to dorsal-ventral compaction of the bone on top of vomeropalatines (Fig. 4 A-B). Comparing the morphology of the anterior portion of the compressed septomaxilla/vomeropalatine mass to the probable septomaxilla of *Coniasaurus gracilodens* (Caldwell, 1999a, fig. 9), where the latter is shaped like an obtuse triangle with a tall, median crest paralleling the internarial bar indicates that the septomaxilla of *Pontosaurus kornhuberi* was similarly shaped and anteriorly located. However, it also must be remembered that this is not a certain identification but rather a discussion of the general similarities between these two taxa; by comparison, there are no preserved remnants of the septomaxillae in *Pontosaurus lesinensis* (Fig. 3 C-D).

### Vomeropalatines

As with the septomaxilla, it is not possible, due to

preservational factors, to determine whether or not the vomers and palatines were separate bones. As it has been shown that the two elements are fused in mosasaurs (Russell, 1967) and *Coniasaurus gracilodens* (Caldwell, 1999a, figs. 10, 11), these two elements are discussed here as though they were a single fused structure (the elements are not distinguishable in *Pontosaurus lesinensis* [see Pierce & Caldwell, 2004]).

The vomeropalatines of MSNM V3662 are elongate, strap-like elements that parallel the sagittal plane but do not appear to meet at the midline (Fig. 4 A-B). The posterior extent of the bone appears to be beneath the frontal (the palatine ramus), but there is some uncertainty as exposed and this statement must be made only tentatively. Anteriorly, at a point equivalent to the anterior termination of the prefrontal, the vomeropalatine extends a lateral process to contact the maxilla (maxillary process of the palatine); at this point the vomeropalatine continues anteriorly following the margin of the maxillary shelf to the medial divergence of that shelf where it forms the premaxillary process (Fig. 4 A-B). The tips of the vomeropalatine appear to diverge away from the midline as they converge towards the premaxillary process. Details such as the position of Jacobson's Organ, or the aperture of the medial palatine sinus, are not visible as preserved.

#### Prefrontal

The prefrontal is an anteriorly elongate element with the anterior process extending at least three-fifths of the length of the narial opening along the medial surface of the side wall of the maxilla. Posterodorsally, the prefrontal contacts the frontal along about one quarter of the length of the frontal and then descends ventrally to contact the anterior tip of the jugal and the posterior process of the maxilla. Overall, the exposed surface of the right prefrontal, as preserved, resembles the sail of a tall sailboat (Figs. 2, 3 A-B, 4 A-B). The articulation with the maxilla is an important and characteristic feature of pontosaurs and is shared in common by both species: the suture is long and low and slopes gently towards the narial opening. The result is that there is no ascending process of the maxilla, creating a similar profile to that observed in many extant snakes; this feature contrasts sharply with that described by Caldwell (1999a) for *Coniasaurus gracilodens* where the maxilla has a well-developed ascending process. The difference between *Pontosaurus lesinensis* and *P. kornhuberi* is that in the former the maxilla and prefrontal comprise equal portions of the margin of the narial opening, whereas, as noted for the latter, the prefrontal is three fifths of the margin of the opening.

#### Nasals

As noted previously, it is not clear from the specimen (Fig. 4 A-B) as to the presence or absence of the nasal bones. This is in direct contrast to the relatively well-preserved nasals of *Pontosaurus lesinensis*, where the nasals are thin, flat and paired, (Pierce & Caldwell, 2004) (Fig. 3 C-D).

#### Lacrimal

It is not possible to identify the presence or absence of a lacrimal in *Pontosaurus kornhuberi* as the area on either side of the skull, ventral to the prefrontals, is heavily crushed and deformed (Figs. 2, 3 A-B, 4 A-B). As was noted by Pierce & Caldwell (2004), Kornhuber (1873) had reported a trace of the right lacrimal posterodorsal to the maxilla and anterior to the jugal, but such an element was not visible to the former authors. The massive size of the prefrontal would suggest, if analogous to snakes, that the lacrimal is absent in both species of *Pontosaurus* as it is in snakes, *Pachyrhachis* (Lee & Caldwell, 1998) and many other squamate groups (Estes *et al.*, 1988).

#### Jugal

Both the right and left jugal are well preserved in *Pontosaurus kornhuberi* (Figs. 2, 3 A-B, 5 A-C). The anterior edge of the jugal arch extends forward to meet the prefrontal anteriorly and the maxilla ventrally and may well have extended anteriorly past the orbit as in other mosasauroids (deBraga & Carroll, 1993); this observation is contra the condition reported in *P. lesinensis* by Pierce & Caldwell (2004) except that the anteriormost tip of the jugal is not visible and so may well have overlapped the maxilla, thus extending anterior to the orbit.

A second difference is also noted between the two species: in *P. kornhuberi* the two rami of the jugal form a distinct angle at the posteroventral corner of the orbit producing a well-developed posteroventral tuberosity. In contrast, in *P. lesinensis* the jugal curves gradually in an anterior direction to contact the lateral process of the postorbital. In all other respects, the jugal of *Pontosaurus lesinensis* is of roughly similar size and shape to that of *P. kornhuberi* (Fig. 3 A-D).

#### Frontal

The frontal is a long, flat element that comprises approximately one-third of the total length of the skull (Figs. 2, 3 A-B, 5 A-B). As is common to pontosaurs and coniasaurs the outline in dorsal view resembles an hourglass that is broadly expanded at both its anterior and posterior ends and is constricted above the orbits (Caldwell, 1999a; Pierce & Caldwell, 2004); this configuration is very similar to that of modern macroteiids (Estes *et al.*, 1988). In *Pontosaurus kornhuberi*, the anterior expansion of the frontal is only marginally more narrow than the posterior expansion at the frontal-parietal suture; this contrasts with the condition in *P. lesinensis* where the anterior expansion is noticeably more narrow than the expansion at the frontal-parietal suture, and with *Coniasaurus gracilodens* (Caldwell, 1999a, figs. 4, 5) where the posterior expansion is twice the width of the anterior expansion.

In *Pontosaurus kornhuberi*, the anterior border of the frontal has only three processes (Figs. 2, 3 A-B, 4 A-B): one large sagittal process and two equal-sized large lateral processes. In contrast, the frontal of *P. lesinensis* has five processes: one large sagittal process, two large lateral processes, and two small parasagittal processes (Fig. 3 C-

D). In both species, the external edge of the lateral processes articulates with the prefrontals, while the internal rim forms the posterior margin of the external narial opening. Pierce & Caldwell (2004) noted that the nasals of *P. lesinensis* were clasped by the unpaired sagittal, and paired parasagittal, processes. The absence of the paired parasagittal processes in *P. kornhuberi* may well relate to the absence of identifiable nasal bones. The sagittal process of *Pontosaurus kornhuberi* is smooth as it is in *P. lesinensis*; in contrast, the sagittal process of *Coniasaurus gracilodens* bears a low but clearly defined sagittal crest that extends posteriorly about one quarter of the length of the frontal.

At its midpoint, the constricted frontal forms the dorsal margin of the orbit. The prefrontal and postorbitofrontal do not meet above the orbits as they do in higher mosasauroids (Russell, 1967), but are widely separated over the orbit as they are in *Pontosaurus lesinensis* (Fig. 3 C-D) and *Coniasaurus gracilodens* (Caldwell, 1999a, figs. 4, 5).

The posterior border of the frontal describes an obtusely angled w-shape along its margin with the parietal; this margin represents a gap of considerable size and is not interpreted as an artifact of preservation, but rather is very well preserved. It is possible that this morphology represents the adult condition and that there was a high degree of mesokinesis in pontosaurs. It is also possible that frontal-parietal ossification was delayed in this animal, either that it was a younger individual or that in fact dermatocranial ossification was delayed in *Pontosaurus kornhuberi*. In comparison, the frontal-parietal margin in *Pontosaurus lesinensis* is relatively simple and straight with the two bones fitting together very tightly (Fig. 3 C-D).

#### Parietal

The parietal is a single element composing approximately one-third of the total skull length (Figs. 2, 3 A-B, 5 C, 6 A-D). In general terms, the suture with the frontal is long and describes an obtuse “w”-shaped outline with large parietal lappets lying below the frontal. Along the lateral edge of the frontal-parietal suture, the anterolateral projection of the parietal is broadly overlapped by the postorbitofrontal. Laterally and ventrally, the parietal is broadly expanded to form a long and deep decensus parietalis (Figs. 3 A-B, 5 C, 6 A) which rises slightly at its midpoint at the sutural contact with an element identified here as the prootic. The dorsal surface of the parietal is not developed into a long thin crest as in *P. lesinensis* (Fig. 3 C-D), but rather is broad, flat table-like surface. The parietal foramen is not as large as that of *P. lesinensis*; it is also an equivalent distance posterior to the parietal-frontal suture in both species.

The prootic margin of the parietal also appears to contact the margin of the supraoccipital; the latter margin is broad and wide in its contact with the parietal and is in the same plane: the supraoccipital does not lie beneath the parietal as in lizards but is in the same plane and articulates along its anterior margin as in snakes. There is also an interdigitating and overlapping sutural contact between the supraoccipital and parietal where the supraoccipital over-

lies the parietal on the midline in large triangular shaped depression (Fig. 6 A-D). This same condition is observed in *Pontosaurus lesinensis* (Fig. 3 C-D). The differences between *P. kornhuberi* and *P. lesinensis* are preservational: in the former, the overlapping portion of the supraoccipital is broken away leaving a fractured surface on the supraoccipital, whereas in *P. lesinensis* the small sagittal-crest like structure of the supraoccipital is still in place.

The parietal ramus for the suspensorium is well developed though only well preserved on the left side of the skull, where it contacts a small supratemporal element and the small, underlying paroccipital process of the exoccipital-opisthotic. The parietal ramus of *Pontosaurus kornhuberi* is broken away and displaced vertically from its position at the posterior edge of the decensus parietalis. In its proper articulation, the parietal ramus would have been oriented obliquely and would have formed a continuous surface with the decensus parietalis as in *P. lesinensis* (Fig. 3 C-D).

#### Postorbitofrontal

The postfrontal and postorbital of *Pontosaurus kornhuberi* appear to have fused to form a single, multi-rami element, the postorbitofrontal; the element is very well preserved on the left side of the skull, but very poorly preserved on the right. All descriptions given here are of the left side of the skull. Close inspection indicates the presence of an unidentified element immediately anterior to the left postorbitofrontal (Figs. 3 A-B, 5 A-C) that is considered here to be the left postfrontal. Squamates show a perplexing and problematic degree of plasticity in the presence, absence, or fusion, of the elements comprising the anterior portions of the supratemporal arcade. For example, some groups possess only a postorbital (snakes), while others possess both postfrontals and postorbitals (e.g., *Pontosaurus lesinensis* [Fig. 3 C-D]), while others, such as species assigned to the varanid genus, *Varanus*, and *P. kornhuberi*, possess a single, apparently fused, postorbitofrontal element. Some possess supernumerary elements, such as pythons, which have added a supraorbital bone. Assuming that the anterior element is not a true postfrontal, the remaining description will focus on the morphology of the left postorbitofrontal.

The left postorbitofrontal is a quadri-radiate element with four distinct rami contacting four very different components of the dermatocranium. The anterior or frontal ramus is a moderately long and thin spline of bone that begins at roughly the frontal-parietal suture and clasps the lateral margin of the frontal to a position roughly near the beginning of the supraorbital constriction (Figs. 2, 3 A-B, 5 A-C). The medial or parietal ramus of the postorbitofrontal is very short and medially directed. It clasps the margin of the parietal table just posterior to the frontal-parietal suture; there is a short section of the postorbitofrontal, between the frontal and parietal rami, that firmly abuts the lateral wing of the parietal immediately posterior to the frontal-parietal suture. The lateral or jugal ramus of the postorbitofrontal projects laterally only a short distance; this ramus is thickened posteriorly with

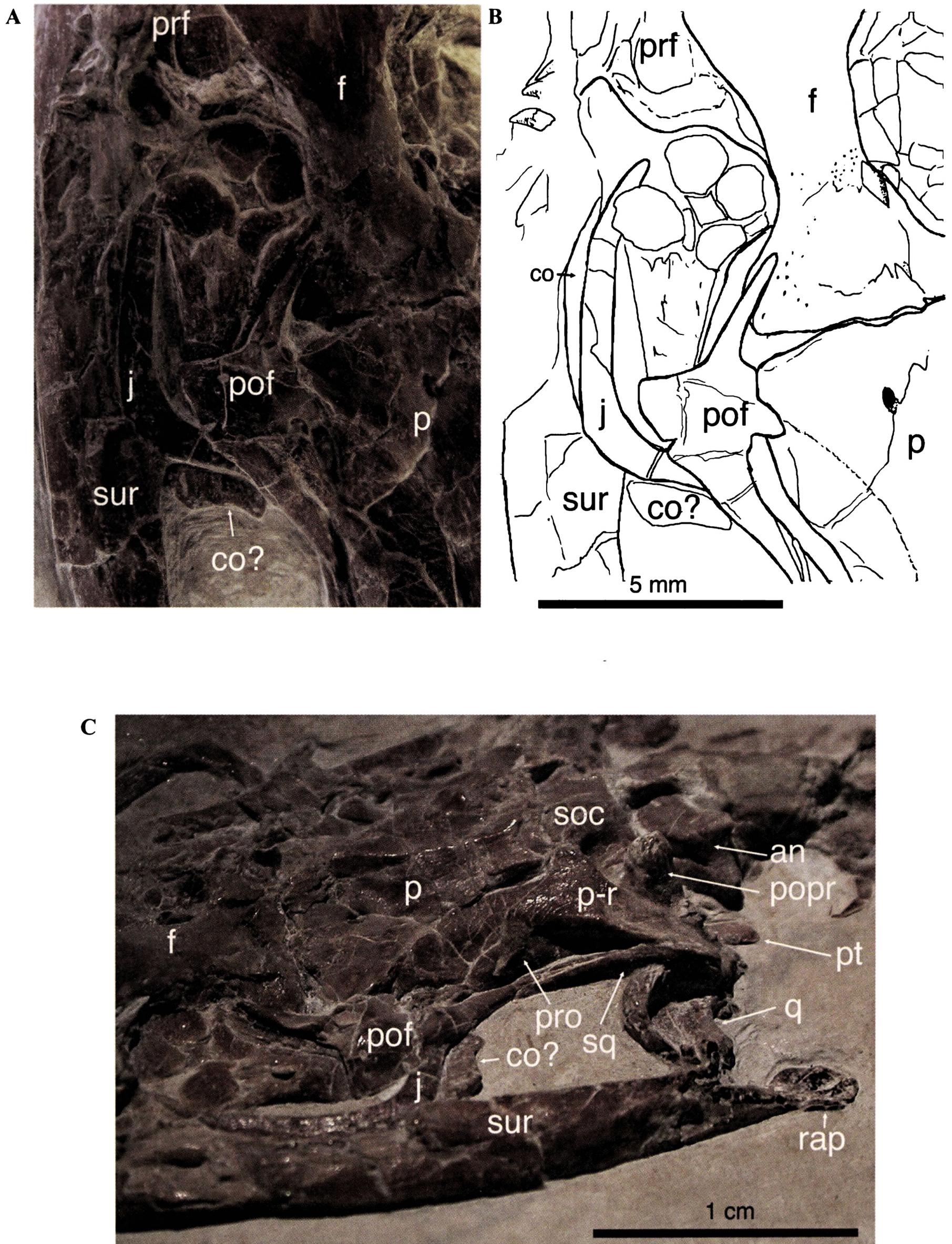


Fig. 5 - Mid-dorsal surface of the dermatocranium of *Pontosaurus kornhuberi*, MSNM V3662. A) Photo detail of left postorbital-frontal-parietal; B) line drawing of same; C) oblique view of left side of skull showing configuration of decensus parietalis and contact with left prootic. Abbreviations: see Fig. 3.

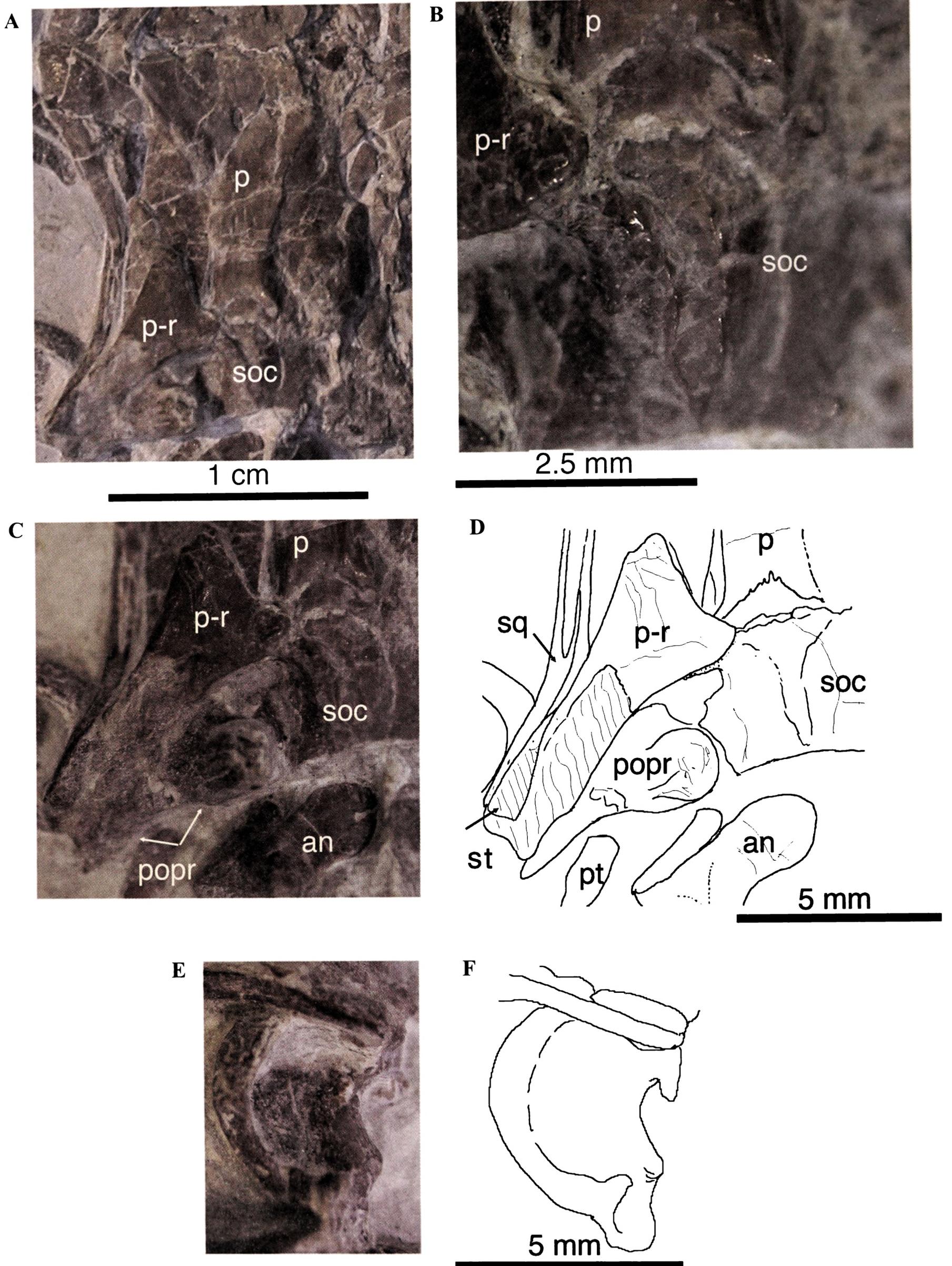


Fig. 6 - Postero-dorsal surface of dermatocranium of *Pontosaurus kornhuberi*, MSNM V3662. A) Overview of parietal; B) detail of supraoccipital and overlapping, interdigitating sutural contact onto parietal; C) detail of parietal ramus, squamosal, exoccipital, supraoccipital; D) line drawing of 'C'. E) left quadrate. F) line drawing of same. Abbreviations: see Fig. 3.

its anteriormost edge beginning parallel to the plane of the frontal-parietal suture. It is not clear if some portion of the jugal ramus was directed ventrally; however, it is possible that the ascending portion of the jugal contacted a small facet on the ventral surface of the jugal ramus similar to some mosasaurs (Russell, 1967) and many squamates (Estes *et al.*, 1988). The posterior or squamosal ramus of the postorbitofrontal is elongate and thin (Figs. 5 A-C, 6 A-C) extending posteriorly to a point equal to the contact of the parietal and supraoccipital. It overlaps the squamosal laterally and dorsally in an interfingering suture. The distance between the postorbitofrontal bar and the parietal crest is rather far even though the supratemporal fenestra appears to be relatively small anteriorly (Figs. 5 A-C, 6 A-C).

