FIELDIANA: GEOLOGY

A Continuation of the

GEOLOGICAL SERIES

of

FIELD MUSEUM OF NATURAL HISTORY

VOLUME 15

TABLE OF CONTENTS

THE NON-THERAPSID REPTILES

OF THE LUFENG BASIN, YUNNAN, CHINA

DAVID JAY SIMMONS

VOLUME 15, NUMBER 1

Published by

CHICAGO NATURAL HISTORY MUSEUM

APRIL 29, 1965

THE NON-THERAPSID REPTILES
OF THE LUFENG BASIN, YUNNAN, CHINA

DAVID JAY SIMMONS

Department of Palaeozoology University of Chicago

Edited by Edward G. Nash

CONTENTS

The Non-Therapsid Reptiles
of the Lufeng Basin, Yunnan, China

INTRODUCTION

The geological investigations of Bien (1941) some twenty years ago demonstrated that the sediments of the Lufeng Basin, Yunnan, China, held a richly varied vertebrate fauna. We are indebted to C. C. Young for our detailed knowledge of the fossil materials. The early taxonomic work progressed so rapidly that by 1940, the principal members of the assemblage were segregated and described briefly in several short preliminary notes (Young, 1939a, 1940b). Seven papers treating the individuals in detail were published in as many years (1941–1948), and in 1951 the fauna was assessed in monographic fashion.

The collection to be described was made in 1948 and 1949 by an expedition of the Fu Jen Catholic University of Peking led by Fr. E. Oehler, S.V.D. A re-examination of the fauna was deemed justifiable on several counts. First, the field work conducted by Young continued sporadically for two seasons during the early war years; lack of funds, transportation and equipment provided such difficult circumstances that the collections were largely cursory and unsystematically procured. Second, new outcrops from which fossils might be obtained were certain to have been exposed in the years intervening between the early and late 1940's. Young's sample is dominated by large saurischians but the scanty and very imperfect remains of smaller forms were reported. The fragment of a jaw symphysis tentatively diagnosed as a small pseudosuchian was of particular interest.

The fossils were lent from the S.V.D. Catholic Universities in 1957 by Fr. H. W. Rigney, S.V.D. The collection is known as the Fossil Collection of the S.V.D. Catholic University of Peking and will bear the provisional designation of CUP in the following report.

I am indebted to Dr. E. C. Olson through whose efforts the materials became available for study, and under whose guidance the

work was completed. I also wish to thank Dr. C. C. Young of the Institute of Vertebrate Paleontology, Peking; Dr. C. C. Mook and Dr. B. Brown of the American Museum of Natural History; Dr. R. Zangerl of Chicago Natural History Museum; Dr. A. S. Romer and Dr. B. Patterson of Harvard University, for their useful comments. Dr. Young kindly provided supplementary drawings used in the taxonomic determinations of many specimens. The bibliographic aid provided by Mrs. Rachel Nichols of the American Museum is gratefully acknowledged. The drawings were prepared by Mrs. Julia Child.

GEOLOGY OF THE LUFENG BASIN

The geology of the Lufeng Basin was described in a paper by Bien (1941); he arranged the list of vertebrate fossils from Young's publication (1939a) in stratigraphic sequence. The stratigraphy of the Basin was again reviewed generally by Young in his summary paper (1951), but the annotated list of fossils was incomplete relative to the newly determined materials.

Lufeng is situated about 60 km. northwest of Kunming, the capital city of Yunnan Province. The tectonic history of Yunnan shows that the Lufeng sediments were deposited in a structural basin formed by the subsidence of the Central Yunnan Swell (Central Yunnan Block) which had oscillated throughout the Paleozoic and had last been revived in the Upper Permian. The structure is clearly recognizable since late middle Sinian time; Misch (1945) states that the structure underwent strong subsidence in the Triassic due to additional sedimentation. Chang (1947) constructed a paleogeographic map (fig. 1) based upon the distribution of marine fossils which delineated the margins of the raised Swell and demonstrated that the Lufeng region was the site of terrestrial sedimentation. The uplift of the Swell in Permian times apparently served as a barrier to the transgressing Triassic sea that entered Yunnan from the south along the Sino-Burmese geosyncline so that it diverged into east and west waterways which continued in a northerly direction. During the Triassic, then, the basin received only sediments of continental origin typical of red bed development and flood plain environments. Interfingering of marine and continental deposits occurs along the borders of the Swell.

In Lufeng, the Lufeng Series has an aggregate thickness of about 1000 meters divided into a Lower Series of alternating beds of dull purplish to dark red clays, siltstones, shales and sandstones, and into

an Upper (Shihmen) Series of greenish-yellow banded bed sandy shales passing to variegated and wine red beds toward the top. The wine red beds contain calcareous and evaporitic matter. A thick green sandstone divides the red beds of the fossiliferous Lower Lufeng Series. The entire column is capped by a sandstone and rests on a basal breccia overlying the Sinian metamorphic rocks.
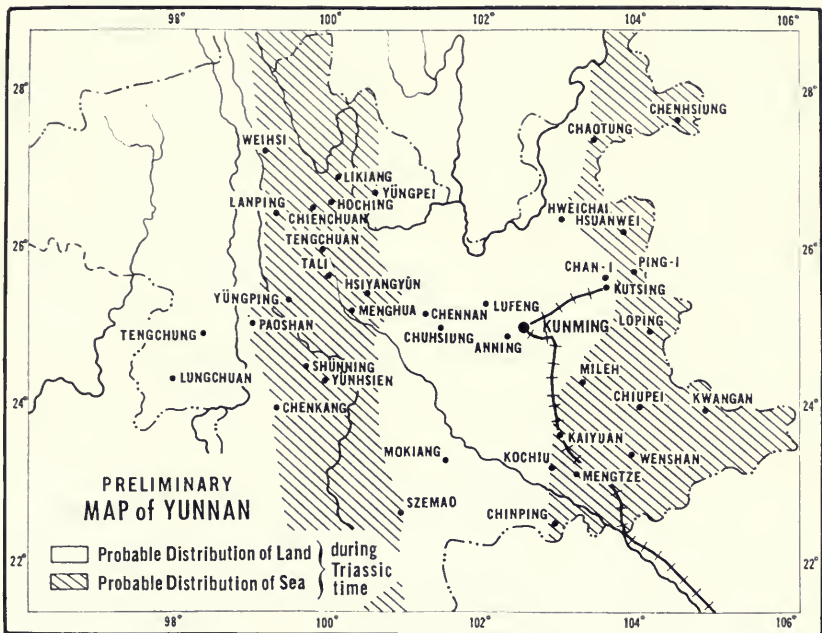
Fig. 1. A paleogeographic map of Yunnan Province showing the relative distribution of land and sea during Triassic time (redrawn from Chang, 1947).