#### Postfrontal?

It is not clear if the postfrontal is present as a separate element in *Pontosaurus kornhuberi* even though it is clearly separate in *P. lesinensis* (Fig. 3 C-D). The postorbitofrontal, described previously, shows the typical squamate morphology of a fused postorbital ramus and body (posterior ramus contacting the squamosal and framing the supratemporal fenestra, main body contacting the jugal) and postfrontal ramus (anterior process clasping the frontal-parietal suture and extending anterolaterally along the frontal). However, there is an extra element in *P. kornhuberi* that lies anterior and lateral to the anterior ramus of postorbitofrontal the identity of which is uncertain (Figs. 2, 3 A-B, 5 A-C). The element is indicated with a “?” on Fig. 3 B. It is possible that it is a fragment of the pterygoid, or perhaps is a displaced palpebral bone, but as most of the skull is very well articulated, the latter possibility is considered remote. The element bears a striking resemblance to, and is in a similar position to, the postfrontal of *P. lesinensis* which is a large boomerang-shaped element (Fig. 3 C-D) that clasps both the frontal and parietal along its medial border and attaches to, but does not fuse with, the postorbital along its posterolateral surface.

The fusion of the postfrontal and postorbital in forming the postorbitofrontal is not a well-understood process, nor is it common among squamates. It is also clear from a survey of modern squamates that there is great deal of plasticity in the formation and fusion of the dermatocranial elements of the supratemporal and postorbital arcades (see Estes *et al.*, 1988). Non-scolecophidian snakes are considered to possess only a postorbital with the exception of *Dinilysia patagonica* which also possesses a discrete postfrontal (Caldwell & Albino, 2002); amphisbaenians and dibamids possess neither element; *Varanus* possesses a single postorbitofrontal element while *Lanthanotus* and *Heloderma* have only a postfrontal with the postorbital having been lost; anguids typically have both a postfrontal and postorbital, as do most other scincomorphs; gekkotans are treated as possessing a postorbitofrontal even though the posterior ramus is missing and iguanians show both a single element and paired element condition.

#### Squamosal

The squamosal is a thin band of bone that forms the posterolateral border of the supratemporal fenestra (Figs. 3 A-B, 5 C, 6 C-D). At the midpoint of the supratemporal fenestra, the squamosal articulates with the ramus of the postorbitofrontal; it underlies that element in a long, clasping articulation (Fig. 6 C-D). At its posterior tip, the squamosal contacts the quadrate laterally and the supratemporal medially. The element is slightly bent laterally at its posterior contact with the supratemporal and quadrate. A similar morphology is observed in *Pontosaurus lesinensis* (Fig. 3 C-D).

#### Supratemporal

The supratemporal is a small wedge of bone that as preserved, appears to articulate with the squamosal, quadrate and parietal ramus. Presumably it also contacted the paroccipital process of exoccipital-opisthotic; however, this is not clear as preserved and it is important to note that the paroccipital process appears to be quite short.

#### Supraoccipital

The supraoccipital of *Pontosaurus kornhuberi* (Figs. 2, 3 A-B, 6 A-D) is nearly identical in its morphology to that of *P. lesinensis* (Fig. 3 C-D) as reported by Pierce & Caldwell (2004); among squamates the pontosaur supraoccipital is a uniquely configured bone. The element broadly contacts the posterior margin of the parietal along its dorsal surface, not ventrally as in most lizard squamate groups. The element is broadly expanded along this contact and is posteriorly also very broad. The posterior margin of the supraoccipital is rounded and smooth and not emarginated as it is in many lizard squamates. There is no evidence that exoccipital-opisthotic bones met at the midline above the foramen magnum; it appears therefore that the dorsal border of the foramen magnum was formed exclusively by the supraoccipital.

Posterolaterally, the supraoccipital contacts the dorsal margin of the exoccipital-opisthotic bone close to the origin of the paroccipital process. Anterolaterally the supraoccipital appears to contact the posterolateral margin of the decensus parietalis to its contact with the prootic, where the supraoccipital appears to contact that margin in a smooth arc (Fig. 6 A-B).

On median dorsal surface of the supraoccipital (Fig. 6 A-B) is a small t-shaped area of roughened periosteum. On first observation this area appears to be a broken surface, but under high magnification it is clear that a small fragment of unossified tissue likely occupied this region and overlapped the parietal on the dorsal surface of that bone. As the supraoccipital is an endochondral element of the chondrocranium, it is not unlikely that the missing tissue was not ossified. Reconstructing the t-shaped portion and the portion that overlaps the parietal presents a final morphology to the supraoccipital of *Pontosaurus kornhuberi* that is identical to that of *P. lesinensis*.

In *Pontosaurus lesinensis* (Fig. 3 C-D) the supraoccipital has a rectangular base and a clover-shaped anteromedial shelf (Fig. 2). The “stem” and the two lateral “leaves” of the shelf rest on top of, and form a v-shaped suture with,

the parietal; this configuration comes close to that of snakes, but the supraoccipital in snakes never sits above the parietal. Instead the supraoccipital in snakes is level with and slightly on-lapped by the parietal. The third medial "leaf" forms a crest that runs down the center of the supraoccipital's rectangular base. The rectangular base gradually slopes caudally underneath the parietal until it contacts the atlas posteriorly, a configuration that typifies non-snake squamates (Estes *et al.*, 1988). On its lateral margin the supraoccipital meets the left and right exoccipital in a straight, anterior-posterior directed suture.

#### Exoccipital

As preserved and exposed the exoccipital-opisthotic is a long, curving acute triangle-shaped element with a short, robust paroccipital process. It contacts the supraoccipital dorsomedially, and the prootic anterolaterally. In *Pontosaurus lesinensis* the exoccipital-opisthotic shows exactly the same acute triangle outline, is broad along its contact with the supraoccipital (Fig. 3 C-D), and bears a large, oval paroccipital process ventrally (this process is derived from the opisthotic portion of the exoccipital bone). In *P. lesinensis* the contact with the prootic is not visible while it is visible, though obscured by crushing, on the right side of the skull in *P. kornhuberi* (Fig. 3 A-B).

#### Prootic?

The right and left prootics are tentatively identified here though it is possible that the fragments identified as prootics are symmetrically fractured portions of the decensus parietalis (Figs. 3 A-B, 5 C). The observable portions of both the right and left prootics are the anterolateral alar processes of the prootic. Ventral to this expansion is an opening or emargination of varying size and shape that serves as the exit point for the V<sup>th</sup> and VI<sup>th</sup> cranial nerves. In lizards such as *Varanus*, the anterior alar process of the prootic contacts the parietal on only a small point at the top of the projection. In snakes, the contact with the decensus parietalis is along the full length of the superior margin of the alar process creating distinct exit points, as foramina for the V<sup>th</sup> and VI<sup>th</sup> cranial. As preserved in MSNM V3662, the type and only specimen of *Pontosaurus kornhuberi*, the decensus parietalis and superior margin of the prootic and alar process also appear to have a continuous sutural contact, unlike the condition in *Varanus*.

#### Quadrate

The left quadrate is almost perfectly preserved in lateral view in *Pontosaurus kornhuberi* (Figs. 2, 3 A-B, 5 C). It is a C-shaped structure with a pronounced suprastapedial process, a well-developed stapedial notch, a very small but present infrastapedial process, and a well-developed tympanic ala or conch, comparable in particular to that of *Pontosaurus lesinensis*, and more generally, to those of other mosasauroids (Russell, 1967; Carroll & deBraga, 1992; deBraga & Carroll, 1993). As was noted by Pierce & Caldwell (2004), the quadrate of the teiid *Dracaena* (FMNH 207657) is strikingly similar as well. As with *Pontosaurus lesinensis*, the quadrate appears to articulate

with the parietal ramus, the squamosal and supratemporal (the latter bone is poorly preserved).

#### Pterygoid

The pterygoids are not well exposed in MSNM V3662 with only a short section, likely the suborbital portion of the left pterygoid, exposed in the floor of the left orbital opening (Figs. 2, 3 A-B, 5 A-C). Little detail is visible that merits description or comparison to either *Pontosaurus lesinensis* or *Coniasaurus*.

#### Epipterygoid

Right and left elements that might be identifiable as the epipterygoid are visible on either side of the parietal, between the anteroventral margin of the decensus parietalis and the postorbitofrontal (Fig. 3 A-B). The element is small and rounded in cross-section and directed anteriorly from its contact with the decensus parietalis; this latter position is a taphonomic artifact. While the elements cannot be identified with certainty, they are in the approximate topological position where disarticulated epipterygoids might be anticipated.

A similar element is well preserved in the type of *Pontosaurus lesinensis* (Fig. 3 C-D). The element is a simple, broad, columnar bone whose dorsal tip has taphonomically rotated out of position and is now contacting the postorbital bone directly in front of the postorbital-squamosal suture.

#### Dentary

The right dentary is not exposed in MSNM V3662, while the left is very poorly preserved and somewhat fractured and fragmented. The left element makes up about two fifths of the length of the mandible (Figs. 2, 3 A-B) and bears at least four mandibular foramina. It is an elongate and very thin element with a large number of teeth; while it is not possible to count the number of tooth positions, it is clear that there is space for approximately twenty teeth. The exposed dentary teeth, like those of the maxilla and those of *Pontosaurus lesinensis*, are laterally compressed, sharp, and weakly recurved with what appear to be shallow furrows or facets. Neither the intermandibular symphysis, nor the intramandibular joint are visible in MSNM V3662 though it seems unlikely that the anatomy of these important joints would have been dissimilar to *P. lesinensis* (Pierce & Caldwell, 2004) or *Coniasaurus gracilodens* (Caldwell, 1999a) and *C. crassidens* (Caldwell & Cooper, 1999).

#### Coronoid?

An element tentatively identified as part of the left coronoid is present just posterior to the left jugal. The bone fragment as exposed is poorly preserved and it is not clear if it connects to the probable coronoid as exposed beneath the left jugal (Fig. 5 A-C). However, if it is the posterior and dorsal portion of the coronoid, then the dorsal process was quite tall. In comparison, the coronoid process of *Pontosaurus lesinensis* is quite small (Pierce & Caldwell, 2004).

### Surangular

The surangular is an extremely long bone whose sutural contacts with the articular/prearticular and angular cannot be ascertained as preserved and prepared. The probable sutural contact with the articular, which would normally be exposed on the posterolateral aspect of the mandible, is broken away just ventral to the articular cotyle and the quadrate (Fig. 5 C); it does appear though that the surangular forms part of the articular surface of the cotyle similar to other mosasauroids. The angular does not appear to be exposed in lateral view. Likewise, no portion of the splenial appears to be visible laterally. The intramandibular joint is also not exposed laterally; unfortunately, at the point where the dentary and surangular meet (Figs. 2, 3 A-C), the bone is broken away and the lateral surface morphology of the joint is obscured. Thus it is not possible to ascertain the presence or absence of the splenial, angular and their contribution to the morphology of the unique mosasauroid and serpentiform joint. The only sutural contact that is relatively well preserved is the surangular-coronoid contact (Fig. 5 A-B); this joint is long and sloping as it rises anteriorly towards the dorsally inflected tip of the jugal. The size and shape of this element is identical to that of *Pontosaurus lesinensis* (Pierce & Caldwell, 2004).

### Articular/Prearticular

Details of the sutural relationships between these elements are not visible in MSNM V3662 and so similarities to the fused elements of *Pontosaurus lesinensis* cannot be identified and confirmed. Posteriorly, the articular widens and forms the articular cotyle for the reception of the quadrate. It terminates in an expanded retroarticular process that is well preserved on both sides of the skull.

### Postcranial skeleton

The postcranial skeleton of *Pontosaurus kornhuberi* is the most complete of any of the known small aquatic squamates (Fig. 1). Though there is some minor surface breakage and crushing throughout, the postcranium of MSNM V3662 is very well preserved down to the last caudal vertebrae and the tip of the tail (i.e., it is carbonized but present). The cervical vertebrae and ribs are preserved in dorsal view as are the dorsal vertebrae and ribs, and the sacral vertebrae and sacral processes (Figs. 7, 8). Posterior to the sacrum and sacral vertebrae, there appear to be only two pygal vertebrae (based on the absence of haemal arches). Posterior to the pygal vertebrae the axial skeleton is rotated laterally so that the tail and its caudal vertebrae are exposed in left lateral view all the way to the tip of the tail.

In general, the forelimb and girdles are much smaller as compared to the rearlimb and girdles. While the condition in *Pontosaurus lesinensis* is unknown due to the absence of the rearlimb, this marked difference in size between the forelimb and rearlimb is common to *Adriosaurus suessi* (Lee & Caldwell, 2000), *Dolichosaurus longicollis* (Caldwell, 2000) and *Aphanizocnemus libanensis* (Dal

Sasso & Pinna, 1997). It is the reverse condition to that of mosasaurs where the forelimb and girdle are much larger than the rearlimb and girdle (Russell, 1967). The condition observed in adriosauroids, pontosaurs, and dolichosaurs also contrasts with nearly identical front and rearlimb proportions in aigialosaurs (Caldwell *et al.*, 1995).

The left pectoral girdle is well preserved and has been slightly translocated so that it is exposed in dorsal view (internal surfaces are exposed); the right pectoral girdle is not visible in any way that permits observation of the elements. Likewise, the left forelimb is much better preserved and is extended lateral to the body wall exposing the elements of the carpus; the right limb is but up and under the body wall with only the distal portion of the manus exposed along the rib cage.

The pelvic girdle is well preserved on the left side of the body but is underneath the sacrum on the right side and is not visible. However, in contrast to the forelimbs, both the left and right rearlimbs are well preserved and exposed in the prepared specimen. The tip of the right femur is hidden beneath the sacrum, whereas the entire femur is well exposed on the left side. The tarsus and metapodium and phalanges are all well preserved and exposed.

### Axial skeleton

#### Cervicals

There are ten preserved cervicals in *Pontosaurus kornhuberi*, beginning with C1, represented by the right and left atlas neural arches, and ending with an anterior fragment of C10, identified as such because there is no evidence of an elongate rib articulating with the sternal cartilages (Figs. 7 A-D, 8 A, 9). The cervical series are all preserved in dorsal view, and for the most part have been sheared through the neural arch lamina leaving only the centrum and fragments of the neural canal; one vertebra, C8, was prepared from the right lateral side to expose the cervical peduncle and unfused hypapophysis.

The cervical vertebrae gradually increase in width and length caudally (Fig. 7 A-C). The right and left neural arches along with the anterior portion of the axis centrum are visible in dorsal view (Fig. 7 A-D). Pre- and postzygapophyses are variably present, depending on preservation, from C3-C10. Synapophyses/parapophyses are present from C3-C10; C1 and C2 do not appear to possess cervical ribs, a condition typical of squamates. Short cervical ribs are preserved from C3 to C7 on the left side, and on C4, C6 and C8 on the right side. It is not clear, due to preservation, if any of the vertebrae possesses zygosphenes or zygantra.

For *Pontosaurus lesinensis* Kornhuber (1873) had originally identified a total of nine cervicals, but what he thought was the atlas-axis complex is actually C3 (see Pierce & Caldwell, 2004). Furthermore, based on morphology and the position of the pectoral girdle, what Kornhuber identified as the first two dorsals corresponds to the last two cervicals. Therefore, by making the appropriate changes, the cervical count increases to twelve. In

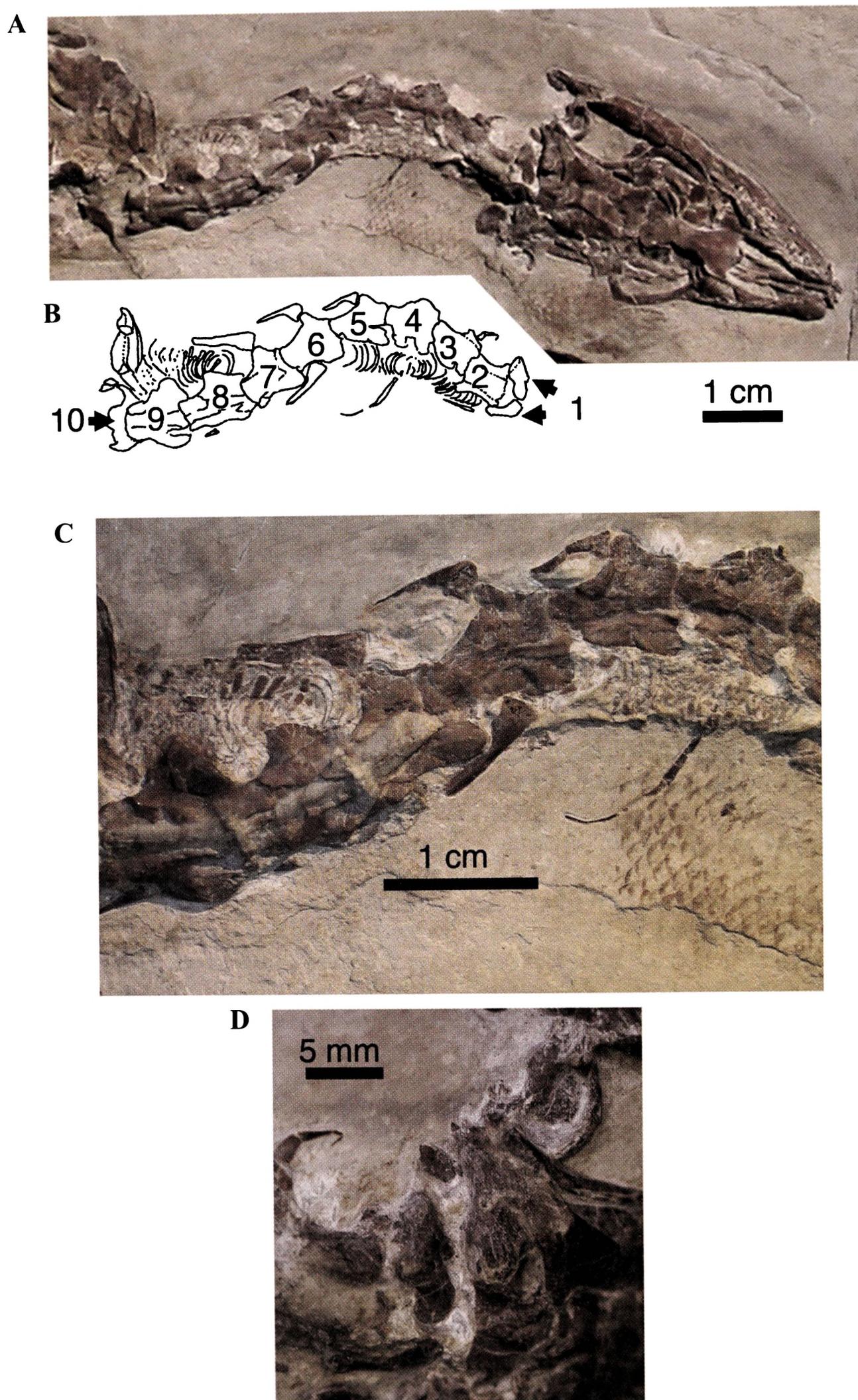


Fig. 7 - Cervical vertebrae of *Pontosaurus kornhuberi*, MSNM V3662. A) Photographic overview of entire cervical column; B) line drawing of only the cervical column (numbers indicate 1-10 cervical vertebrae); C) detail of mid and posterior vertebrae in cervical column showing cervical ribs, neck scales, and tracheal rings; D) detail of C1 (note right and left atlas neural arches are flattened and compressed).

squamates, a cervical count greater than ten has only ever been observed in pachyophiids (Lee & Caldwell, 1998; Lee *et al.*, 1999), pontosaurs and dolichosaurs (Dal Sasso & Pinna, 1997; Caldwell, 2000; Lee & Caldwell, 2000; Pierce & Caldwell, 2004).

### Dorsals

There are twenty-six dorsal vertebrae present in MSNM V3662 (Figs. 1, 8 A-B, 10 A). The first and last three dorsal vertebrae in the series are poorly preserved but the ribs associated with the left synapophyses are present and quite well preserved making the count of dorsals quite accurate. In general, the vertebrae and ribs increase in size and in degree of pachyostosis from the first dorsal to approximately the twenty-first to twenty-second vertebra; at this point there is a marked reduction in the degree of pachyostosis and overall size of both the ribs and vertebrae (Figs. 8 A-B, 9, 10 A, 11 A). The 23<sup>rd</sup>-26<sup>th</sup> ribs decrease in size and thickness posteriorly and extend laterally from the centra in a narrow downward arch folding towards the mid-line and forming a somewhat laterally constricted frame; these last three ribs do not show any notable degree of pachyostosis (Fig. 11 A). In *Pontosaurus lesinensis* a corresponding decrease in pachyostosis begins at dorsal vertebra 21.

Pre- and post-zygapophyses are present, but for the most part poorly preserved. In the few vertebrae with preserved zygapophyses, the facets do not appear to incline above the horizontal; however, it must be remembered that there is considerable compression of the specimen in addition to the fracturing present on most vertebrae. Accessory articulations, specifically zygosphene-zygantral facets are present in the dorsal column but can only be observed in the mid-dorsal region on vertebrae fifteen through twenty.

For *Pontosaurus lesinensis*, Kornhuber (1873) originally counted 30 dorsals, but with the modified count in the cervical region given by Pierce & Caldwell (2004), the dorsal count is now recognized to be 28, for a total of 40 presacral vertebrae. For *P. kornhuberi* the count is similar: 10-11 cervicals plus 26-27 dorsals for a total of 36-38 presacrals. The dorsal vertebrae of both species are larger than the cervicals in width and length and are more robustly ossified (Figs. 1 A-B, 7 A-D, 8).

### Sacrals

In *Pontosaurus kornhuberi* the left pelvic region is very well preserved, but the sacral vertebrae are missing completely even though fragments of the first sacral transverse process and a complete second sacral transverse process are present (Figs. 8 A, 11 A-B). Based on the articulations of the first and second transverse processes, there are clearly only two sacral vertebrae, a feature common to most squamates with a sacrum. The transverse process of the first sacral vertebra is largely broken away where it would have overlain the ischium; however, there are some remnants of the proximal portions of the process between the ischium and the vertebra. The second sacral vertebra's transverse process is missing as well, but an excellent natural mold of the ven-

tral surface of the process is preserved; the distal tip of the mold still retains some fragments of bone such that the articulation with the ilium is preserved. A third vertebra and transverse process is located next to the ilium (Fig. 11 A-B) but is not fused to it and is interpreted here as the first pygal vertebra. In *Pontosaurus lesinensis* the specimen is broken through the sacrum preserving very few details of the anatomy of this region. Pierce & Caldwell (2004) reported the presence of two fragmentary transverse processes that they interpreted as belonging to sacral vertebrae.

### Pygals?

There appear to be only two pygals, contra Dal Sasso & Renesto (1999) who identified three, in *Pontosaurus kornhuberi* (Figs. 8 A, 11 A-C) based on the absence of haemal arches; pygal vertebrae in pythonomorphs are differentiated from caudals based on the absence of haemals. However, it is important to point out that the ventral surfaces of these two most postsacral vertebrae are not observable and thus haemapophyses and their attendant haemals cannot be ruled out completely. The difference in haemal counts between this study and that of Dal Sasso & Renesto (1999) is based on the position of the first preserved haemal between the transverse processes of the third and fourth vertebrae posterior to the sacrum (Figs. 8, 11 C). I tentatively identify these two vertebrae as pygals.

These two probable pygals, like the sacrals and dorsals, are broken through the neural arches and preserve little information on the morphology of the zygapophyses and neural arches. Unlike the caudals, the pygals are not preserved in lateral view and so the left transverse processes are well preserved displaying their dorsal surfaces. The first pygal vertebra's transverse process has an unusual morphology as compared to that of the second pygal (Fig. 11 A-C); the process is anteriorly directed and narrows towards the tip resembling a small "j"-shape. This morphology is not atypical of pygal or first caudal vertebrae as these transverse processes are usually modified to support lymph node clusters located superior to the cloaca; such transverse processes are referred to as lymphapophyses. By comparison, the transverse process of the second pygal is directed laterally, is narrow at the distal tip and widest proximally. The next most posterior vertebra is also preserved in oblique dorsal view but is identified here as the first caudal based on the estimation that its posteroventral margin articulated with the large disarticulated haemal arch located to the left of it (Figs. 8 A, 11 C).

### Caudals

The tail is extremely well preserved, numbering 163 caudal vertebrae from the last pygal to the tip of the tail; at the tail tip the vertebral count is problematic due to the extremely small size of these most-caudal elements (Fig. 8 A, C-F). Overall, the caudal vertebrae are strongly laterally compressed and longer than they are tall and wide. The tips of the haemals are fused so that they form a true haemal arch, however the arches articulate with the haemapophyses instead of being fused to them. Haemals

are present along the tail to caudal vertebra 139. For approximately the first 55 caudal vertebrae, the haemal arches are nearly twice as long as the neural spines; by about vertebra 55-60, the haemals and neural spines are nearly the same length. From this point, to vertebra 139, where preserved, the haemals and neural spines are of equal length. The anteriormost 60 vertebral elements make up slightly more than half the length of the tail, with the remaining half of the length containing the other one hundred and three vertebrae. The effect on the aspect of the tail is that for at least the first half of its length, the hypaxial depth is nearly twice that of the epaxial depth based on osteology alone; factoring in the soft-tissue effect on tail aspect, it becomes clear that ventral to the haemal arches the tail is at least that same haemal depth again (Fig. 8 C-D). Epaxially, the marginal squamation indicates a soft tissue depth equal to the height of the neural spines. Thus, between its osteology and soft tissue anatomy, the tail of *Pontosaurus kornhuberi* was at least twice as deep as the osteology would suggest.

The first and second caudals possess large transverse processes and are preserved in dorsal view. However, each has a large transverse process, equivalent in length to those of the two pygal vertebrae (Fig. 11 A-C). For all four of these vertebrae it is likely that the varied heads of the *m. caudofemoralis* originated here. This muscle body is integral to strong tail driven propulsion and requires significant origin sites if it is to be a useful locomotory muscle.

All caudal centra are longer than they are tall, which is the opposite condition to that observed in mosasaurids and aigialosaurids (Russell, 1967; deBraga & Carroll, 1993). Another interesting feature is the rather steep posterior angle of all neural spines along the column. This inclination would suggest fairly strong ligamentous connections of the varied *m. spinocaptis* muscles between vertebrae.

The very small vertebrae of the distal tip of the tail are slightly disarticulated and bent backwards on each other so that in a very small area (approximately 1.5 cm) there are thirteen caudal vertebrae. The distal carbonized tip of the tail contains no vertebral centra (Fig. 8 F).

### Pectoral girdle and forelimb

The left pectoral girdle is relatively well preserved and exposed in internal view. Fragments of the scapula are preserved, as are portions of the clavicle, interclavicle, coracoid, supracoracoid and sternal cartilage (Figs. 9, 10 A). The right forelimb is not well exposed in *Pontosaurus kornhuberi*, having twisted beneath the body during burial. However, the left forelimb is very well preserved and is exposed in palmar view (Fig. 10 A-E). This description will therefore focus on the left forelimb.

#### Scapula and coracoid

The scapula and coracoid may well be fused into a single scapulocoracoid element similar to that of the aigialosaur *Opetiosaurus* (Carroll & DeBraga, 1992; DeBraga & Carroll, 1993) and *Pontosaurus lesinensis*,

but as preserved, it is not absolutely clear; the alternative, as in most aigialosaurs (Carroll & DeBraga, 1992) and both *Coniasaurus gracilodens* (Caldwell, 1999) and *Dolichosaurus longicollis* (Caldwell, 2000) is that the two elements are separate. Evidence suggesting that there was fusion of these two elements is derived from the absence of an identifiable sutural contact along the anterior margin of the coracoid. Additionally, because the scapula is a small element in *P. kornhuberi* and is not well preserved, it is not clear if it is emarginated (in *P. lesinensis* it is not emarginated). Similar to mosasaurs (Russell, 1967; DeBraga & Carroll, 1993), *Haasia* (Polcyn *et al.*, 1999), *Coniasaurus gracilodens* (Caldwell, 1999) and *Aphanizocnemus* (Dal Sasso & Pinna, 1997), the coracoid portion is significantly larger, possesses an anterior (primary) emargination and a fan-like posterior margin. A single coracoid foramen is present in the middle portion of the element.

#### Supracoracoid cartilage

The exact outline of the supracoracoid cartilage is not clear as its contact with the sternal cartilage is not well-preserved; the only point where its contact with the sternal cartilage is clear is immediately to the right of the humerus where the supracoracoid cartilage is seen to extend past and overtop of the sternal cartilage (Fig. 9). However, the semi-circular outline of the supracoracoid cartilages contact with the coracoid is well defined, indicating that the coracoid was mobile within the supracoracoid cartilage assembly.

#### Interclavicle

The interclavicle is represented by the left transverse process lying to the left of C10 and immediately anterior to the element identified as the clavicle (Fig. 9), and by the sagittal ramus extending parallel to the long axis of the body immediately to the right of the supracoracoid cartilage. As exposed, the sagittal ramus of the interclavicle only extends posteriorly to the mid-point of the coracoid; likely, as preserved and prepared, the distal extent of the ramus is incomplete. The interclavicle of *Pontosaurus lesinensis* is similar in shape but slightly longer as preserved (Pierce & Caldwell, 2004).

#### Clavicle

The clavicle is a relatively robust element that is broken on both its proximal and distal extremities leaving little to describe of its anatomy other than to say it shows a sloping curvature at midlength.

#### Sternal cartilage

The sternal cartilage is calcified, exposed in internal view, with only the left side of the element exposed in MSNM V3662. There are three posteriorly directed articular points for costal cartilages (Fig. 9). The element is not exposed far enough posteriorly to determine if the third costal articulation point is the last, minus the xiphisternal cartilage articulations, as observed in *Dolichosaurus longicollis* (Caldwell, 2000) which also only has three costal car-

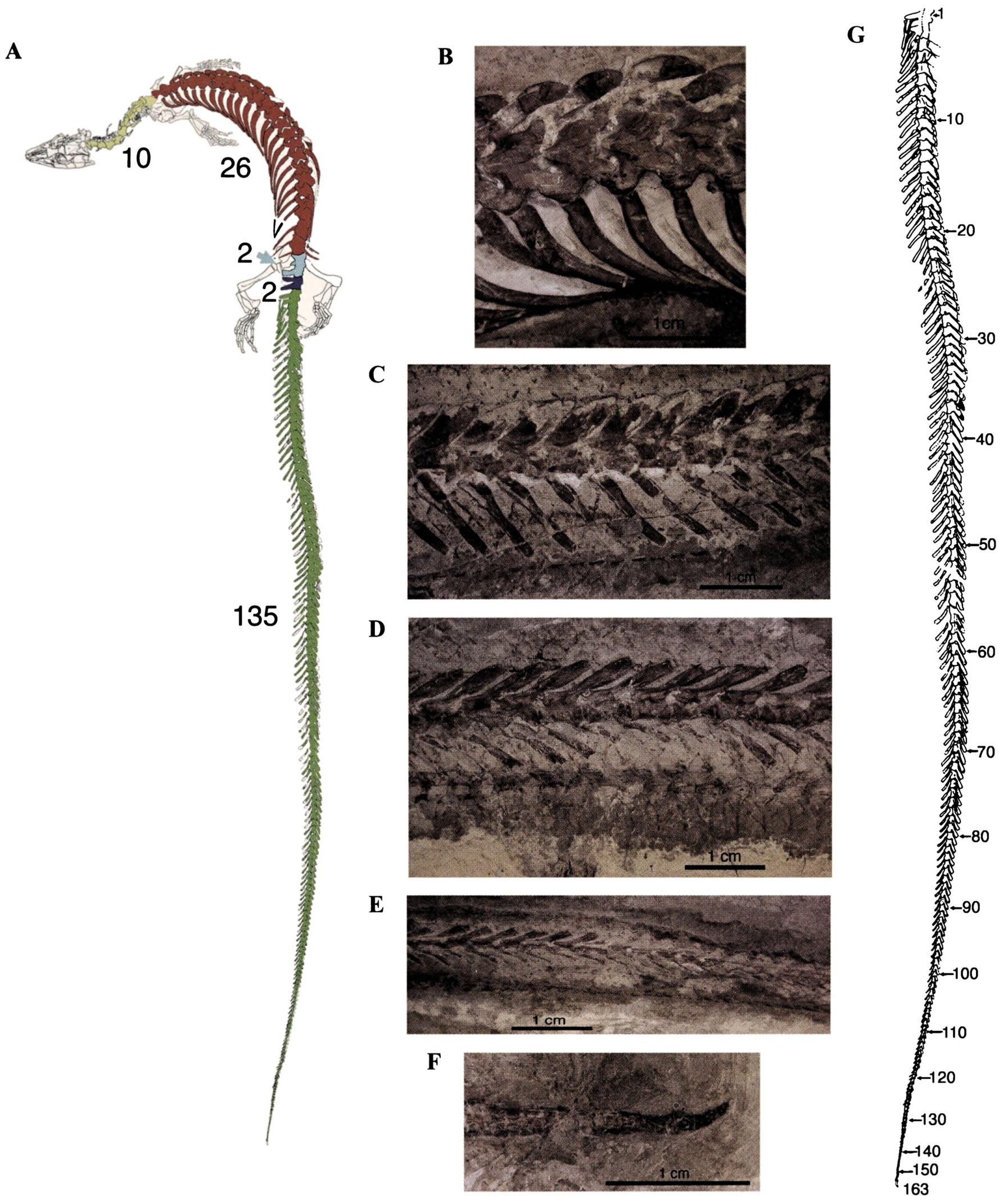


Fig. 8 - Axial skeleton of *Pontosaurus kornhuberi*, MSNM V3662. A) Line drawing of MSNM V3662 with axial skeletal regions colour coded (yellow=cervical; red=dorsal; light blue=sacral; dark blue=pygal; green=caudal); B) detail of dorsal vertebrae and ribs; C) anterior caudals; D) mid-caudal vertebrae; E) distal caudals; F) distal-most caudals to soft-tissue tip of tail; G) line drawing of caudal skeleton indicating numbers of vertebrae along the column (1-163).

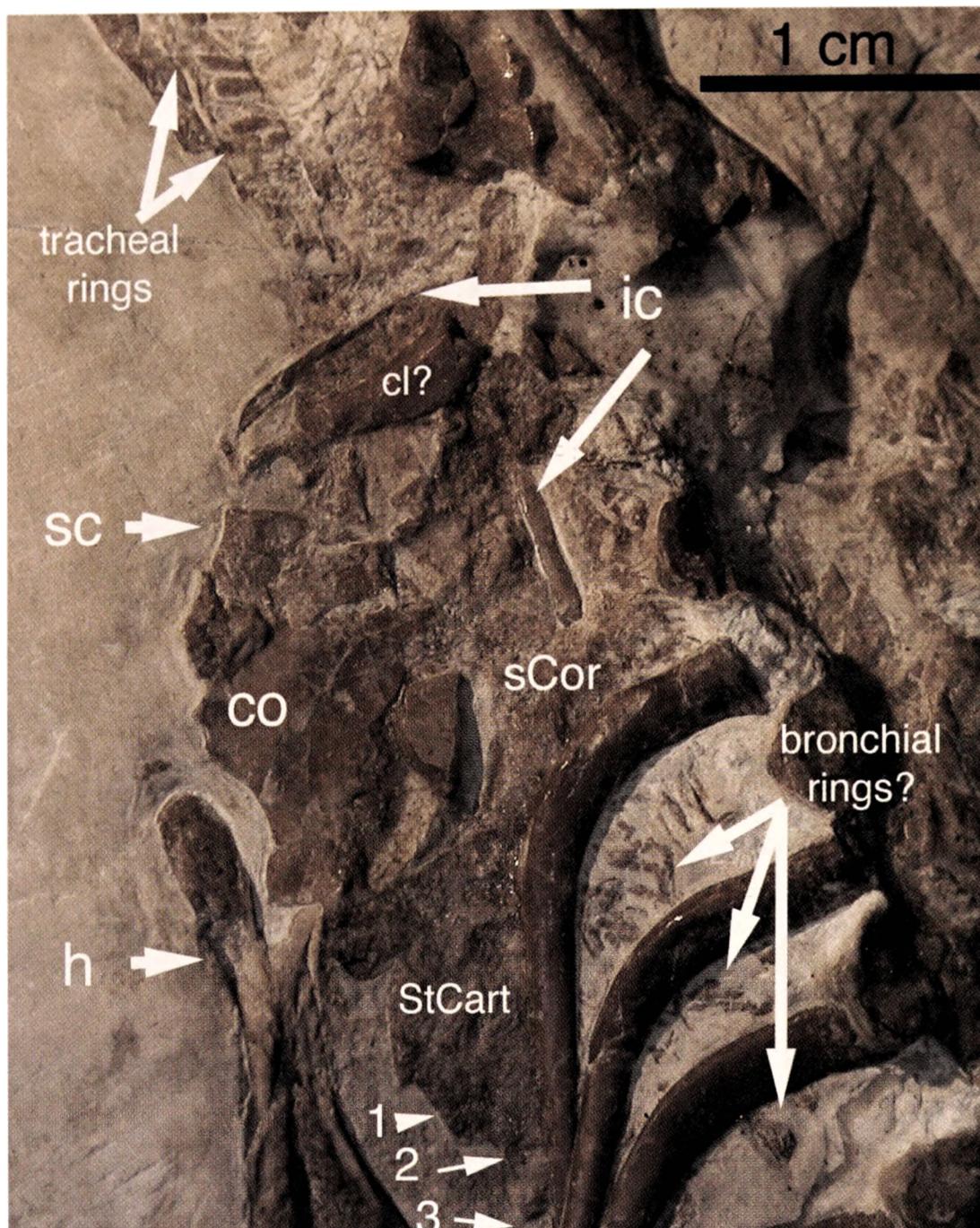


Fig. 9 - Pectoral girdle of *Pontosaurus kornhuberi*, MSNM V3662. Abbreviations: cl?, clavicle; co, coracoid; h, humerus; ic, interclavicle; sc, scapula; sCor, supracoracoid cartilage; stcart, sternal cartilage; 1-3, costal cartilage articulation points.

tilage articulations on the sternal cartilage. The number contrasts with the aigialosaur *Carsosaurus marchesetti* (Caldwell *et al.*, 1995) where there are at least five costal cartilage articulation points in addition to the xiphisternal cartilages.