The Lufeng Series *in toto* is conformable with the Ipinglang Coal Series below and with the Shihmen sandstone above (Misch, 1945). Bien (1941) regarded the Shihmen as disconformable with the Lufeng Series in Lufeng, but Misch held that the sandstone is "one horizon in the upper part of the Upper Red Beds" of Yunnan and not a separable unit. The apparent local discordance indicates that deposition of the Upper Lufeng Series was interrupted prior to the introduction of sand. The Shihmen sandstone is current cross-bedded and passes from a basal lenticular pebble to massive boulder conglomerate with shaley intercalations toward the top. The Upper Lufeng Series is also more highly variegated than most of the "Red Beds of Yun-

nan" and the calcareous clays and sandstones (with limestone bands) are apparently of a finer texture in Lufeng.

The thick Lower Lufeng Series is characterized by saurian remains. The thinner Upper Series contains fish (*Hybodus*, *Lepidotus*), an indeterminate chelonian, fresh-water ostracods and minute pelecypods and gastropods. The abrupt shift in the pattern of sedimentation and faunas perhaps indicates that conditions favored the establishment of shallow water environments, small lakes or pools fed by streams bearing dissolved calcium salts that produced at times the strongly indurated limestone bands of the upper-middle part. The algal deposition of carbonate and evaporitic matter is also conceivable. The fossil content and high degree of variegation is attributable to either a facies change, and/or to a change in the source area, or to the inclusion of organic materials resulting in the partial reduction of iron. The second of these is indicated by the apparent regularity of the bedding and by the reported absence of plant remains to serve as reducing agents. The fauna indicates a facies shift; the beds pass upward conformably to unfossiliferous strata of the same general description as the bone-bearing beds of the Lower Lufeng Series.

Bien (1941) assigned an Upper Triassic age to the whole of the Lower Lufeng Series where saurian remains are found and called the Shihmen Jura-Cretaceous. Misch correlated the very thick Upper Red Beds of Yunnan, of which the Lufeng beds were considered a part, to the red beds of the neighboring province of Szechuan and suggested that they comprised "much of the Jurassic if they do not even in some parts extend beyond it." Chang (1947) notes that definitive Rhaetic beds have not yet been discovered in Lufeng. Misch categorized the Lufeng sediments as T4, purple marly shale (from a section at Taoyuan, about 8 km. north of Kunming). Since beds of this description are only characteristic of the Upper Lufeng Series, the idealized traverse is less than satisfactory. The more massive Lower Lufeng Series, perhaps equal to T4 (purple sandy shale interbedded with thin bedded sandstone) or T6 (red shale), should have been included with the middle upper Triassic Noric Beds which apparently embrace the Ipinglang Coal Series. Young's taxonomic studies on the saurian elements indicate that the Lower Lufeng Series had to have been deposited not earlier than Noric or post-Noric time.

The stratigraphic column and a map of the Lufeng Basin (figs. 2, 3) showing the leading collecting localities, have been redrawn from Bien (1941). The vertebrate remains have been gleaned from four

	Thickness in Meters	LITHOLOGY	NATURE of CONTACTS	AGE
SHIHMEN SERIES	100±	Capping Escarpment Sandstone	DISCON-FORMITY	POSTLIAS
UPPER LUFENG SERIES	80±	Wine - Red Beds		LIAS
	130±	Variegated Beds		
	70±	Greenish - Yellow Banded Beds		
	5 - 10	Red Sandstone	DISCON-FORMITY	
LUFENG SERIES / LOWER LUFENG SERIES	150±	Dark Red Beds		UPPER TRIAS
	30+	Massive Green Sandstone		
		Dull Purplish Beds		
		Tali		
		Hei Kao Peng		
	550±	Dull Purplish Beds		
		Tachung		
		Dull Purplish Beds		
	5 - 30	Basal Brecia	UNCOMFORMITY	
META-MORPHIC SERIES		Metamorphic Series		PRE-CAMBRIAN

Fig. 2. Stratigraphic section of the Lufeng Series showing the principal collecting localities, Tachung, Hei Koa Peng and Ta Ti. (redrawn and modified from Young, 1951).

rather narrow horizons, Fossiliferous Beds 1–4, ordered stratigraphically from the lowest to the highest levels. The saurian elements are known from the first and second zones traversing the Basin in a north-northwest direction. The third and fourth zones are less extensively developed and are concentrated in the variegated beds of the Upper Series; these have been correlated across to the sediments of the nearby Anning Basin by the common occurrence of *Hybodus*.

STRATIGRAPHIC SECTION OF THE LUFENG BASIN
(Young, 1951)

Top

Upper Lufeng Series

8. Wine Red Beds (30 meters)

Alternating bright wine red clays, shales and sandstones with occasional purplish earthy limestone. Rock salt, brine and gypsum occurs at Yuanyungching, North of Ipinglang.

7. Variegated Beds (120 meters)

Upper two-thirds—Limey beds of purple, mauve, greenish and pink sediments.

Lower one-third—Purplish limey beds with honeycomb weathering.

Lowest—Greenish mottled limey beds with fresh water unioids and ostracods, *Hybodus*, *Lepidotus* and an indeterminate Chelonian.

6. Green-yellow banded beds (70 meters)

    Dark red shales and ripple marked siltstones at the base passing upwards to regular greenish yellow shale bands.

5. Red Sandstone (5–10 meters)

<div align="center">DISCONFORMITY</div>

Lower Lufeng Series

4. Dark Red Beds (150 meters)

    Alternating beds of clays, shale, siltstone and sandstone with two subordinate layers of dull purplish elements. Fossils occur 70M above Bed No. 3.

3. Massive Green Sandstone (20 meters)

    Sediments contain occasional angular fragments of rocks, a breccia at Yaochan. Quartzite and quartz derived from Sinian rocks.

2. Dull Purplish Beds (550 meters)

    Alternating clays, shales, silstones and sandstone. Green sandstone bands occur near the base. Calcareous nodular concretions are common as knobs or tubular masses. The beds are penetrated by calcite
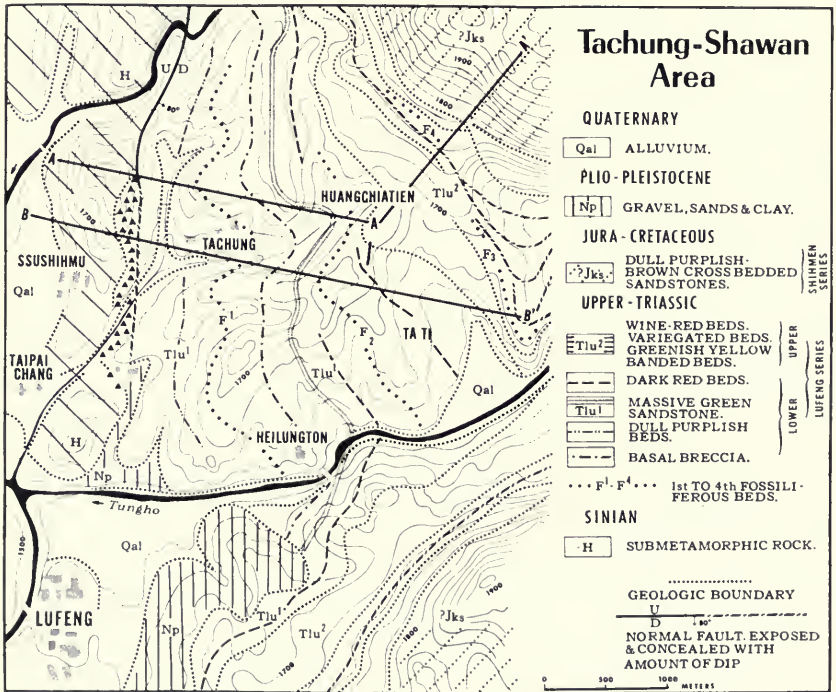

Fig. 3. Map of the Lufeng Basin showing the distribution of the fossiliferous horizons and principle collecting localities (redrawn and slightly modified from Young, 1951).

streaks, veins or mottlings. Fossils occur 300M below Bed 3 and 200M above Bed 1.

1. Breccia (5–20 meters)
    Phyllite derived from the underlying rocks. Yaochan sediments contain a quartzite and quartz brecchia.

PRESERVATION OF BONE

With few exceptions, the bones occur as weathered-out nodular materials invested by a heavy scale of matrix and scattered about on the surface of the ground. The rocks are so heavily indurated with iron compounds that quarrying was difficult and articulated skeletons were obtainable in only a few instances. Some remains are suggestive of coprolitic material.

The field notes did not define the precise area of each collecting site or the relative concentration and association of bone in every case. Many individual fragments bearing the same field number were either referred to several genera, or these contained specimens of the same species but of different ontogenetic development. The proper identification of other disarticulated but otherwise complete bones was difficult because of the unavailability of comparative materials and the morphologic similarity of the known Lufeng prosauropods and carnosaur. For these reasons, a number of specimens could not be treated effectively and were not considered in this paper.

Table 1 lists the fauna recognized by Young and also that newly determined by this study. It will be noted that Oehler's collection sampled most of the previously recognized non-Therapsids (?parasuchian) and yielded many heretofore unrecognized forms. The new finds are principally pseudosuchians and coelurosaurs. Their discovery in effect, fulfills Young's first charge to future collectors (1951, p. 92) that "special attention should be paid to the less known forms such as parasuchians, pseudosuchians, possibly protosuchians. . . ."

TABLE 1.—FAUNAL LIST OF THE NON-THERAPSIDS OF THE
LOWER LUFENG SERIES

YOUNG (1951)	NEW MATERIAL
THECODONTS	
Pseudosuchia	

Platyognathus hsui Young:
    anterior part of the jaw symphysis.
	Platyognathus hsui Young:
	    a nearly complete skeleton.
	    CUP 2083

YOUNG (1951)

NEW MATERIAL

Strigosuchus licinus:
jaw. CUP 2082

Dibothrosuchus elaphros:
a nearly complete skeleton.
CUP 2081

?Pseudosuchian:
a fragment of an ilium and femur.
CUP 2084

Parasuchia

Pachysuchus imperfectus Young:
jaws.

. . . .

Protosuchia

Microchampsa scutata Young:
vertebrae and dorsal armor.

Microchampsa scutata Young:
vertebrae and dorsal armor.
CUP 2085, 2086

SAUROPODS

Coelurosaurs

Lukousaurus yini Young:
anterior half of a skull and jaws;
several limb fragments.

Lukousaurus yini Young:
anterior half of a skull and jaws.
CUP 2092

. . . .

?Coelurosaur:
distal end of a femur and metacarpals. CUP 2089

. . . .

?Coelurosaur:
distal end of a femur. CUP 2091

. . . .

?Coelurosaur:
metatarsals. CUP 2090

Carnosaurs

Sinosaurus triassicus Young:
a nearly complete skeleton.