#### Humerus

The humerus is a short element (16.5 mm long), crushed throughout most its length, and is slightly constricted at mid-shaft and expanded at both ends. There is no evidence of a proximal epiphysis though the humeral head is slightly broken away medially (Fig. 9). The distal expansion appears to possess a small-ossified epiphysis at the contact with the ulnar head (Fig. 10 A). Both the ectepicondylar and entepicondylar foramina are absent. Proximally, near the broken portion of the head, there is a stout tubercle and small crest for the attachment of the deltoid musculature. Distally, there is a large somewhat flattened capitulum and a troclea; although the dimensions are smaller, the distal epiphysis resembles that of *Opetiosaurus* (deBraga & Carroll, 1993) and *Haasia* (Polcyn *et al.*, 1999).

#### Radius and ulna

The radius and ulna are of similar size and are distally divergent along their contact with the proximal row of carpals (Fig. 10 A-C); proximally the two elements are in close contact along the distal margin of the humerus. The effect of this divergence is that the antebrachium, and thus forearm, is extremely wide and flattened. It is also likely that pronation of the forearm was not possible thus impeding forelimb assisted terrestrial locomotion. This form of distal divergence is observed in most mosasaurs (Russell, 1967) and the dolichosaurs *Adriosaurus* (Lee & Caldwell, 2000) and *Pontosaurus lesinensis* (Pierce & Caldwell, 2004). Divergent epipodials also characterize aigialosaurs such as *Carsosaurus marchesetti* (Caldwell *et al.*, 1995) and *Opetiosaurus buccichi* (Carroll & deBraga, 1992) but to a much lesser extent and it appears as though pronation of the manus was possible due to the configuration of the radius.

In *Pontosaurus kornhuberi* the radius is a simple rod-like element that is slightly curved along its antebrachial margin. The ulna is thickened proximally forming a weak olecranon process, is narrow through the antebrachial portion of the shaft, and then expands somewhat at the contact with the ulnare.

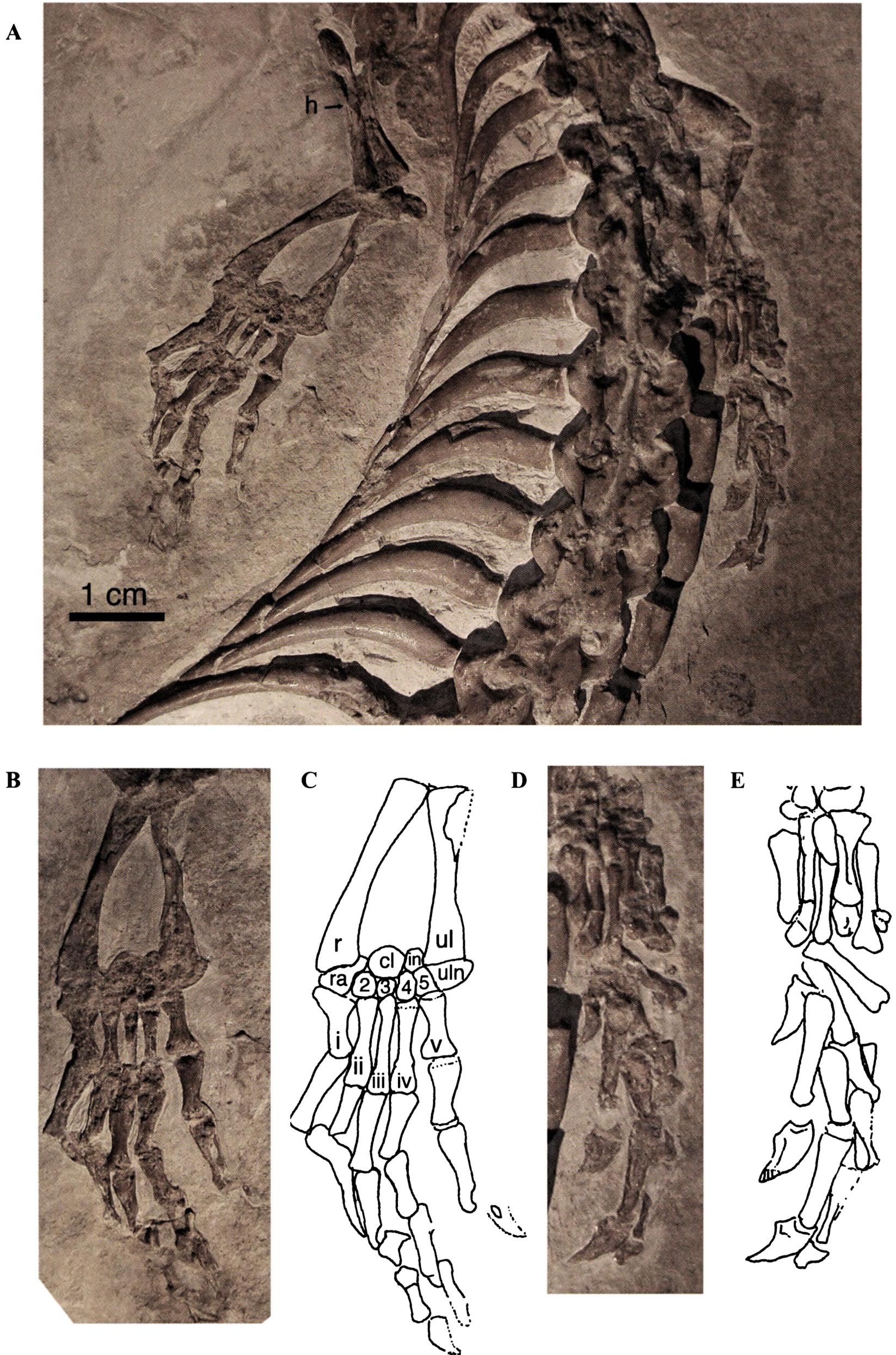


Fig. 10 - Forelimbs of *Pontosaurus kornhuberi*, MSNM V3662. A) Overview of anterior trunk and right and left forelimbs; B) photodetail of left forelimb; C) line drawing of left forelimb; D) photodetail of right forelimb; E) line drawing of right forelimb. Abbreviations: cl, centrale; h, humerus; in, intermedium; r, radius; ra, radiale; ul, ulna; uln, ulnare; i-v, metacarpals 1 through 5; 2-5, distal carpals 2 through 5.

In general, the propodial and epipodials are comparable to those of *Pontosaurus lesinensis* (Pierce & Caldwell, 2004) and the dolichosaur *Adriosaurus* (Lee & Caldwell, 2000) in terms of proportions. Comparisons of this sort highlight several interesting trends. Of importance to note in *P. kornhuberi* are the relative proportions of the podial elements: the humerus (propodial) and ulna/radius (epipodials) are of equal length and make up two fifths of the length of the limb, while the hand (mesopodium, metapodium and phalanges) comprises the other three fifths of the limbs overall length. There are three apparent trends in the evolution of the pontosaur limb: 1) overall reduction of the limbs relative to body size; 2) size reduction of the forelimb in relation to the rearlimb; 3) increased size of the manus/pes in relation to the propodials and epipodials.

#### Mesopodium (carpus)

The mesopodium possesses both a proximal and distal row of carpals (Fig. 10 A-C). The proximal row includes the radiale, medial centrale, and intermedium, while the distal row includes the ulnare and distal carpals two through five. There is no pisiform as preserved and prepared though it is possible that the postaxial tip of the ulnare is the pisiform (the surface of most of the bones of the epipodium and mesopodium is broken away and so sutures are hard to identify).

The radiale and ulnare are the largest mesopodial elements in the carpus and are both irregularly shaped, lozenge-like elements. The radiale articulates with both the centrale and distal carpal two; the centrale appears to contact the radiale, distal carpals 2 through 4, as well as the intermedium. The intermedium is a small element displaced postaxially by the large centrale (Fig. 10 B-C). The mid-antebrachial placement of the centrale, and the comparatively small size of the intermedium, is a consistent feature among aigialosaurs (Caldwell *et al.*, 1995; Caldwell, 1996) and now pontosaurs (see Pierce & Caldwell, 2004).

#### Metapodium

All five metacarpals are present (Fig. 10 A-E). The first and fifth are shorter than two, three and four, and as a result are more hourglass-shaped than the longer and slimmer metacarpals two through four. The fifth metacarpal articulates with distal carpal five but not the ulnare. Likewise, metacarpal one articulates with only the radiale, while the remaining metacarpals articulate with their respective distal carpals.

#### Phalanges

The phalangeal formula appears to be 2-3-4-5-3, a count that is primitive for all lepidosauromorphs (Fig. 10 A-E). The distal phalanges of digits three, four and five are not well preserved but a count is still possible from the natural molds. The phalanges of all digits are roughly the same shape: proximally expanded, narrow shaft, and distal condyle with two condylar heads. The terminal phalanx or ungual is a well-defined claw with a proximal and ventral tubercle.

### Pelvic girdle and rearlimb

The right pelvic girdle is not exposed (Fig. 8 A). However, the left girdle is more complete and reasonably well preserved. The left pubis is well preserved as is the left ischium; the left ilium is preserved throughout most of its posterior length as a natural mold of the ventral portion of the bone within only the acetabular portion preserved as a fragment of bone.

#### Ilium

The ilium of *Pontosaurus kornhuberi* is slightly expanded at the contact with the ischium and pubis; posterior to the acetabular fossa (not well preserved in its entirety in MSNM 3662) the ilium is posteriorly elongate (i.e., the posterior superior iliac crest), articulates with two sacral processes and overlaps at least one pygal vertebra, possibly two (Fig. 11 A-C). There is no evidence of an anterior superior iliac crest, as the bone appears to terminate at the contact with the pubis in the middle of the acetabular fossa. This same anatomy (posterior iliac crest, no anterior crest) is shared with all aigialosaurs (Caldwell *et al.*, 1995) and *Dolichosaurus longicollis* (Caldwell, 2000) and contrasts with the anteriorly directed superior iliac crest/spine of mosasaurs (Russell, 1967) and the condition in modern terrestrial lizards where both crests are present (though the anterior is smaller, e.g., *Varanus*).

#### Pubis

The pubis is small as compared to extant terrestrial lizards, but still displays the typical hatchet-shaped morphology; there is a large pubic foramen at the center of the proximal head of the bone (Fig. 11 A-B). Distal to the pubic head, the element narrows to a long medially directed shaft that expands slightly where it contacts the right pubis at the midline. The head of the pubis bears two principal facets: 1) laterally for the head of the femur, 2) medially, for articulation with the ilium. The ischiadic facet is not visible as preserved and prepared.

#### Ischium

The ischium is slightly shorter than the pubis and has been displaced from its ventral and posterior position (Fig. 11 A-B). The element is curved along its anterior margin and steeply angled along its posterior margin to form an equine-ankle like shape. The proximal portion is narrower than the distal tip (ischiadic footplate), the latter of which articulates with the opposite footplate of the right ischium.

#### Femur

The femur is a long (33 mm long) and relatively robust bone (Fig. 12 A) that is nearly twice the length of the epipodium (tibia and fibula are each 18 mm in length). As compared to the humerus (16.5 mm long) it is twice the length of that bone, and compared to the ratio of nearly 1:1 between the humerus and radius/ulna, the femoral/tibia-fibula ratio is quite different at roughly 1.8:1.

The proximal tip of the left femur preserves a rounded epiphysis still in articulation with the acetabular fossa (Figs. 11 A-B, 12 A). The proximal portion of the element is rela-

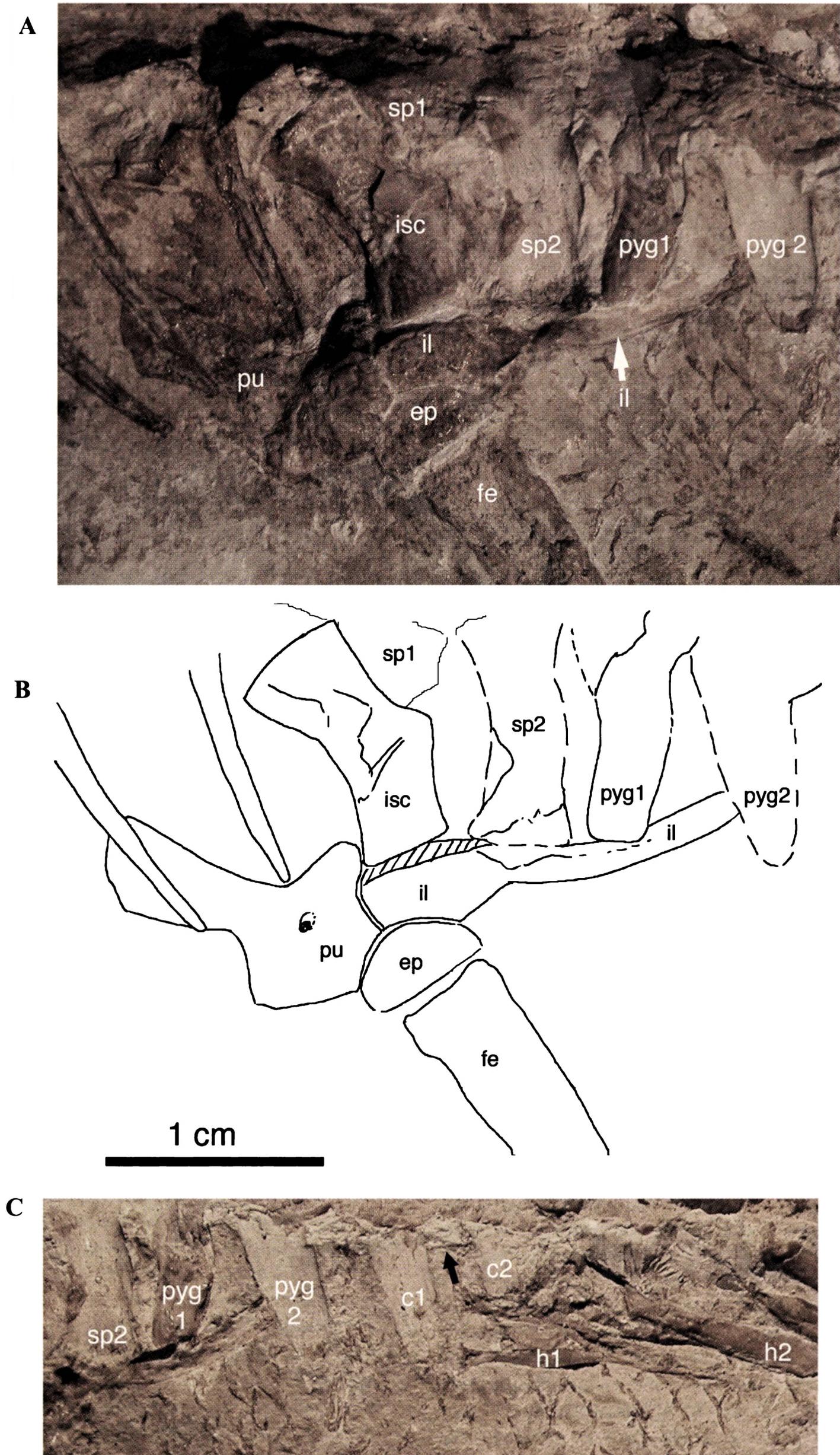


Fig. 11 - Pelvic girdle of *Pontosaurus kornhuberi*, MSNM V3662. A) Photodetail of left pelvis; B) line drawing of same; C) photo detail of pygal region. Abbreviations: c1-2, first and second caudal vertebrae; ep, epiphysis; fe, femur; h1-2, haemal arches; il, ilium; isc, ischium; pu, pubis; pyg 1, 1<sup>st</sup> pygal vertebra; pyg 2, 2<sup>nd</sup> pygal vertebra; sp1-2, sacral processes 1 and 2.

tively narrow compared to the expanded distal portion. There are no strongly developed trochanters on the proximal head, nor are there any well developed femoral condyles at the articulation with the tibia and fibula. The only relatively well-developed feature visible on both the right and left femora is a slight anterior curvature of the shaft of the bone. The surface bone of the right femur is better preserved than the left and indicates that the mid-line of the shaft bears a long proximal-distal crest, postaxial to which is an equally long and shallow fossa. It is likely that this portion of the femur served as the insertion point for the *m. caudofemoralis* discussed previously in terms of the pygal and anterior caudal vertebrae and their transverse processes.

#### Tibia and fibula

The tibia and fibula, like the radius and ulna, are of similar size and are distally divergent along their contact with the proximal tarsal row (Fig. 12 A-C); proximally the two elements are in close contact along the distal margin of the femur. The effect of this distal divergence is that the antebrachium, and thus lower limb, is wide and flat as noted previously for the forelimb (Fig. 10 A-E) and in mosasaurs and other dolichosaurs. In *Pontosaurus kornhuberi* the tibia is a simple rod-like element that is slightly curved along its antebrachial margin and is much more gracile than the fibula. The fibula is much more narrow at its proximal end than the distal end (2:1 ratio) that expands into a large fan-shape distally. The fibula articulates with both the calcaneum and astragalus.

#### Mesopodium (tarsus)

The tarsus possesses both a proximal and distal row of tarsals (Fig. 12 A-C) and is the best-preserved tarsus of any known member of the Dolichosauridae, *sensu* this study (see also Caldwell, 1999a, 2000; Lee & Caldwell, 2000). The proximal row includes the postaxially located calcaneum, the astragalus, situated in the antebrachial space, and an extra element identified in Fig. 12 B-C with a "?". This extra element is common to both the right and left pes and is in articulation in the left pes where it is located ventral to the tibia and preaxial to the astragalus; in the right pes this element has been disarticulated into the antebrachial space by the distal movement of the tibia (Fig. 12 A-C). The identity of this extra element is problematic. In the left pes it would be easy to dismiss this bone as a tibial epiphysis. However, in the right pes, this is clearly not the case. Instead, the possibility is raised that this preaxial element is a separate center of astragalar cartilage ossification, or, that it is a distal tarsal two that has been displaced.

The morphology of the astragalus is similar to that known for pythonomorphs (see Caldwell, 1996, fig. 15) where the element is not fused to the calcaneum as in modern squamates, but instead is a large element, dominating the proximal tarsal row, bears a "u"-shaped emargination of finished perichondral bone across the distal expanse of the antebrachium, and has a distinct tibial and fibular facet of roughly equal size and articulates with a small, lozenge-shaped to irregularly shaped calcaneum (Fig. 12 A-C).

The distal tarsal row includes only two elements, distal

tarsal three and four (Fig. 12 A-C). Distal tarsal four is the larger of the two as preserved in the right pes (Fig. 12 A, C) and articulates preaxially with the smaller distal tarsal three. However, postaxially distal tarsal four also appears to be in contact with a bony mass of uncertain identity (Fig. 12 A-C). In comparison, in the left pes, distal tarsal four is again well preserved, but distal tarsal three is not preserved or is preserved unprepared below the tip of metatarsal three, such that this articulation is not obvious. However, there is a distinct ossification postaxial to distal tarsal four that may be the same element as indicated in the right pes. In mosasaurs the tarsus only ever includes a small calcaneum, large astragalus and distal tarsal four (Caldwell, 1996). In aigialosaurs (Caldwell *et al.*, 1995) the tarsus includes a small calcaneum, large astragalus and distal tarsals three and four. The tarsus of *Pontosaurus kornhuberi* shares the presence of an ossified third tarsal with aigialosaurs to exclusion of this element in mosasaurs.

The additional postaxial element may well be the poorly ossified portion of the hook on the fifth metatarsal or it may represent the actual fifth metatarsal with the element so identified in *Pontosaurus kornhuberi* being the first phalanx (Fig. 12 A-C). If this is the case, then this anatomy would be consistent with that seen in mososaurids (Caldwell, 1996) where the hooked fifth metatarsal, a usually consistent feature of squamates, is absent, but there the fifth metatarsal is a small, compressed element that articulates distally with a first phalanx that is of subequal size and shape to the other metatarsals.

#### Metapodium

Five metatarsals are identified with the caveat as identified previously, i.e., that the actual fifth metatarsal might be the element identified with a "?"-mark in Fig. 12 A-C. However, using the identities as illustrated, in the manus, the first and fifth are shorter than two, three and four, and as a result are more hourglass-shaped than the longer and slimmer metatarsals two through four. An important difference is that the fifth is shorter than the first and is much less robust while the first is the thickest and most robust element in the pes. Due to some slight disarticulation and dissociation, the articulations of the metatarsals with the more proximal elements of the tarsus are not clear.

#### Phalanges

The phalangeal formula appears to be 2-3-4-5-3 thus showing a limited form of phalangeal reduction of the fifth digit by loss of one phalanx (Fig. 12 A-C) unless the argument rendered previously is accurate and the fifth metatarsal is represented by the broken fragments in Fig. 12 A-C. If this is the case, then the phalangeal formula is not derived, but rather is the primitive configuration of 2-3-4-5-4.

The phalanges of the pes are morphologically similar to those of the manus: proximal expansion, narrowed shaft, and distal condyle with two condylar heads. Again, the terminal phalanx or ungual is a well-defined claw with a proximal and ventral tubercle for ligamentous attachment and a sharp tip.

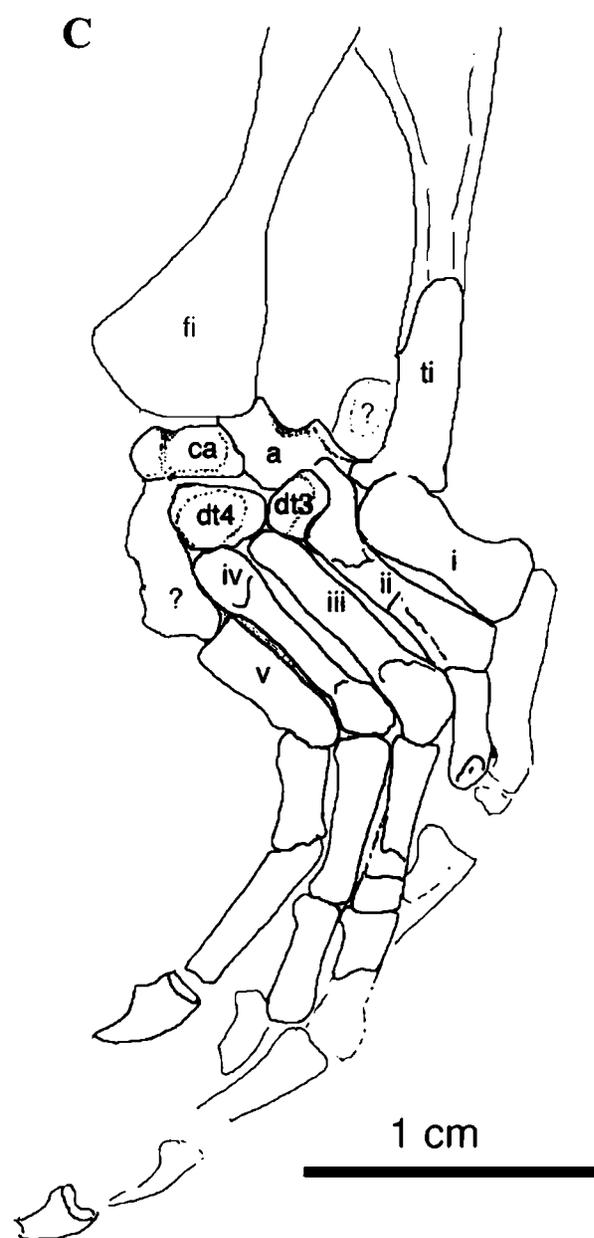
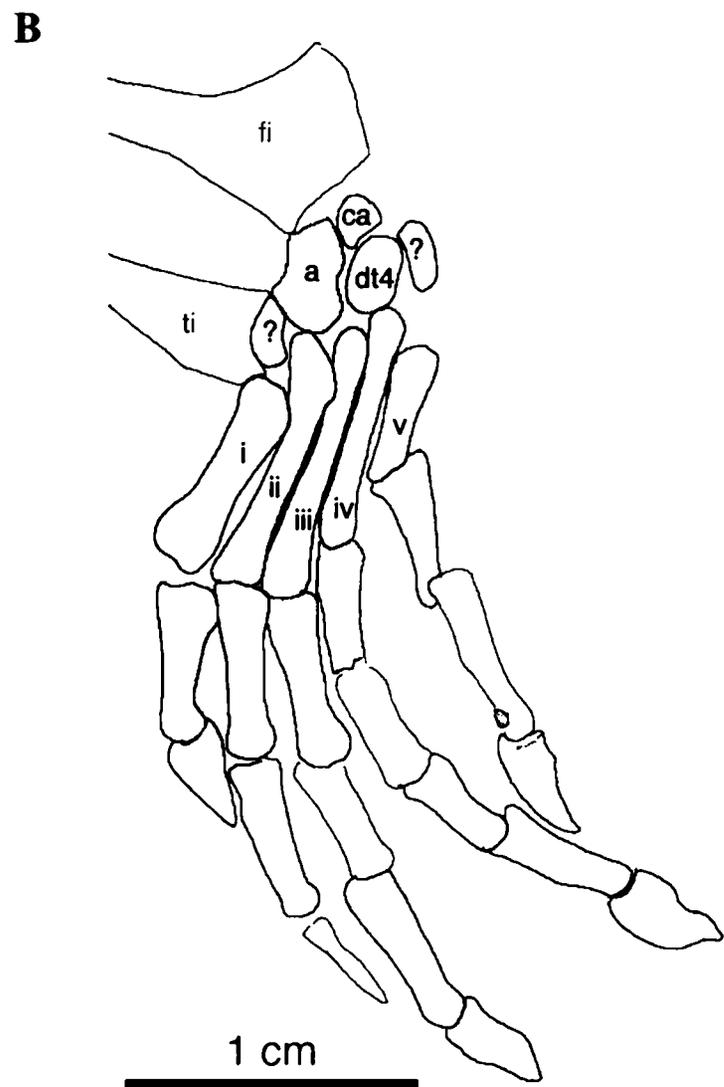
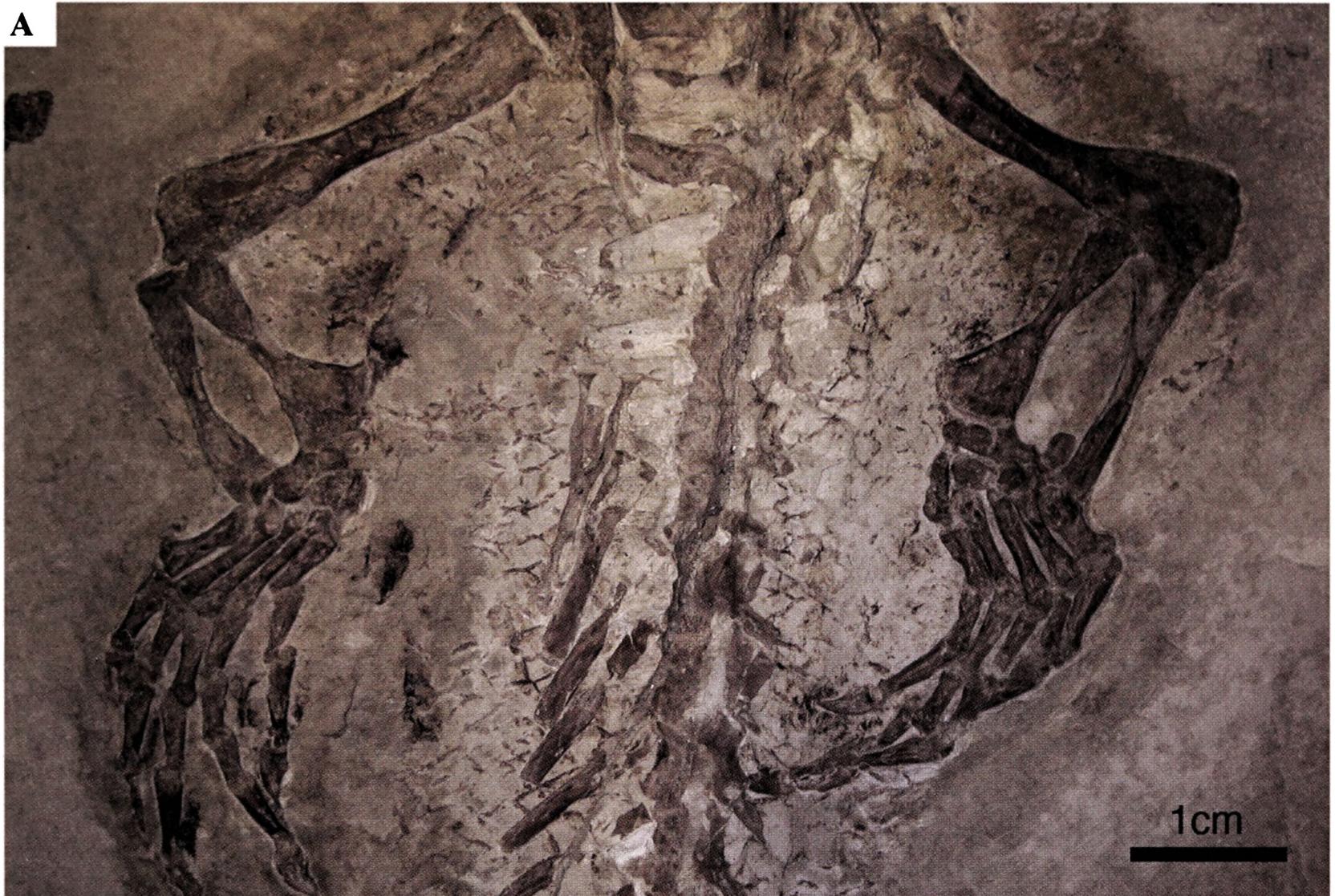


Fig. 12 - Rearlimbs of *Pontosaurus kornhuberi*, MSNM V3662. A) Overview of rearlimbs, pelvis, and anterior cauda; B) line drawing of left rearlimb; C) line drawing of right rearlimb. Abbreviations: a, astragalus; ca, calcaneum; dt3, distal tarsal 3; dt4, distal tarsal 4; fi, fibula; ti, tibia; i-v, metatarsals 1 to 5; ?, anterior astragalar ossification.

## SQUAMATION AND TRACHEAL RINGS

Caldwell & Dal Sasso (2004) recently described the squamation of *Pontosaurus kornhuberi* and compared it to the scales of a number of extant squamates. In association with the osteological description presented here, I present a summary of Caldwell & Dal Sasso's (2004) descriptions as well as additional details not given by those authors.

### Squamation

Most of the scales of MSNM V3662 are preserved as articulated sections of orange to brown permineralized or perhaps carbonized integumentary remnants (Figs. 2, 7, 8, 11-15), while some sections such as those on the cheek, appear to be external casts. Scales range in size from small head scales (1-2 mm) with irregular polygonal outlines (Figs. 2, 13), to regularly organized networks of large diamond-shaped scales on the neck, body, hindlimbs, and tail (Figs. 7, 8, 11, 12, 14, 15); these latter scales appear to be very well imbricated or overlapping.

A number of features separate the various scale regions from each other. The head scales all appear to be non-overlapping structures while all the body scale regions, from the neck to the tip of the tail are imbricated. The transition from non-overlapping to overlapping is abrupt and appears to occur immediately posterior to the presumed location of either an external auditory meatus (Fig. 13 A-C), marked here by the posterior margin of the quadrate. In the cheek to gular region, the gular or neck scales are diamond-shaped while the cheek scales are polygonal and non-overlapping.

The balance of the body margin of MSNM V3662 is well defined by the squamation (Figs. 8, 14, 15). Where preserved, there are large, articulated patches of scales in particular along the posterior half of the specimen and down to the tip of tail (Figs. 1 A-B; 8, 11, 12, 14, 15). In the mid-trunk region, the body margin scales are not well preserved, likely due to preparation of the specimen before the recognition that scales were present. However, in some body regions, for example the tail, the preserved integumentary margins indicate very clearly that the dorsoventral expansion of the tail is twice as deep as the skeletal outline (Figs. 1 B, 8, 15).

The head scales include cheek and jaw scales and possibly a short section of labial scales. Labial scales are located near the jugal and are preserved as a sequence of small, subrectangular scales, each of which bears a tiny protuberance or tubercle at its center (Fig. 13 A, C-D). Cheek and jaw scales vary in size and are elliptical to hexagonal in outline (Fig. 13 A, C-D); these scales compare well with those of the monitor lizard, *Varanus niloticus* but not with those of the Yellow-bellied Sea Snake, *Pelamis platurus* (see Caldwell & Dal Sasso, 2004). Neck scales in MSNM V3662 (Fig. 13 A-B) are small, diamond-shaped, overlapping, and arranged in oblique rows; neck through to tail scales for both *V. niloticus* and *P. platurus* are markedly different (see Caldwell & Dal Sasso, 2004).

The body scales of MSNM V3662 are uniformly sized,

diamond-shaped scales that are arranged in oblique rows (Figs. 8, 14, 15). Comparisons to other fossil pythonomorphs with scales show similarities to those of the fossil mosasaur *Tylosaurus proriger* (Snow, 1878) and the fossil aigialosaur *Carsosaurus marchesetti* (Caldwell & Lee, 2001). Comparisons to extant squamates show marked similarities to many terrestrial alethinophidian snakes as well as aquatic alethinophidians such as the Banded Sea Krait, *Laticauda colubrina* (UAMZ 762).

Caudal scale morphology differs from body scale morphology in the hypaxial region of the tail, whereas epaxial caudal scales are comparable in size and organization to the body scales (Figs. 8 C-F, 15 D-E). In MSNM V3662, immediately below the caudal vertebrae, and on top of and below the haemal spines, there are two to three horizontal rows of scales, each of which bears a "keel" (Fig. 15 D-E); the keels on these caudal scales compare well with the keels of the body scales of *Tylosaurus proriger*. Immediately below the keeled tail scales of MSNM V3662 is a single row of tall, overlapping, columnar scales that extend to the ventral margin of the tail. It appears as though these large ventral-most scales (Fig. 15 D-E) were bilaterally paired, though this cannot be positively determined. It is also a possibility, though less likely, that these ventral columnar scales were large, single scales that crossed the ventral caudal midline. The hypaxial caudal scales of MSNM V3662 are similar to those of *Laticauda colubrina* that possesses two or three rows of hexagonal scales (though in *Laticauda* they do not bear a keel), and a single row of bilaterally paired columnar scales that meet at the ventral midline, similar to *Pontosaurus kornhuberi*.

The scales of MSNM V3662 appear to be a blend of the scale types present in extant lizards and snakes. As was discussed by Caldwell & Dal Sasso (2004), small, irregular, non-imbricated head scales associated with small labial scales are observed in iguanids, chamaeleonids, agamids, gekkotans, and varanids, and in acrochordid snakes; in contrast to MSNM V3662, several other squamates, i.e., some iguanids and some snakes (e.g., boas, vipers) combine irregular, non-imbricated head scales with large labial scales. The remaining lizards and most snakes, with the exception of scolecophidians, have large scales on the head and labial margins, which in some are imbricated, but in many are not. The tiny protuberance in the middle of the labial scales appears to be unique to *Pontosaurus*.

Scales on posterior body parts of MSNM V3662 are similar to the imbricated scales of many scincids and iguanids; trunk scales are similar to those of many extant snakes with the exception of scolecophidians and some marine elapids (e.g., *Pelamis platurus*). Interestingly, the amphibious seakrait has scales similar to those of terrestrial snakes, mosasaurs, aigialosaurs, and MSNM V3662. In contrast, body scales of MSNM V3662 are very different from those of extant varanoids such as *Varanus*, *Heloderma*, and *Lanthanotus*.

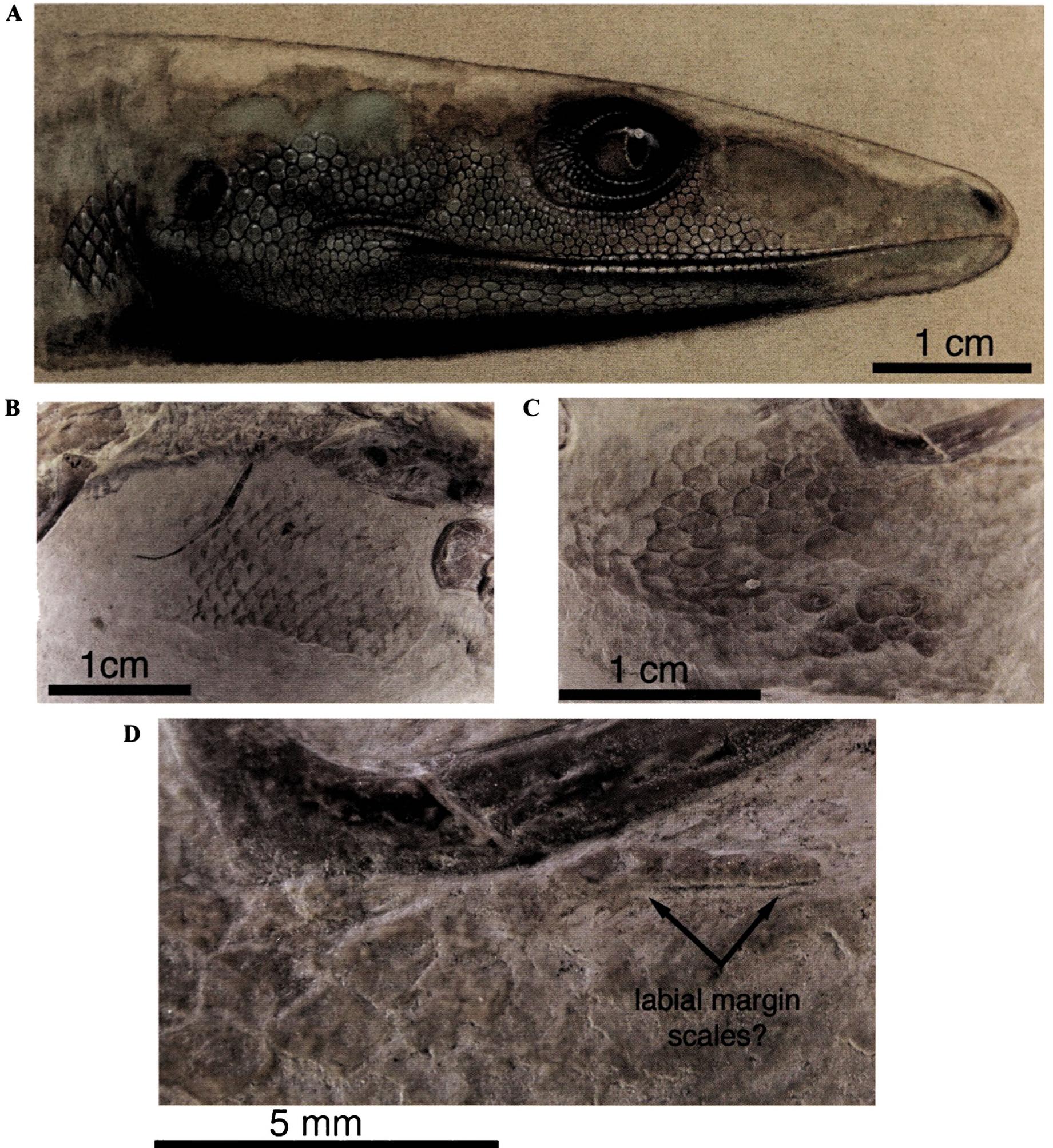


Fig. 13 - Scales on the head and neck region of *Pontosaurus kornhuberi*, MSNM V3662. A) Reconstruction of the head (artist: Fabio Fogliazza); B) detail of neck scales; C) detail of cheek scales; D) detail of lower portion of jugal bar illustrating possible labial scales.