Sinosaurus triassicus Young:
jaws, teeth and postcranial elements.
CUP 2097

Prosauropods

Lufengosaurus hueni Young:
several nearly complete skeletons.

Lufengosaurus hueni Young:
jaws and postcranial bones.

Lufengosaurus magnus Young:
jaws and postcranial elements.

Lufengosaurus magnus Young:
jaws and postcranial elements.

Yunnanosaurus huangi Young:
several nearly complete skeletons.

Yunnanosaurus huangi Young:
a juvenile skull and postcranial elements.

Yunnanosaurus robustus Young:
a nearly complete skeleton.

Yunnanosaurus robustus Young:
postcranial elements.

Gyposaurus sinensis Young:
many nearly complete skeletons.

Gyposaurus sinensis Young:
skull and jaw fragments and postcranial elements.

ORNITHISCHIA

. . . .

Tatisaurus oehleri:
a left jaw. CUP 2088

SYSTEMATIC CONSIDERATION OF THE
NON-THERAPSID REPTILES OF THE LUFENG FAUNA

Order **Thecodonta**

Suborder **Pseudosuchia**

Family **Ornithosuchidae**

Genus **Dibothrosuchus**, gen. nov.

Diagnosis.—Skull elongate and extensively excavated by a large triangular preorbital fenestra, a round orbit and a long infratemporal vacuity; roofing bones depressed below the superior margin of the orbit. Lower jaw slender, possessing a long narrow lateral fenestra. Teeth laterally compressed, finely denticulated and somewhat recurved.

Neck short, cervical vertebrae not elongate; their centra sharply compressed and keeled, and the anterior zygapophyses very steep. The dorsal vertebrae less sharply compressed backward. Three sacral vertebrae possessing broadly triangular ribs. The presacral series show costal articulations oriented in an upward and backward direction. The first seven caudals are in natural connection with the sacrum and are not especially elongate.

The appendicular skeleton, consisting of the forelimb and several metacarpals, is slender and the bones are thin-walled and hollow.

Dibothrosuchus elaphros, sp. nov.

Holotype.—A partially complete skull and jaws, a series of articulated vertebrae from the cervical, dorsal, sacral and caudal regions of the column, and a fragment of the forelimb and hand. The bones are of a reddish color encrusted with a thick greenish matrix. Catalog no. CUP 2081.

Horizon and locality.—Ta Ti, Dark Red Beds, Lower Lufeng Series.

Diagnosis.—Same as for genus.

DESCRIPTION

Skull (fig. 4,A): The skull is lightly built and broadly fenestrated; the roofing elements are thin and crushed, and the paired bones overlap. The ventral surface bears grooves interpreted as impressions of the nasal tracts and cortical regions of the brain; the

nasal, prefrontal, and frontal bones must be represented in part but sutural contacts are obliterated. The supraorbital contours of the frontals and prefrontals form elevated ridges which pass forward and become confluent with the nasals above the preorbital fenestra. The median suture is slightly depressed and the frontal is plicated by an additional pair of furrows mediad to the supraorbital ridges. The supraorbital eminences project downward to sheath the dorsal orbits externally so that the eye muscles reside in deep pockets bordered internally by the ventrolateral furrows delimiting the brain structures.

Premaxilla (fig. 4,B2): The extreme tip of the snout is lacking and the relationship of the premaxilla to the external nares and maxillary is uncertain. The dentition indicates that the bone is present but probably exclusive of its suture with the nasal. The nasal tracts are seen on the median side by a concavity bounded from below by a palatine fragment; the external nares, then, lay laterally on the snout at the same level as or slightly lower than the antorbital fenestra.

Maxilla (fig. 4,B2): The maxilla projects dorsally about the anterior corner of the triangular preorbital fenestra and terminates posteriorly under the anterior orbit. The bone is gradually replaced by the jugal and its inferior border is downturned.

Jugal (fig. 4,B2): The jugal is a triradiate bone. It replaces the maxilla anteriorly and forms the two ascending bars delimiting the orbit from the antorbital and infraorbital fenestrae. The bone projects posteriorly and somewhat outwardly to bound the infratemporal opening from below and to contact the quadratojugal element. The inferior surface is flat.

Quadrate (fig. 4,B2): The quadrate has been displaced during preservation, and lies horizontally above the surangular-angular complex of the jaw. It is a triangularly concave bone which bears a gently curved, broad articular facet, and a distinct vertical anterior supporting ridge on the lateral side. The inner surface is rugose and probably fragmented.

Pterygoid (fig. 4,B2): An irregularly shaped flat element, perhaps the quadrate process of the pterygoid, lies in front of and touches the quadrate. The straighter anterior part has a finished border and may represent the incipient flange of the lateral process.

Quadratojugal: A problematic quadratojugal fragment lies above the surangular-angular complex of the jaw and contacts the quadrate and pterygoid. Its features are quite indistinct.