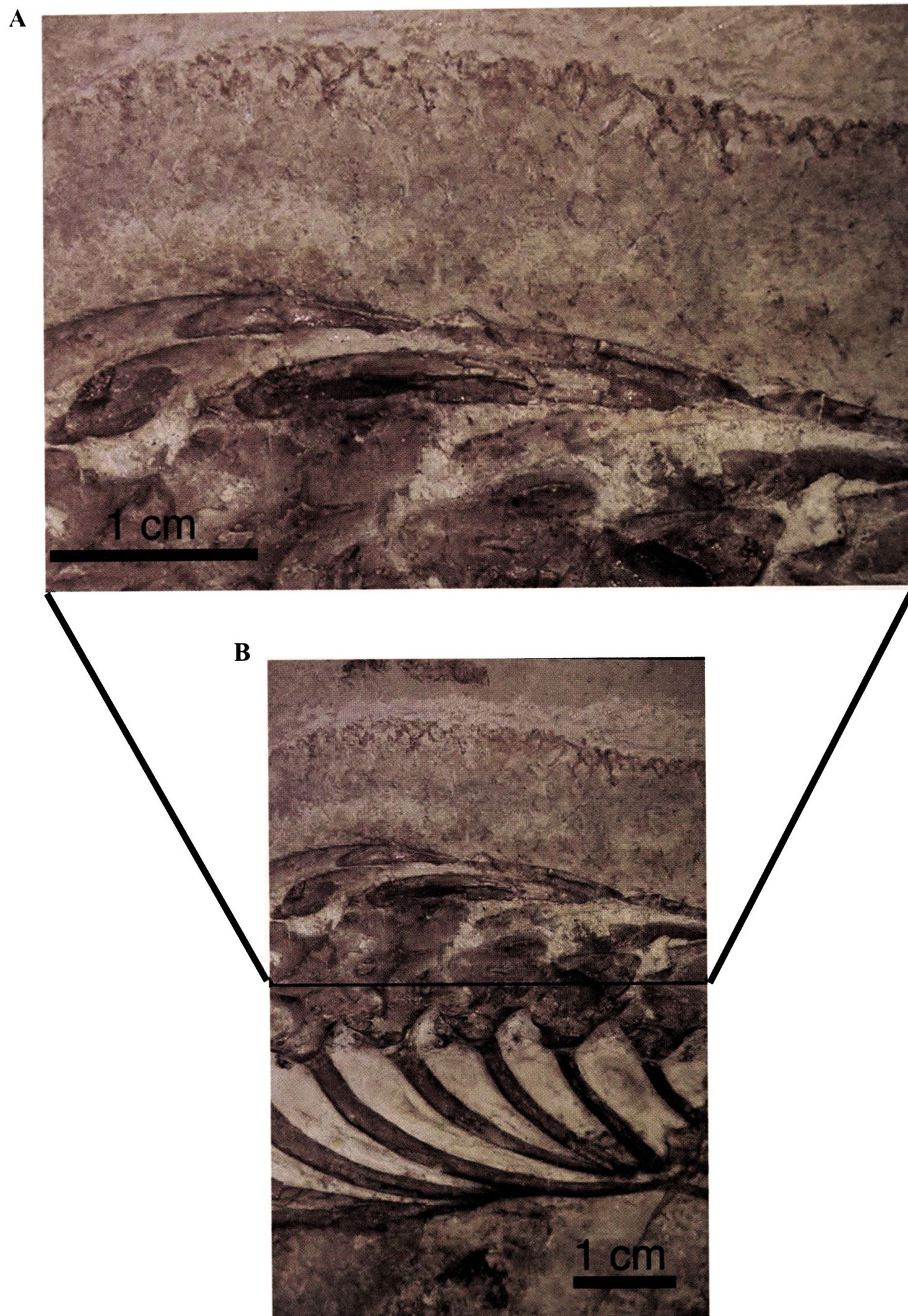


Fig. 14 - Scales on the trunk of *Pontosaurus kornhuberi*, MSNM V3662. A) Detail of scales at mid-trunk, vertebrae 17-21; B) photo of mid-trunk region. 'A' is a magnified portion of the upper part of photo 'B'.

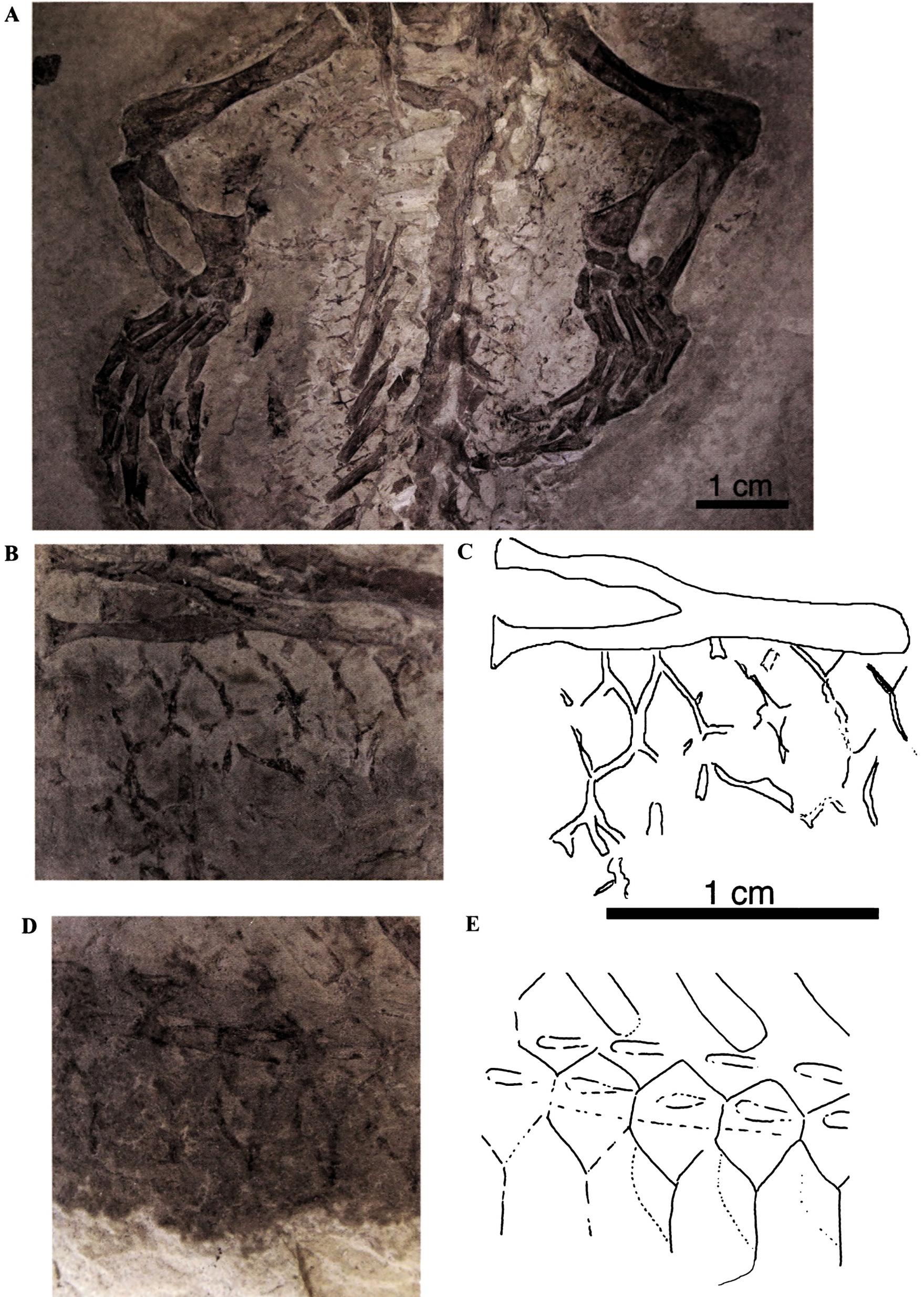


Fig. 15 - Pelvic and caudal scales of *Pontosaurus kornhuberi*, MSNM V3662. A) Overview of rearlimbs, pelvis, and anterior cauda; B) photo detail of anteriormost and ventral caudal scales; C) line drawing of photo 'B'; D) photo detail of midcaudal scales and ventral columnar scales; E) line drawing of photo 'D'.

### Tracheal and ?bronchial? rings

The trachea, as represented by the preserved tracheal rings present in the cervical region and the anteriormost portion of the trunk, was naturally long, but also had a rather large diameter (Fig. 16) at approximately 3-4 mm. The preserved tracheal rings are exposed to the right of the axis cervical vertebra (Fig. 7 A-C) and are exposed on the right side of the specimen through to C5 where they disappear under C6-7 reappearing at C8 and crossing the internal surface of the clavicle-interclavicle (though not well preserved here) to reappear between the left side ribs of the first, second and third dorsal vertebrae (Fig. 9). At this point, it is tempting to refer to these rings as preserved portions of the left bronchus since presumably at this point, the trachea had bifurcated into the right and left bronchi. This series of tracheal and perhaps bronchial rings is the best-preserved and most continuous sequence for any known pythonomorph and possibly any lepidosauromorph.



Fig. 16 - Tracheal rings of *Pontosaurus kornhuberi*, MSNM V3662.

## PHYLOGENETIC ANALYSIS

Of the squamate synapomorphies recognized by Estes *et al.* (1988), *Pontosaurus kornhuberi* possesses the following: reduced nasals, transverse frontoparietal suture, angular not reaching mandibular condyle, single headed ribs, cervical intercentra form prominent hypapophyses, loss of entepicondylar foramen in humerus, enlarged distal epiphysis of ulna, loss of gastralia, proatlas absent, premaxillae fused, parietal fused, jugal forms anteroventral border of orbit, procoelous vertebrae, dorsal intercentra lost, and an anterior coracoid emargination. As a result, it is accepted *a priori* that it is a squamate, a statement that need not be tested phylogenetically.

Additionally, *Pontosaurus kornhuberi* also possesses the following anguimorph synapomorphies as recognized by Estes *et al.* (1988): cervical intercentra sutured to posterior part of preceding centrum and more than 26 presacral vertebrae.

### Methodology

Phylogenetic relationships of *Pontosaurus kornhuberi* and *Pontosaurus lesinensis* were examined by integrating the detailed osteological description presented here into a highly modified version of Pierce & Caldwell's (2004) data matrix (characters and state codings) of pythonomorph squamates (a modified analysis of Lee & Caldwell's [2000] squamate data matrix). A large number of characters were uninformative when balanced against the reduced ingroup used here and so were deleted. Several character states were modified, in particular for *Pontosaurus lesinensis*, and some character descriptions were also modified.

The analysis presented here only includes the ingroup pythonomorphs as identified by Pierce & Caldwell

(2004): aigialosaurs and mosasaurs (Lee & Caldwell, 2000), *Pachyrhachis problematicus* (Lee & Caldwell, 1998), *Pachyophis woodwardi* (Lee *et al.*, 1999), *Aphanizocnemus libanensis* (Dal Sasso & Pinna, 1997), the Dolichosauridae [which includes *Dolichosaurus longicollis* and *Coniasaurus crassidens/Coniasaurus gracilodens* (Caldwell 1999, 2000; Caldwell & Cooper, 1999)], *Adriosaurus suessi* (Lee & Caldwell, 2000), *Pontosaurus lesinensis* (Pierce & Caldwell, 2004), and *Pontosaurus kornhuberi* (this study). These taxa were coded for 77 osteological characters (Appendix I) modified from the character descriptions listed by Pierce & Caldwell (2004). Cladograms were produced using the Branch-and-Bound algorithm as written into the computer software application PAUP Version 4.0b10 (Swofford, 2002). All characters were analyzed unordered and unweighted; terminal polymorphisms were interpreted as "uncertainty regarding the primitive state" when calculating tree lengths. The modern varanid lizard *Varanus* sp. was coded for these same 77 characters and used as the outgroup taxon for rooting the tree and polarizing character state transformations. The selection of *Varanus* as outgroup in this analysis follows the justifications as given by Tchernov *et al.* (2000) in their analysis of snakes, and the findings of Rieppel & Zaher (2000) regarding varanid-mososaurid relationships as presented in their critique of Lee (1998).

### Results

Cladistic analysis of the data matrix (Appendix II) resulted in 9 equally most-parsimonious cladograms with tree lengths of 119 steps, Consistency Indices (C.I.) of 0.773, Homoplasy Indices (H.I.) of 0.226, and a Retention

Indices (R.I.) of 0.727. Aigialosaurs and mosasaurs form a resolved clade in all nine cladograms as do the ophidians, *Adriosaurus* and the two pontosaurs; the Dolichosauridae are consistently reconstructed as the sistergroup to all other non-mosasauroid pythonomorphs (see the Strict Consensus Tree, Fig. 17 A). The unstable taxon is the Lebanese marine

lizard, *Aphanizocnemus libanensis*. In three trees it is the sistergroup to all non-mosasauroid pythonomorphs, in three more it forms a clade with the Dolichosauridae, and in the final three it is resolved as the sistergroup to all pontosaurs, *Adriosaurus* and ophidians.

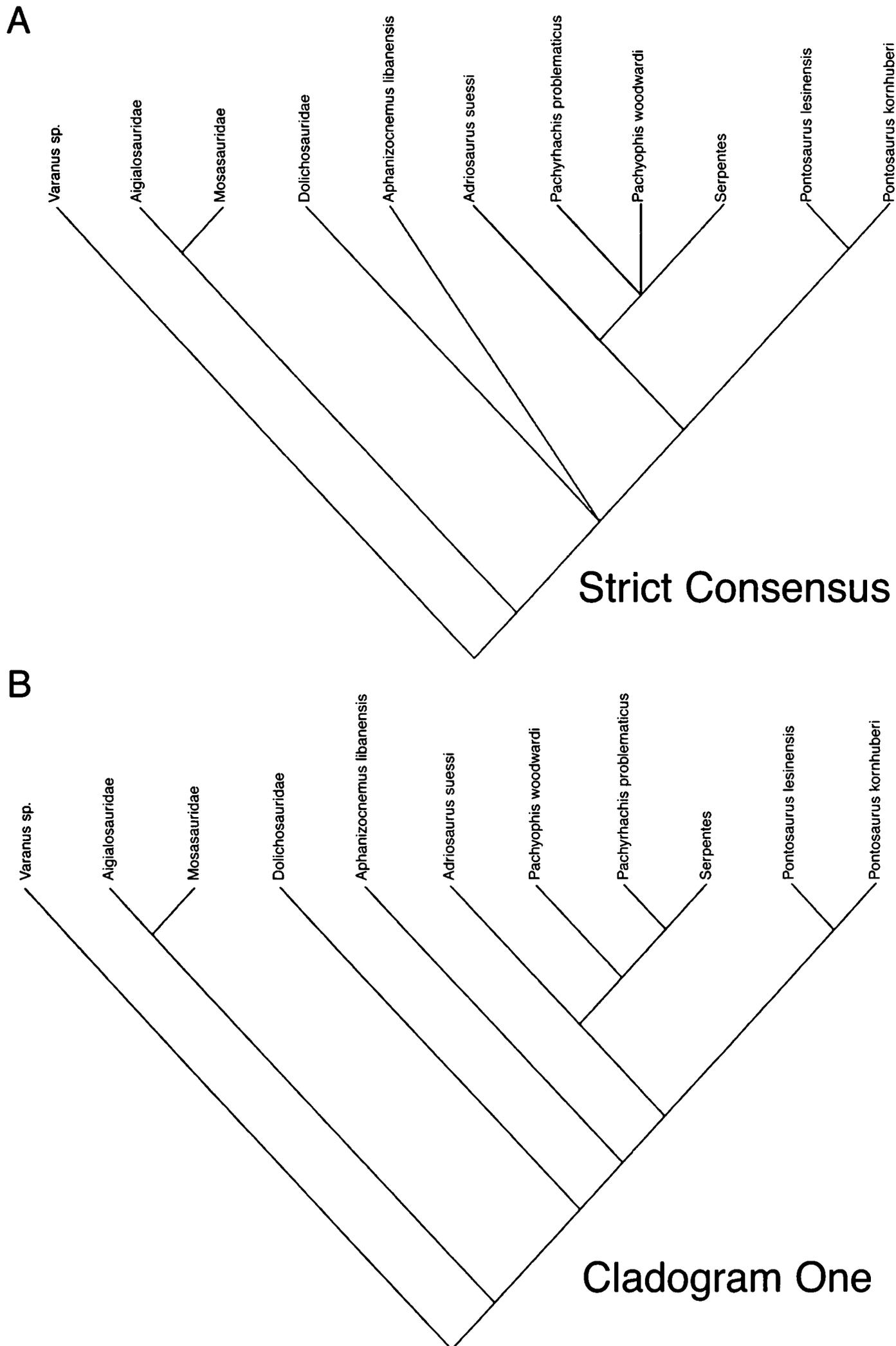


Fig. 17 - A) Strict consensus phylogeny and B) Cladogram Number One, resulting from cladistic analysis of ten pythonomorph squamate taxa using 77 osteological characters. This analysis resulting in nine most parsimonious trees (Tree length, 119 steps; Consistency Index (C.I.) = 0.773); Homoplasy Index (H.I.) = 0.226; Retention Index (R.I.) = 0.727).