The skull is lightly built on the ornithosuchian pattern. The orbital contours are similar to *Ornithosuchus* and *Hesperosuchus agilis*
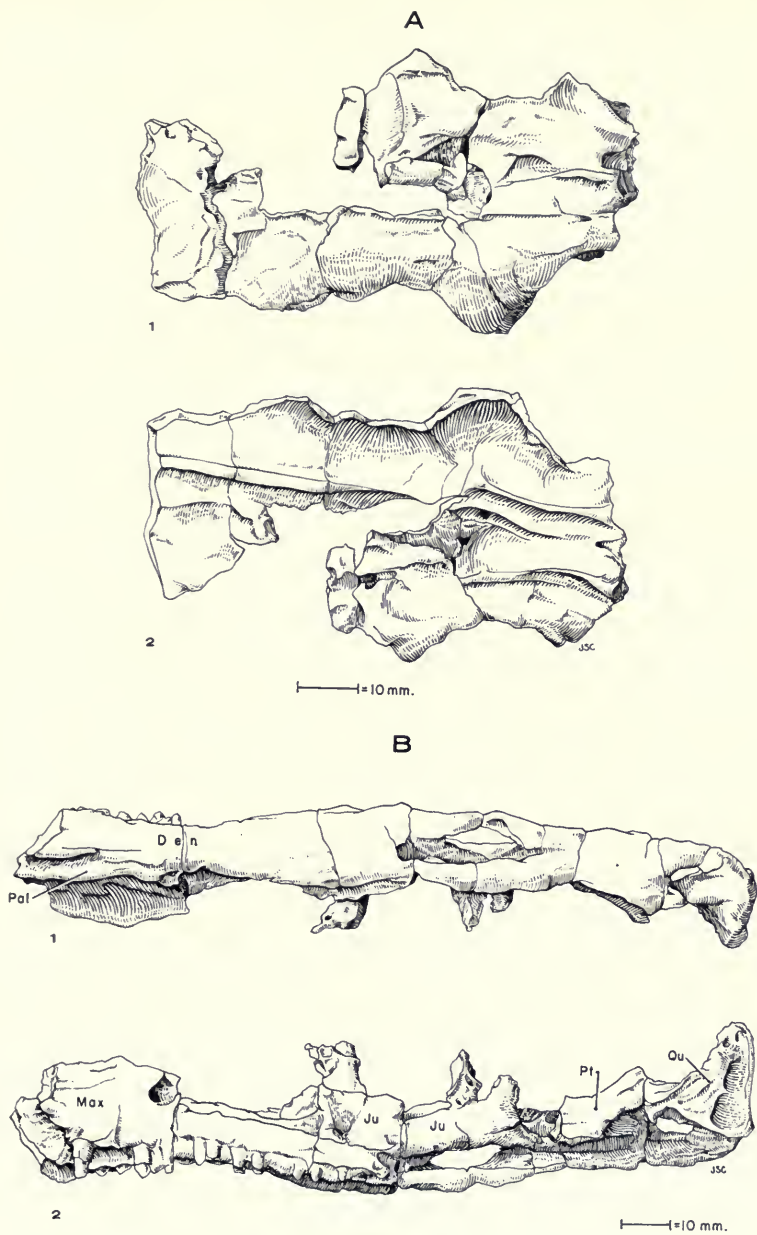
FIG. 4. *Dibothrosuchus elaphros* (gen. et sp. nov.). A, Fragment of the skull roofing bones—dorsal (1) and ventral (2) views. B, Left lower (1) and upper (2) jaws. (CUP 2081).

15

TABLE 2.—MEASUREMENTS OF *DIBOTHROSUCHUS ELAPHROS*
(in mm.)

SKULL

Length of the skull "cap"....................................	83.0
Preserved length along the inferior margin.....................	128.0
Ventral length of the preorbital fenestra.......................	38.5
Maximum breadth (anteroposterior) of the orbit...............	28.5
Ventral length of the infratemporal fenestra...................	23.0
Length of the maxilla.......................................	73.0

JAW	left	right
Preserved length...................................	157.0	101.0
Height: broken anterior end........................	11.2	. . . .
20 mm. back of symphysis..................	10.2	. . . .
anterior margin of the lateral fenestra........	20.0	. . . .
constriction posterior to the fenestra.........	14.3	. . . .
Length of the mandibular fenestra..................	29.0	. . . .
Length of the tooth row...........................	. . . .	34.6

MAXILLARY TEETH	left	right
Fragment of the largest robust tooth...............	5.0	. . . .
basal breadth...................................	5.0	. . . .
length (lacking tip)............................	7.3	. . . .
Basal breadth of the crown at the symphysis.........	. . .	2.5
Length of the crown at the jaw symphysis...........	. . . .	10.0

Right Side	length	breadth
1..	7.8	3.4
2..	7.0	3.1
3..	7.0	3.2
4..	7.0	3.0
5..	6.8	3.0
6 (replacement ?)............................	3.0	. . .
7..	5.2	2.8
8..	2.9	1.9
9..	4.1	2.0
10...	3.6	1.9

MANDIBULAR TEETH	length	breadth
Length of the tooth at the symphysis (lacks the crown)..	7.0	2.3

Colbert (1952) and the ventral skull of the latter features nearly identical endocranial impressions. The position of the external nares high on the skull, either dorsally in *Cerritosaurus binsfeldi* Price (1946) or above the anterior angle of the preorbital fenestra in *Saltoposuchus connectens* and *S. longiceps* Huene (1921), excludes these forms from direct comparison. The preorbital fenestra in *Dibothrosuchus* is neither aetosaurid-like as in *Erpetosuchus granti* Newton (1894), nor crescent-shaped as in *Prestosuchus chiniquensis* Huene (1936, drawing by Price, 1946), nor as tiny as that of *Cerritosaurus.* Broadly oval orbits are known for *Saltoposuchus connectens, Sclero-*

mochlus taylori (Huene, 1914–15) and *Hesperosuchus*, but the supraorbital borders are "wulstig erholt" or padded in the latter two forms, and elevated above the roofing bones in *Ornithosuchus* and *Hesperosuchus*.

The infratemporal region of the skull of *Hesperosuchus* was not preserved, but the associated fenestra lies slightly below and back of the orbit in *Dibothrosuchus*. Conversely, the orbit overlaps the interoanterior angle of the fenestra in *Scleromochlus*, or lies high above the fenestra in *Prestosuchus*, due to the depression of the inferior skull contours.

The quadrate bones of *Hesperosuchus* and of the present form are very similar although the articular surface is broader and the supporting ridge is better developed and more anteriorly located in *Dibothrosuchus*. The skulls of each *in toto* are equal in length to nine to ten dorsal vertebrae.

Maxillary Dentition (fig. 4,B2): The left maxilla holds 12 imperfectly preserved thecodont teeth which become successively smaller posteriorly. The stoutest and largest lies 10.0 mm. in front of the preorbital and is succeeded by a gap accommodating two teeth. A less robust tooth lies below the anterior corner of the preorbital, followed by nine to ten teeth with alveolae for three to four others. The complete maxillary series numbers 16 to 18 teeth; the anteriormost slope backward but the others are erect. The teeth are broad laterally compressed, slightly recurved with sharp and finely denticulated (16/1.0 mm.) posterior edges.

The right maxilla (fig. 5,A) holds well-preserved teeth which are laterally compressed but slightly convex, pointed and equipped with sharp trenchant edges. The crowns of two slender premaxillary teeth are embedded in the matrix of the symphyseal fragment.

The left dentary (fig. 4,B1) holds the roots of 10–11 teeth of uniform size which are weaker than the maxillary series. The fourth root opposing the robust maxillary tooth is also the largest. The complement of the right jaw is masked by the opposed maxillary series.

The development of canine-like teeth in the front of the maxilla is common among Pseudosuchia. The individual teeth compare more favorably with those of the coelurosaur *Halticosaurus orbitoangulatus* Huene (1932) than with the lanceolate type in *Hesperosuchus*, but the overall pattern—a needle-like premaxillary tooth passing to a more robust tooth posteriorly—is hesperosuchid.

TABLE 3.—MEASUREMENTS OF THE CERVICAL VERTEBRAE OF *DIBOTHROSUCHUS ELAPHROS* (in mm.)

Position in Series	Centrum						Neural Arch				
	*V.L.	A.H.	A.B.	M.B.	P.H.	P.B.	Ht.Az+C.	Div.Pz.	L.Pz.	L.Az-Pz.	L.Az.
ISOLATED CENTRA											
1	14.9	13.9	9.1	5.8	11.6	13.9	27.4	8.6	....	....	11.2
2	13.0	14.5	12.5	...	13.5	11.7	27.1	?10.0	9.0	27.4	4.5
ARTICULATED COLUMN											
1	12.0	14.0	12.7	5.3	14.9	12.8	28.0	10.0	7.3	26.7	8.0
2	13.4	15.3	13.0	6.8	14.2	12.3	31.5	9.2	4.5	21.7	6.8
3	?13.5	?14.2	14.7	6.0	...	....	29.6	9.0	4.0	20.0	5.7
4	12.5	?13.0	....	5.9	11.5	11.0	25.0	...	...	....	4.6
TERMINAL CERVICAL											
	13.0	12.5	13.5	5.3	....	....	24.5	...	....	....	...

ANTERIOR CERVICAL RIBS (in mm.)

Ventral length.................... 20.8
Height—tuberculum to the ventral
surface..................... 12.4
Tubercular width.............. 5.8
Tubercular depth.............. 3.2

POSTERIOR CERVICAL RIBS (in mm.)

Head (capitular breadth, tubercular breadth).. 6.2, 5.7
Breadth of the neck............... 6.8
Shaft: breadth at mid-length........... 3.3
    breadth at tip.............. 3.3
Preserved length (1st, 2nd)............ 70.4, 80.0

*V.L.: Ventral length
A.H.: Anterior height
A.B.: Anterior breadth
M.B.: Median breadth
P.H.: Posterior height
P.B.: Posterior breadth

Ht.Az+C.: Height, ant. zygapophysis + centrum
Div.Pz.: Maximum spread of the post. zygapophyses
L.Pz.: Length, post. zygapophyses
L.Az-Pz.: Length, tip ant. zygapophysis to tip post zyga-
    pophysis
L.Az.: Length, ant. zygapophysis

18

VERTEBRAL COLUMN AND RIBS

Cervical Series (Table 3): Seven vertebrae were found with the skull. The anterior two are isolated. A fragmented series of four vertebrae is presumably from the more posterior region of the neck. A single, and the last cervical, articulates with the dorsal column.

Centra (figs. 5,B,C,): The centra are of moderate length, are strongly compressed, ventrally furrowed, and have flat articular surfaces. The anteriormost develop a prominent longitudinal ventral ridge which is less manifest in the last. The vertebrae are separated at the neurocentral suture by relatively wide spaces which indicate a regional specialization and functional involvement with the passage of the spinal nerves to the forelimb.

Parapophyses: The parapophyses lie on the anterior ventrolateral margin of the first centra, but they migrate upward to the neurocentral suture (fourth vertebra present) to form the base of the anterior supporting lamella of the transverse process. The parapophyses undergo a concomitant outward rotation posteriorly and they are triangular in cross section.

Transverse Processes: The transverse processes of the isolated vertebrae are flat and broad structures which project downward over the neurocentral suture and parapophyses. They lie higher upon the neural arch of the second–fourth vertebrae of the articulated series, and are supported by lamellae which converge from the margins of the suture; these are stouter structures and rotate upward and outward posteriorly in the series. The processes lie just back of the parapophyses in the first articulated vertebrae, over the parapophyses in the fourth, and behind in the last cervical.

Zygapophyses: The anterior zygapophyses are high on the isolated centra; they project forward beyond the margin of the centra, but at somewhat a lower angle than those of the articulated column. Concomitant with the rotation and upward migration of the diapophyses posteriorly, they become progressively lower and little more than medial extensions of the dorsal surface of the diapophyses. Their facets are oblique and inwardly directed anteriorly but more outwardly diposed posteriorly.

The posterior zygapophyses are continuous with the diapophyses. In the articulated series, they diverge sharply and extend beyond the limits of the centra at successively lower levels. Since the fourth articulated centrum is also the shortest, the adjustment in zygapophysial height might limit the amplitude of lateral motion of the neck.

Neural Spines: Although these are all broken off at their bases, they are all apparently erect or slightly anteriorly directed. Their cross sections are roughly triangular, sharp in front and broader in back, i.e., about 2.0 mm. and 4.0 mm. respectively.

Ribs: An isolated rib (Table 3; fig. 5,B1) embedded in a rock fragment shows that the anterior ribs are plow-shaped in typical archosaur fashion. The rib has a ventrolateral longitudinal groove formed by an expansive inferior surface.