### Character distributions

The synapomorphies supporting the various clades are the only important components of any phylogenetic statement as derived from a cladogram, or series of cladograms (i.e., a consensus tree interpreted as a phylogeny). As cladograms are constructed by character state distributions, the nature of the characters and states as described, and subjective decisions that were made in their delineation and construction, are the key elements of any phylogenetic hypothesis. Statistical support, other than the information supplied by consistency and homoplasy indices, is not given in this study. From my point of view, a character may well be homoplastically distributed and not at all "robust" on a statistical basis. However, this lack of robustness may stem from at least two alternatives in terms of phylogenetic history or non-history: 1) the taxic sample is incomplete but the character is accurately described; 2) the character is inaccurately described and the taxic sample is incomplete. In either case, because we are testing sistergroup relations, not heuristically recovering ancestors, we must always assume that the taxic sample is incomplete. What is likely impossible to determine is the delineation and character state subdivision of the feature being characterized. No statistical test, administered subsequent to the cladistic parsimony analysis, can determine the phylogenetic value of a character statement. In other words, I do not accept the value of decay indices such as Bremer Support etc., and have not applied such tests to the analysis of character distributions, the characters of which, and their states, are still the object of great scrutiny.

The following review of synapomorphy/apomorphy distributions reflects the character distributions for cladogram number one (Fig. 17 B).

**(Aigialosauridae, Mosasauridae)** - This clade is supported by six synapomorphies: 6 (0=>1), Jugal extends anteriorly past orbit; 48 (0->1), Coronoid anteromedial margin does not contact splenial; 49 (0=>1), Surangular forms half of articular cotyle (1); 60 (0=>1), Transverse processes of cervicals on middle of centrum; 61 (0=>2), Cervical intercentra (excluding atlas and axis intercentra) not sutured or fused to preceding centrum; 72 (1=>2), Number of rib attachment points to sternum, five pairs.

**(Dolichosauridae, (Aphanizocnemus ((Pontosaurus lesinensis, Pontosaurus kornhuberi) (Adriosaurus (Pachyophis (Pachyrhachis, Serpentes))))))** - This clade is supported by 17 synapomorphies: 1 (1->0), Premaxillary lateral foramina absent; 20 (0->1), Supratemporal in superficial position, on dorsolateral surface of parietal; 27 (1->2), Decensus parietalis, prominent flanges form sidewall of braincase contacting entire dorsal margin of prootic; 29 (0->1), Optic foramina enclosed partly or entirely by frontals; 30 (0->1), Trigeminal foramen or foramina, anterior margin enclosed by descending flange of parietal; 31 (0->1), Crista prootica (ridge on lateral surface of the prootic, overhanging foramen pro nervi facialis) reduced to weak ridge, or absent; 32 (1->0), Basisphenoid without long posterolateral flanges; 33 (0->1), Supraoccipital situated posterior to parietal, forms part of posterior skull roof; 34 (0->1), Post-temporal fenestra completely closed via sutural contact of the skull roof and otic region of braincase; 35 (1->2), Opening of

Jacobson's organ enclosed fully by vomer and septomaxilla only, not confluent with choana; 38 (1->0), Palatine as long as vomer; 39 (0->1), Palatine with distinct rectangular process projecting medially from the middle portion of the palatine to the skull midline; 59 (0->1), Number of cervical vertebrae ten to eleven; 66 (0=>1), Scapulocoracoid present but reduced; 69 (0->1), Interclavicle present but reduced; 73 (0=>1), Forelimbs small (1); 76 (0->1), Scleral ossicles thirteen or fewer.

**(Aphanizocnemus ((Pontosaurus lesinensis, Pontosaurus kornhuberi) (Adriosaurus (Pachyophis (Pachyrhachis, Serpentes))))))** - This clade is supported by 6 synapomorphies: 2 (0->1), Premaxilla-maxilla contact mobile and non-sutural; 12 (0->1), Frontoparietal suture, in dorsal view, complex curved or interdigitating contact; 26 (0->2), Ventromedial processes of frontals contacting parabasisphenoid below olfactory tracts; 42 (0->1), Mental foramina on lateral surface of dentary, two or fewer foramina; 44 (1->0), Subdental shelf weakly developed; 71 (0->1), Ossified sternum absent.

**((Pontosaurus lesinensis, Pontosaurus kornhuberi) ((Adriosaurus (Pachyophis (Pachyrhachis, Serpentes))))))** - This clade is supported by 3 synapomorphies: 46 (0->1), Splenial, small, only reaching middle of tooth row (1); 62 (0=>1), Pachyostosis of mid-dorsal vertebrae and ribs, present; 63 (0=>1), ribs, long, not curved, body laterally compressed.

**(Adriosaurus (Pachyophis (Pachyrhachis, Serpentes)))** - This clade is supported by 17 synapomorphies: 4 (1->0), Posterior process of maxilla long, reaching or extending past middle of ventral margin of orbit; 8 (1->0), Antorbital ridge absent; 9 (0=>1), Frontals, paired elements; 15 (0=>1), Postorbital ventral process prominent, forming half or more of posterior orbital margin, postorbital primarily an orbital bone; 23 (0->2), Quadrate, distinct tympanic crest absent and external surface of quadrate only weakly concave; 24 (1->0), Quadrate shape without large, posteroventrally curved, suprastapedial process; 28 (0->1), decensus parietalis contacting parabasisphenoid; 36 (0->1), Vomer entirely medial to palatine; 37 (0->1), Palatine-vomer contact mobile, non-sutural contact; 40 (1->0), Interpterygoid vacuity ("pyriform recess" of Estes *et al.*, 1988) open and wide; 44 (0->2), Subdental shelf absent; 45 (1->2), Posterior margin of lateral surface of dentary, deep notch present; 48 (0->1), Coronoid anteromedial margin does not contact splenial; 51 (1->2), Articular fused with prearticular and surangular; 55 (0->1), Palatine teeth present; 68 (0->1), Clavicle absent; 75 (0->1), Scleral ossicles absent.

**(Pachyophis (Pachyrhachis, Serpentes))** - This clade is supported by 14 synapomorphies: 5 (0=>1), Lacrimal absent, never present as a discrete element; 10 (0->1), Frontal excluded from orbital margin, prefrontal contacts postfrontal or postorbital; 17 (0=>1), Pineal foramen absent; 18 (0=>2), Parietal table and jaw adductor muscles, parietal table has a narrow sagittal crest, jaw adductors extend over entire dorsal surface of parietal; 19 (0=>1), Upper temporal arch incomplete, upper and lower temporal fenestra confluent; 52 (0->1), Retroarticular process size short, < articular cotyle; 57 (0->1), Vertebral articular surfaces vertical, condyles (if present) facing

posteriorly, much of the articulatory surface is visible in ventral view; 58 (0=>3), Number of presacral vertebrae 120 or more; 59 (1=>2), Number of cervical vertebrae more than twelve; 64 (0=>1), Distally forked cloacal ribs (“lymphapophyses”) present; 66 (1=>2), Scapulocoracoid absent; 73 (1=>2), Forelimbs absent; 74 (1->0), Epipodials parallel; 77 (0=>1), Epiphyses on appendicular skeleton absent.

(*Pontosaurus lesinensis*, *Pontosaurus kornhuberi*) - This clade is supported by 10 synapomorphies: 3 (1=>0), Dorsal process of maxilla on middle or anterior end of maxilla; 21 (1=>0), Supratemporal small, less than half the maximum width of the skull; 22 (1->0), Quadrate suspension, mobile, articulates dorsally with squamosal, supratemporal and opisthotic; 41 (1->0), Pterygoid, anterior (palatine) process merges gradually, in a gentle curve, with the lateral (ectopterygoid) process; 50 (1->0), Adductor fossa faces dorsomedially; 52 (0=>2), Retroarticular process size long, >2 times articular cotyle; 61 (0=>1), Cervical intercentra (excluding atlas and axis intercentra) sutured to preceding centrum (1); 65 (0->1), very laterally compressed, transverse processes reduced anteriorly, absent posteriorly, chevrons and neural spines elongated; 69 (1->0), interclavicle present.

## Discussion

The phylogenetic analysis presented here supports Nopcsa’s (1903) claim that *Pontosaurus* is more closely related to other dolichosaurs and snakes than to the aigialosaurs (Kramberger, 1892); the varanoid question debated by Kornhuber (1873) and Kramberger (1892) was not tested here. The phylogenetic position of *Pontosaurus* further reinforces the assertion that dolichosaurs are the sister group to all modern and extinct snakes as recently suggested by Pierce & Caldwell (2004) and Lee & Caldwell (2000), and more historically, by Nopcsa (1908, 1923).

As was argued by Pierce & Caldwell (2004), the analysis presented here also supports the idea that the family Dolichosauridae is a paraphyletic assemblage as indicated by the following sistergroup structure from Cladogram 1 [(*Dolichosaurus*, (*Aphanizocnemus* ((*Pontosaurus lesinensis*, *Pontosaurus kornhuberi*) (*Adriosaurus* (*Pachyophis* (*Pachyrhachis*, *Serpentes*))))))] (Fig. 17 B).

It should be noted however, that the paraphyly of Nopcsa’s Dolichosauridae, inclusive of “dolichosaurs” other than *Dolichosaurus* and *Coniasaurus*, could be a con-

sequence of the taxa and/or characters used in this analysis; alternatively, if arguments presented by Rieppel & Zaher (2000) are ever tested by original analysis then it is possible the topology hypothesized here will be found to be polyphyletic and that the Dolichosauridae is in fact a monophyletic assemblage exclusive of snakes. As noted, Rieppel & Zaher’s (2000) contention has not yet been corroborated by the presentation of a testable hypothesis.

In terms of the selection of taxa and characters, it is important to point out that there are nine known species of non-mosasauroid and non-aigialosaur Cenomanian-aged marine squamates that are referred to as “dolichosaurs”; however, only five were incorporated into the above analysis. A detailed re-examination of all known dolichosaurs, such as *Acteosaurus tommasinii* (Meyer, 1860) and *Eidolosaurus trauthi* (Nopcsa, 1923), is necessary in order to complete the data set.

For example, recent re-assessment of *Acteosaurus crassicosatus* by Caldwell & Lee (2004) indicated that the taxon is not diagnosable and that the specimens assigned to the species by Calligaris (1993) are diagnosable as *Adriosaurus suessi*. Attempts to code *E. trauthi* resulted in only 18% of the 159 characters being coded; the characters and the taxon were removed from the final matrix due to the inordinately high amount of missing data.

What is ultimately needed is a detailed examination and test of the monophyly of the Pythonomorpha (mosasaurs, aigialosaurs, dolichosaur, pontosaurs, adriosaurus, acteosaurus, and snakes). Rieppel & Zaher (2000) recently re-examined and criticized Lee’s (1998) character evidence as used in support of the hypothesis of a monophyletic Pythonomorpha. Their analysis found pythonomorphs to be non-monophyletic, with the Mosasauroidae nested within varanoids and snakes nested with a clade including amphisbaenids and dibamids; all of these squamates were found to be anguimorphs. Although Rieppel & Zaher (2000) used the results of their analysis to reject Lee’s (1998) assertion of a monophyletic Pythonomorpha, they did not accept their own phylogenetic tree as an accurate representation of squamate relationships; this makes their “falsification” unacceptable. A critical review of the character codings used in this study and those employed by Rieppel & Zaher (2000) along with an additional analysis including all known pythonomorphs is necessary to resolve the monophyly of the Pythonomorpha. A rigorous analysis of mosasaurs, aigialosaurs, dolichosaurs, pachyophiids, and snakes might alter both our understanding of pythonomorph phylogeny and by extension snake origins.

## FUNCTIONAL MORPHOLOGY

Aquatic environments present very specific physical and environmental constraints on the successful adaptation and evolution of the inhabitant organisms. For secondarily aquatic tetrapods the parameters of these constraints influence anatomies related to buoyancy control, respiration, locomotion, vision, hearing, chemosensory perception, feeding, and reproduction (Pl. 1).

For example, extinct aquatic squamates responded to these constraints and the selection pressures imposed by them, through the evolution of pachyostosis in the ribs and vertebrae in order to solve problems of buoyancy. In some groups, such as dolichosaurs, they evolved elongate necks and snouts to address the constraints of ambush feeding underwater. Mosasaurs solved locomotory problems in a

viscous fluid via modifications to the axial skeleton to support carangiform locomotion, and by modifying the limbs into hydrofoils/paddles by shortening the upper and lower limb, and lengthening and broadening the hand and foot.

Similar evolutionary solutions to these physical and environmental constraints are preserved in the fossilized skeletons of early aquatic snakes (Caldwell & Lee, 1997; Rage & Escuillié, 2000; Tchernov *et al.*, 2000; Rieppel & Head, 2005), dolichosaurs (Caldwell, 1999, 2000; Caldwell & Cooper, 1999; Lee & Caldwell, 2000) (e.g., MSNM V3662), aigialosaurs (DeBraga & Carroll, 1993; Caldwell & Lee, 2001), and in particular, the giant marine mosasaurs (Russell, 1967; Bell, 1997).

### *Pontosaurus*

The anatomy and morphology of the complete tail of *Pontosaurus kornhuberi*, as exemplified by MSNM V3662, with 163 vertebrae comprising 68% of the total body length (TBL), suggests that this structure was the primary propulsive organ for aquatic locomotion (Fig. 18 A). Because pontosaurs and dolichosaurs are among the earliest known aquatically adapted lizards (Kornhuber, 1873; Pierce & Caldwell, 2004) along with pachyophiid snakes (Lee & Caldwell, 1998), and have been hypothesized to be the sister-group to snakes (Lee & Caldwell, 2000), the adaptations of pontosaurs and dolichosaurs provide important insights into aquatic evolution and adaptation in early marine squamates.

A useful comparison of body proportions gives some insight into the functional morphology of *Pontosaurus*. Caldwell & Dal Sasso (2004) compared *Pontosaurus kornhuberi* to two modern, aquatic squamates, the Galapagos Marine Iguana and the Yellow-bellied Sea Snake (Fig. 18 A-C). Those authors showed that the tail of *Pontosaurus* is proportionately longer, and is dorsoventrally deepened along most of its length as compared to either a sea snake or the marine iguana. This is an important distinction as it indicates that seasnakes locomote not with their tail (carangiform locomotion) but with their entire bodies (anguilliform locomotion); by comparison, the marine iguana, which swims in a carangiform-subcarangiform mode, does so with a proportionately shorter tail. Another level of comparison can be made between pontosaurs and mosasaurs in the percent total body length (TBL) of the tail, which ranges between 30% and 48% in the latter (Russell, 1967). In other words, pontosaurs had very short bodies, long necks, and extremely long tails as compared to the more derived mosasaurs, to their sister group, the snakes, and to the modern marine iguana.

Comparing the osteology of the tail of a marine iguana with the tail of *Pontosaurus kornhuberi*, it is evident that the latter is much more laterally compressed; comparison with the sea snake indicates a similar degree of compression to pontosaurs. The anterior-most haemal arches and transverse processes of MSNM V3662 present a broad and deepened set of surfaces for the insertion of a large and powerful caudofemoralis musculature (lateral to the hypaxially oriented anterior haemals immediately posterior to the reduced ischium) that would have been

used to “drive” the movements of the tail. The adaptive importance of the tail as the aquatic locomotory organ for Cretaceous marine squamates cannot be overemphasized; even in later groups of marine lizards such as mosasaurs, which evolved paddle-like limbs, the primary locomotory organ was clearly the tail. A brief examination of caudal osteology in mosasaurs highlights a number of features shared with *Pontosaurus kornhuberi*, but also reveals the presence of a large and variable number of pygal vertebrae (i.e., caudals without haemal arches).

The transverse processes of the two pygal vertebrae are very large and would have served as an enormous and very long series of attachment sites for the caudofemoralis musculature (ranging from 15-50% of total tail length). Additionally, the long pontosaur tail would have been essential to tail-driven locomotion since the body was likely made more rigid by the high degree of pachyostosis. This rigidity may have decreased the severity of lung compression, allowing limited respiration during powerful surface locomotion.

A second feature of the axial skeleton of *Pontosaurus kornhuberi* that is likely related to tail driven locomotion is the anatomy of the ilium (Fig. 11), specifically the iliac crests. In *P. kornhuberi* the only crest and process that is well developed is the posterior superior iliac crest, thus giving a broad proximal attachment surface for the femoral flexors. There is no anterior extension of the ilium that would serve as the proximal attachment site for the femoral extensors. The overdevelopment of the posterior attachment sites, as compared to the underdevelopment of the extensor attachments, may well represent a functional focus on the limb flexor musculature synergistically associated with the flexion of the caudofemoralis. Contractile flexion of the caudofemoralis musculature would adduct the femora towards lateral surface of the tail. Synergistic flexion of the femur and tibia, by contraction of the femoral and tibial adductor musculature proximally attached to the posterior iliac crest (e.g., *adductor femoris*, *flexor tibialis internus* and *externus*), may well have contributed to the caudal powerstroke driven by contraction of the *caudofemoralis*. Retraction of the femur would have been largely passive thus re-building elastic kinetic energy into the muscles of the opposite and stretched muscles fibers prior to the next contraction. This anatomy also suggests that the synergistic powerstroke was rapid, strong and provided a burst of speed, pursuits designed for ambush style predation.

Building on this functional model, the anatomy of the pubis and ischium present a broad contact along the ventral aspect of midline of the body. This morphology indicates that the *puboischiofemoralis* and *puboischiotibialis* were all well-developed in their proximal attachments. These muscles serve to pull the lower limb towards the midline of the body, again, likely in synergy with the *caudofemoralis*; again, retraction of the femur and tibia would be passive and occurring in opposing waves, right to left.

For slow swimming, it seems reasonable to model gentle caudal driven locomotion with the limbs held tightly against the body. For high speed sudden power bursts, the functional model suggested here would likely involve

strong contractions, in opposite waves, where the limbs were strongly adducted and retracted, adducted and retracted in a right-left pattern.

Following on the use of the rearlimbs in the sudden burst, tail driven locomotion, is the aspect of that limb and how it would have interacted with the water. Both the front and rear limbs are extremely reduced in size in *Pontosaurus kornhuberi*; additionally, the forelimb shows negative allometric growth in relation to the rearlimb. Some of this size difference can be attributed to the anatomy and inferred function of the rearlimb musculature in locomotion as discussed previously. However, despite the size and functional difference between the two limbs, they are similar to each other in terms of their degree of flattening in the lower limb region, the width of the antebrachium, and the elongation and flattening of the manus/pes (Figs. 10, 12). As discussed previously, this flattening and the widening of the limb likely prevented pronation of the forelimb via rotation of the radius. This would effectively have limited the ability of *P. kornhuberi* to locomote efficiently in terrestrial environments using its limbs; there is no indication that this animal could not have propelled itself effectively using axial locomotion, similar to a modern legless lizard (e.g., *Ophisaurus apodus*) or a sea krait (e.g., *Laticauda colubrina*). Similarities of body morphology and proportion link legless lizards and *P. kornhuberi* while the ventral scales of *P. kornhuberi* are similar to those of sea kraits (Caldwell & Dal Sasso, 2004) which also are able to move about on land, unlike true sea snakes.

The other feature of limb morphology in *Pontosaurus kornhuberi* that is important to consider, is the hydrofoil potential of a broad and flattened lower limb and manus/pes. This is particularly important for the rearlimb as functionally reconstructed in the caudal powerstroke. If the limb was passively retracted due to muscle fiber stretching in response to total fiber recruitment during powerful contractions, then it would have been efficient as a hydrofoil if it presented a low hydrofoil aspect preaxially to postaxially. The widening of the antebrachium and flattening of the elements supports this functional model for the rearlimb.

As a result of its small limbs, more rigid trunk, and extremely long tail, it seems likely that *Pontosaurus kornhuberi* had reduced potential for terrestrial locomotion but was likely an excellent swimmer, employing its unique anatomies to problems of aquatic locomotion. It possessed at least several rows of caudal scales that may have assisted in reducing drag; later groups such as mosasaurs appear to have covered the entire body with keeled scales. Pontosaurs also evolved incredibly long tails that were laterally very compressed and thus presented a high surface area for power strokes during lateral undulatory locomotion. Finally, the anterior-most caudals show an osteology that is very suggestive of the presence of large caudofemoralis muscles (a small number of pygals and the presence of large transverse processes); these muscles are critical to tail-driven locomotion and became very important in the later, and very successful, giant mosasaurs.