The more posterior cervical ribs become greatly elongate and slender. A capitular fragment is associated with the second vertebra of the articulated series in hemapophysis fashion. The heads of two nearly complete ribs lie between the second and third and the third and fourth centra and their shafts are fused to the anterior dorsals. During preservation, the column was broken and the posterior cervicals lay at an acute angle to an articulated fragment of the anterior dorsal column. Measurements of the distances between the tuberculum and capitulum (7.0–8.0 mm.) show that these ribs were associated with the second and third articulated cervical centra.

Summary: The cervical column tends to become slightly shorter backwards. The anterior zygapophyses are high and forwardly projecting in front but become shorter and more erect backwards. The parapophyses migrate upward to the neurocentral junction. Anteriorly, the transverse processes are directed downward; posteriorly, these become stouter and rotate upward, outward, and, in the last cervical, somewhat forward. The neural spines are missing but must have been erect or slightly anteriorly directed.

Dorsal Series (Table 4; figs. 5,D,E): The dorsal columb is near ly completely represented by eleven vertebrae in two articulated series, each of which contains fragments of a single centrum. Since these fragments do not fit together, it is likely that there was a single intervening dorsal to bring the number in the column to fourteen. The reconstructed series may be divided into two segments such that in one, the first nine dorsals, the parapophyses and diapophyses are separate. Costal union probably occurred in the tenth vertebra since the processes are co-joined from the twelfth to the fourteenth.

Centra: The centra are weakly constricted and are distinguished from the cervical series by their smooth, round, unfurrowed surfaces.

While the costal articulations are poorly preserved on the left side and are masked by the associated cervical ribs on the right, it is certain that the migration of the parapophyses from the centra to the neural arch was completed in the last cervical vertebra.
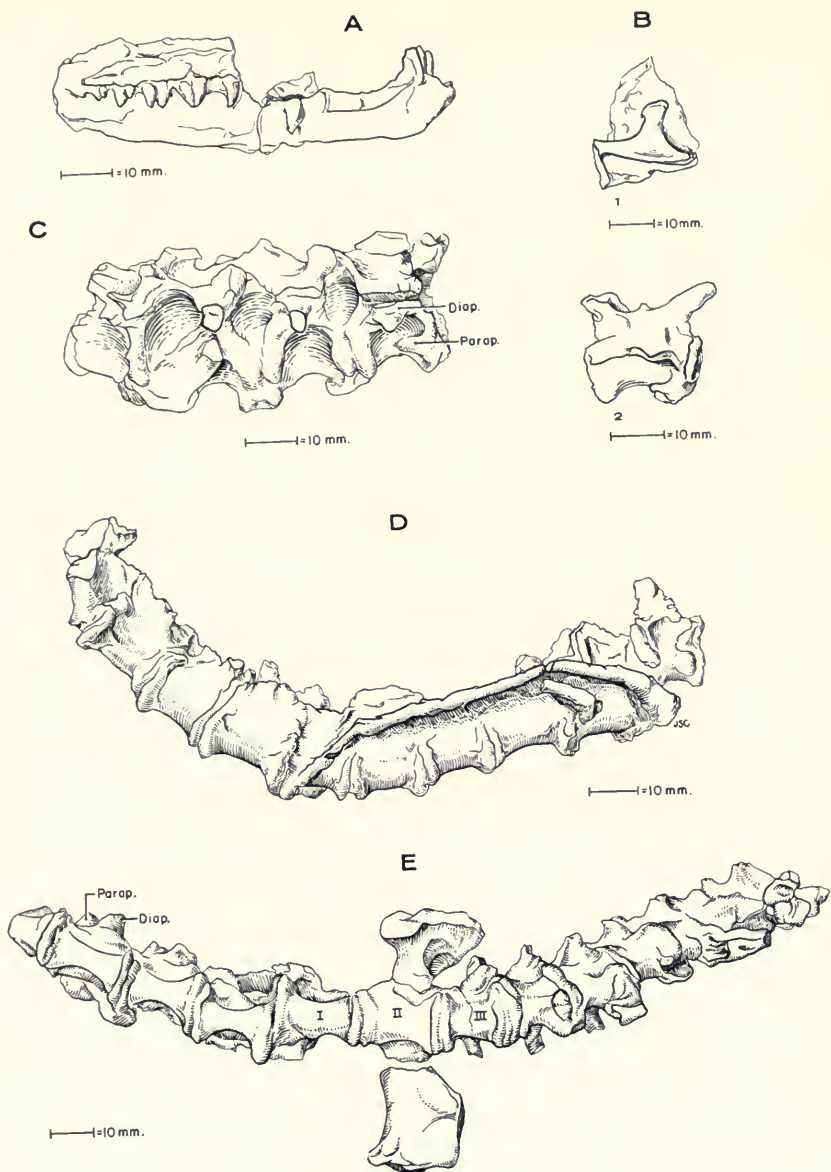
FIG. 5. *Dibothrosuchus elaphros* (gen. et sp. nov.). A, maxilla and dentary fragment. B, cervical rib (1) and vertebra (2). C, A series of four posterior cervical vertebrae viewed from the right side. D, A fragment of the dorsal vertebral column viewed from the right side including the last cervical vertebra and two cervical ribs. E, An articulated series of posterior presacral, sacral, and anterior caudal vertebrae viewed obliquely from below. The sacral ribs and hemapophyses are shown. (CUP 2081).

21

TABLE 4.—MEASUREMENTS OF THE DORSAL SERIES OF *DIBOTHROSUCHUS ELAPHROS* (in mm.)