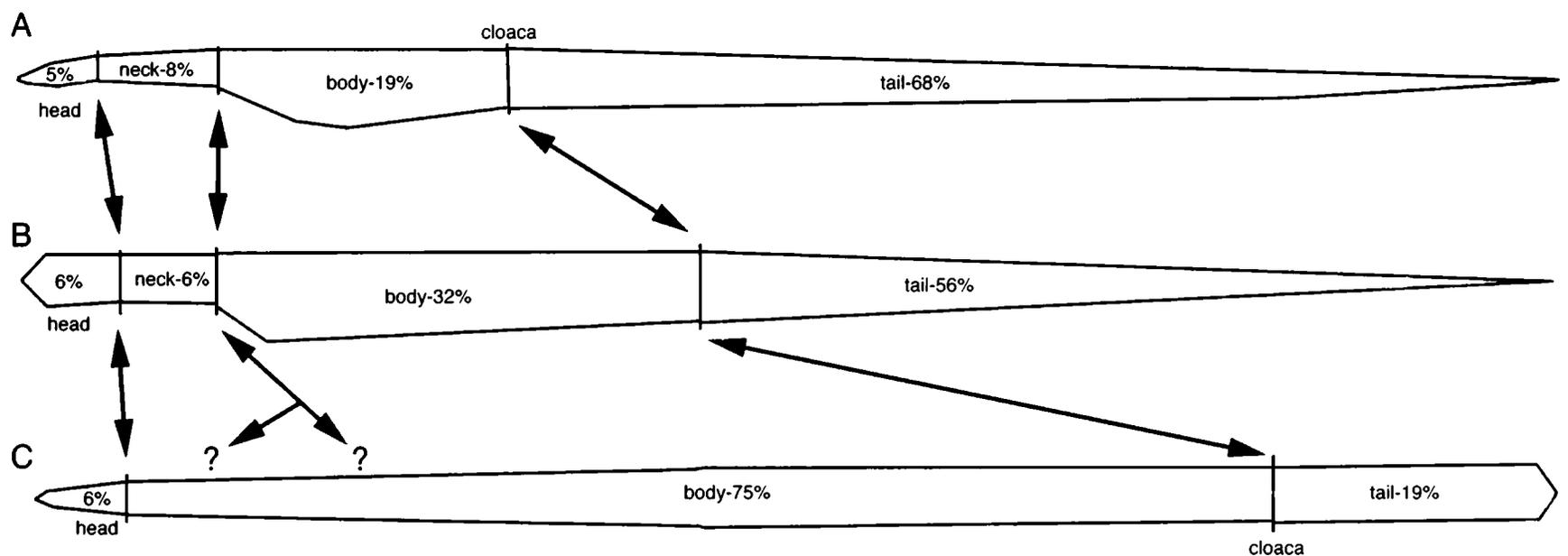


Fig. 18 - Body proportions of fossil and extant marine squamates. A) *Pontosaurus kornhuberi*, MSNMV3662; B) *Amblyrhynchus cristatus*, modern Galapagos Marine Iguana; C) *Pelamis platurus*, modern Yellow-bellied Sea Snake.

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A new species of *Pontosaurus* (Squamata, Pythonomorpha) from the Upper Cretaceous of Lebanon  
and a phylogenetic analysis of Pythonomorpha

Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano  
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## APPENDIX I

## Character List

## (a) skull roof

1. Premaxillary lateral foramina. Absent (0); present (1).
2. Premaxilla-maxilla contact. Immobile and sutural (0); mobile and non-sutural (1). The coding for *Pontosaurus lesinensis* as given by Pierce & Caldwell (2004) was recoded from state (0) to state (1).
3. Dorsal process of maxilla. On middle or anterior end of maxilla (0); on posterior half of maxilla (1). The coding for *Pontosaurus lesinensis* as given by Pierce & Caldwell (2004) was recoded from state (1) to state (0).
4. Posterior process of maxilla. Long, reaching or extending past middle of ventral margin of orbit (0); short, not reaching middle of ventral margin of orbit (1).
5. Lacrimal. Present, either permanently separate or fusing with prefrontal during ontogeny (0); absent, never present as a discrete element (1).
6. Jugal. Does not extend anteriorly past orbit (0); extends anteriorly past orbit (1).
7. Nasals. Paired elements (0); single median element (1).
8. Antorbital ridge. Absent (0); present, extending anteriorly from dorsal margin of orbit (1).
9. Frontals. Single median element (0); paired elements (1).
10. Frontal. Enters orbital margin, prefrontal does not contact postfrontal or postorbital (0); excluded from orbital margin, prefrontal contacts postfrontal or postorbital (1).
11. Frontals. Lateral orbital margin deeply concave (0); lateral orbital margin straight or only very slightly concave (1). The coding for *Pontosaurus lesinensis* as given by Pierce & Caldwell (2004) was recoded from state (1) to state (0).
12. Frontoparietal suture. In dorsal view, simple straight transverse contact (0); in dorsal view, complex curved or interdigitating contact (1).
13. Palpebral (superciliary) ossifications on dorsal margin of orbit. Present (0); absent (1).
14. Postorbital. Present (0), absent (1).
15. Postorbital ventral process. Small, forming less than half of posterior orbital margin, postorbital primarily a temporal bone (0); prominent, forming half or more of posterior orbital margin, postorbital primarily an orbital bone (1). The coding for *Pontosaurus lesinensis* as given by Pierce & Caldwell (2004) was recoded from state (1) to state (0).
16. Posterior margin of orbit. Present and continuous (0); present but with small gap (1); very incomplete, less than 50% of posterior orbital margin bordered by bone (2).
17. Pineal foramen. Present (0); absent (1).
18. Parietal table and jaw adductor muscles. Parietal table moderately wide, jaw adductors extend onto lateral margin only of dorsal surface of parietal (0); parietal table very wide, jaw adductors restricted entirely to ventral surface of parietal (1); parietal table a narrow sagittal crest, jaw adductors extend over entire dorsal surface of parietal (2). The coding for *Pontosaurus lesinensis* as given by Pierce & Caldwell (2004) was recoded from state (2) to state (0).
19. Upper temporal arch. Complete, upper and lower temporal fenestrae separated (0); incomplete, upper and lower temporal fenestra confluent (1).
20. Supratemporal. In deep position, on ventrolateral surface of parietal (0); in superficial position, on dorsolateral surface of parietal (1).
21. Supratemporal. Small, less than half the maximum width of the skull (0); large, at least half the maximum width of the skull (1).
22. Quadrate suspension. Mobile, articulates dorsally with squamosal, supratemporal and opisthotic (0); mobile, articulates dorsally with supratemporal, little or no contribution from other elements (1); mobile, articulates dorsally with opisthotic, little or no contribution from other elements (2). The coding for *Pontosaurus lesinensis* as given by Pierce & Caldwell (2004) was recoded from state (?) to state (0).
23. Quadrate. Tympanic crest (outer conch) directed laterally and a well-developed wall (0); tympanic crest directed laterally but a low ridge (1); distinct tympanic crest absent and external surface of quadrate only weakly concave (2).
24. Quadrate shape. Without large, posteroventrally curved, suprastapedial process (0); with large, posteroventrally curved, suprastapedial process (1).
25. Mandibular articulation of quadrate. Saddle-shaped, with lateral and medial condyles (0); flat, a single continuous condyle (1).

## (b) braincase and associated structures

26. Ventromedial processes of frontals. Not contacting anything below olfactory tracts (0); abutting or sutured with each other below olfactory tracts (1); contacting parabasisphenoid below olfactory tracts (2).
27. Decensus parietalis. Weakly developed ridges/flanges on ventral surface of parietal (0); prominent flanges descending from lateral margins of dorsum of parietal (1); prominent flanges form sidewall of braincase contacting entire dorsal margin of prootic (2). The coding for *Pontosaurus lesinensis* as given by Pierce & Caldwell (2004) was recoded from state (0) to state (1).
28. Decensus parietalis. Not contacting parabasisphenoid or orbitosphenoid (0); contacting parabasisphenoid (1).
29. Optic foramina. Not enclosed in bone (0); enclosed partly or entirely by frontals (1).
30. Trigeminal foramen or foramina. Anterior margin not enclosed in bone (0); anterior margin enclosed by descending flange of parietal (1).
31. Crista prootica (ridge on lateral surface of the prootic, overhanging foramen pro nervi facialis). Well-developed lateral flange (0); reduced to weak ridge, or absent (1).
32. Basisphenoid. Without long posterolateral flanges (0); with long posterolateral flanges (1).
33. Supraoccipital. Situated ventral or posteroventral to parietal, does not form part of posterior skull roof (0); situated posterior to parietal, forms part of posterior

- skull roof (1).
34. Posttemporal fenestra. Present as an opening (0); completely closed via sutural contact of the skull roof and otic region of braincase (1).
- (c) palate and associated structures
35. Opening of Jacobson's organ. Enclosed fully by maxilla and vomer, sometimes with a tiny contribution from the septomaxilla, not confluent with choana (0); enclosed partly by maxilla and vomer, confluent posteriorly with choana (1); enclosed fully by vomer and septomaxilla only, not confluent with choana (2).
36. Vomer. Anterior or anteromedial to palatine (0); entirely medial to palatine (1).
37. Palatine-vomer contact. Immobile, sutural contact (0); mobile, non-sutural contact (1).
38. Palatine. Long - as long as vomer (0); short - half as long as vomer (1).
39. Palatine. Without distinct medially-directed process (0); with distinct rectangular process projecting medially from the middle portion of the palatine to the skull midline (1).
40. Interpterygoid vacuity ("pyriform recess" of Estes *et al.*, 1988). Open and wide (0); open and narrow (1).
41. Pterygoid. Anterior (palatine) process merges gradually, in a gentle curve, with the lateral (ectopterygoid) process (0); anterior process distinctly set off from lateral process, the two portions meeting at a distinct "corner" (1).
- (d) lower jaw
42. Mental foramina on lateral surface of dentary. Three or more foramina (0); two or fewer foramina (1).
43. Dentary. Curved in lateral view, with concave dorsal (alveolar) edge (0); straight in lateral view, with straight dorsal edge (1).
44. Subdental shelf. Weakly developed (0); large (1); absent (2).
45. Posterior margin of lateral surface of dentary. Shallow notch present (0); no notch present (1); deep notch present (2).
46. Splenial. Large, extending anteriorly past middle of tooth row (0); small, only reaching middle of tooth row (1).
47. Splenial-angular contact. Not, or very slightly, exposed in lateral view (0); greatly exposed in lateral view (1).
48. Coronoid. Anteromedial margin contacts splenial (0); anteromedial margin does not contact splenial (1).
49. Surangular. Does not form large portion of articular cotyle (0); forms half of articular cotyle (1).
50. Adductor fossa. Faces dorsomedially (0); faces dorsally (1).
51. Articular. Separate from both prearticular and surangular (0); fused with prearticular but not surangular (1); fused with prearticular and surangular (2).
52. Retroarticular process size. Intermediate, between 1 and 2 times articular cotyle (0); short, < articular cotyle (1); long, >2 times articular cotyle (2).
- (e) dentition
53. Maxillary teeth. Thirteen or more tooth positions (0); between twelve and nine tooth positions (1); eight or fewer tooth positions (2).
54. Dentary teeth. Thirteen or more tooth positions (0); twelve to nine tooth positions (1); eight or fewer tooth positions (2).
55. Palatine teeth. Absent (0); present (1).
56. Pterygoid teeth. Present (0); absent (1).
- (f) axial skeleton
57. Vertebral articular surfaces. Slightly anterodorsal, condyles facing slightly dorsally, only the ventral edge of the articular surface is visible in ventral view (0); vertical, condyles (if present) facing posteriorly, much of the articular surface is visible in ventral view (1); anterodorsal, condyles facing very dorsally, none of the articular surface is visible in ventral view (2).
58. Number of presacral vertebrae. 27 to 50 (0); 50 to 119 (1); 23 to 25 (2); 120 or more (3).
59. Number of cervical vertebrae. Seven (0); ten to eleven (1); more than twelve (2).
60. Transverse processes of cervicals. On anterior end of centrum (0); on middle of centrum (1).
61. Cervical intercentra (excluding atlas and axis intercentra). Fused to preceding centrum (0); sutured to preceding centrum (1); not sutured or fused to preceding centrum (2).
62. Pachyostosis of mid-dorsal vertebrae and ribs. Absent (0); present (1).
63. Body shape. Round, ribs smoothly curved (0); laterally compressed, middle and distal regions of ribs totally straight (1).
64. Distally forked cloacal ribs ("lymphapophyses"). Absent (0); present (1).
65. Tail. Cylindrical or only slightly lateral compressed, transverse processes well-developed, chevrons and neural spines not elongated (0); very laterally compressed, transverse processes reduced anteriorly and absent posteriorly, chevrons and neural spines elongated (1).
- (g) shoulder girdle and forelimb
66. Scapulocoracoid. Present and large (0); present but reduced (1); absent (2).
67. Anterior (primary) coracoid emargination. Present (0); absent (1).
68. Clavicle. Present (0); absent (1).
69. Interclavicle. Present (0); absent (1).
70. Interclavicle. Cross-shaped, with lateral processes (0); simple rod, without lateral processes (1).
71. Ossified sternum. Present (0); absent (1).
72. Number of rib attachment points to sternum. Four pairs (0); three pairs (1); five pairs (2); two pairs or fewer (3).
73. Forelimbs. Large (0); small (1); absent (2).
74. Epipodials. Parallel (0); distally diverging (1).
- (h) pelvic girdle and hindlimb
75. Scleral ossicles. Present (0); absent (1).
76. Scleral ossicles. Fourteen (0); thirteen or fewer (1); fifteen or more (2).
77. Epiphyses on appendicular skeleton. Present (0); absent (1).

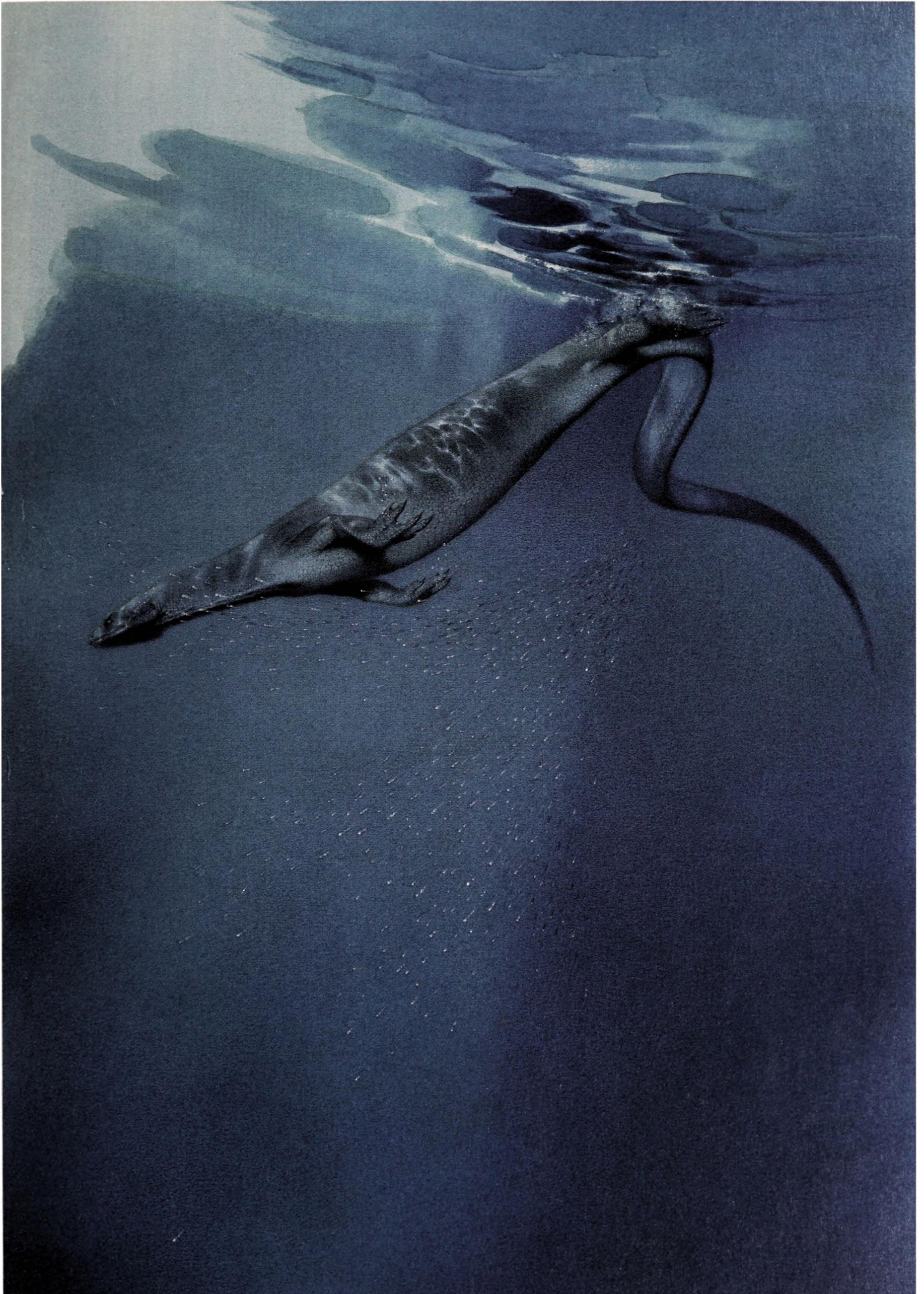
## APPENDIX II

## Character Matrix

	1	10	20	30
Varanus sp.	1	0	1	1
Aigialosauridae	?	0	1	1
Mosasauridae	1	0	1	1
Dolichosauridae	?	0	1	1
Aphanizocnemus libanensi	?	?	?	?
Adriosaurus suessi	?	1	1	&
Pachyrhachis problematic	?	1	1	0
Pachyophis woodwardi	?	?	?	?
Serpentes	&	1	0	&
Pontosaurus lesinensis	0	1	0	1
Pontosaurus kornhuberi	0	1	0	1

	31	40	50	60
Varanus sp.	0	1	0	0
Aigialosauridae	?	?	?	?
Mosasauridae	0	1	0	0
Dolichosauridae	?	?	?	?
Aphanizocnemus libanensi	?	?	?	?
Adriosaurus suessi	?	?	?	?
Pachyrhachis problematic	?	?	1	1
Pachyophis woodwardi	?	?	?	?
Serpentes	1	0	1	1
Pontosaurus lesinensis	?	0	1	?
Pontosaurus kornhuberi	?	?	1	?

	61	70	77
Varanus sp.	0	0	0
Aigialosauridae	2	0	0
Mosasauridae	2	0	0
Dolichosauridae	0	0	0
Aphanizocnemus libanensi	2	0	0
Adriosaurus suessi	?	1	1
Pachyrhachis problematic	0	1	1
Pachyophis woodwardi	?	1	1
Serpentes	0	0	0
Pontosaurus lesinensis	1	1	1
Pontosaurus kornhuberi	1	1	1



Pl. 1 - Reconstruction of *Pontosaurus kornhuberi*. Painting by Fabio Fogliazza.