Position in Series	CENTRUM						NEURAL ARCH				
	*V.L.	A.H.	A.B.	M.B.	P.H.	P.B.	Ba.B. Tr.P.	Lat.Ext. Tr.P.	B.Ns.	Ht. C+Az.	L. Pap-Diap.
1	...	...	...	6.0	...	...	7.2	...	?8.1	...	?19.0
2	14.9	13.1	11.9	5.6	...	...	...	...	?9.1	24.2	?20.0
3	14.5	13.4	11.6	6.4	...	...	8.4	...	...	24.2	?19.0
4	14.0	14.7	10.8	6.4	...	...	8.3	11.2	11.9	23.3	21.4
5	14.7	12.8	11.3	6.5	...	...	?8.6	?7.7	11.4	22.0	21.2
6	16.4	12.5	...	6.3	...	...	...	...	11.9	...	...
7	15.2	12.0	12.3	6.1	...	...	6.9	8.2	...	22.6	23.6
8	15.9	12.1	12.4	7.6	...	...	6.6	8.0	...	22.5	...
9	...	12.1	...	7.5	...	...	6.2	5.9	...	?21.0	...
10	...	...	...	7.3	...	...	...	...	...	...	...
11	...	...	...	7.2	...	...	...	...	...	...	...
12	15.8	12.3	12.9	7.6	...	...	8.2	11.8	...	23.3	23.2
13	15.2	12.6	11.1	7.4	...	...	8.0	...	12.9	25.6	23.3
14	15.4	13.4	13.4	7.9	...	...	8.8	...	...	24.4	21.2

*V.L.: Ventral length
A.H.: Anterior height
A.B.: Anterior breadth
M.B.: Median breadth
P.H.: Posterior height
P.B.: Posterior breadth

Ba.B.Tr.P.: Basal breadth, transverse process
Lat.Ext.Tr.P.: Lateral extension, transverse process
B.Ns.: Breadth of the neural spine
Ht.C+Az.: Height, centrum + ant. zygapophysis
L.Pap-Diap.: Length, parapophysis—diapophysis

With the exception of the last or fourteenth dorsal, the costal articulations and the posterior zygapophyses of each vertebra are connected by a bony lamella directed upward and backward. The lamella of the fourteenth is relatively parallel to the long axis of the column. The relation of the parapophyses to the anterior zyga-pophyses is somewhat variable throughout.

Parapophyses: The bony lamella essentially passes through the midplane of the parapophysis. The processes are rounded (4.0 mm. in diameter) with concave facets for the capitula of the ribs and they extend outward some 8.0 mm. In the first six dorsals, the para-pophyses lie just back of the anterior margin of the centra and under the posterior half of the anterior zygapophyses. In the seventh and eighth they migrate slightly backward. In the ninth dorsal it lies under the zygapophysis.

The costal articulations fuse rather abruptly at the level of the tenth or eleventh vertebra; the distance between the parapophyses and diapophyses does not appear to decrease gradually in the latter part of the column, i.e., 1–9 (?10).

Transverse Processes: The lateral projection and basal breadth of the processes are progressively reduced from the first–ninth verte-brae. They are supported by two rather vertical lamellae on the second dorsal. The processes are flattened above from the twelfth–fourteenth dorsal.

Zygapophyses: In the first six dorsals, the anterior zygapophyses are low as in the posterior cervicals, but become progressively higher from the seventh–thirteenth. Early, their facets are oblique, but they rotate outwardly in the last half of the series. The posterior zygapophyses are longer than the anterior processes and project be-yond the end of the centra. The articulation between the thirteenth and fourteenth dorsals is nearly horizontal. Such an arrangement would tend to reduce the vertical motion of the posterior presacrals.

Neural Spines: The neural spines are relatively long, low and broad. They project forward only slightly, but are more generally erect from the eleventh–fourteenth dorsal. Only a few are com-pletely preserved.

Ribs: Several proximal fragments of broad flat ribs were fused during preservation to the neural spines of the thirteenth and four-teenth dorsal vertebrae.

Summary: There is a general tendency for the vertebrae to in-crease in length throughout the dorsal column although the sixth

dorsal is the longest.   The costal articulations become fused toward
the sacrum and the zygapophysial articulations become more hori-
zontal to restrict the vertical motion of the spine.   Several broad rib
fragments are associated with the last two presacral vertebrae, but
it is questionable whether these can be considered to belong to this
specimen.

Sacral Series (Table 5; fig. 5,E): The sacrum is composed of
three vertebrae with broadly rounded ventral surfaces.   The first
two are articulated but the third has been transversely broken at its
mid-length.   The total length of the articulated sacrum is 56.3 mm.
(1st, 18 mm.; 2nd, 14.5 mm.; 3rd, 13.8 mm.) along their ventral
lengths.   The successive vertebrae decrease in length; the neural
complex of the second and third are fused.   The first and third centra
are more strongly compressed than the second which is compara-
tively massive.

None of the neural spines has been preserved save that of the
first which is supported by high lamellae most probably continuous
with the posterior zygapophyses.

The anterior zygapophyses lies at the level of the sacral ribs on
the first vertebra but are raised high above the neurocentral suture
in the second and third.   The zygapophyses of the first vertebra ap-
pear to be partially fused to the posterior zygapophyses of the last
presacral.   The neural articulations of the second and third sacrals
also seem to be fused.

The posterior zygapophyses of the first and second sacrals are
elevated high above the neurocentral junction and are continuous
with the lamellae supporting the neural spines.   They originate at
the posterior border of the sacral ribs.

Ribs (fig. 5,E): The first sacral lacks ribs.   These, however, are
represented by a scar at the anterior margin of the neurocentral
suture (height, 11.3 mm.; breadth, 8.0 mm.).

The second left sacral rib lies on the posterior half of the vertebra.
It is dorsoventrally flat and irregularly triangular.   The anterior
border extends outward and slightly backward for half its length,
and turns forward distally; the posterior border is straight and pro-
longed backward.   The facet receiving the ilium is expansive and
lies at the anterior corner.   Distally, the rib becomes rather flat but
the facet receiving the ilium of the pelvis is expansive at the anterior-
most corner.

The third sacral bears a fragmented narrow transverse process
opposing the posterior border of the second rib.

TABLE 5.—MEASUREMENTS OF THE SACRAL SERIES OF
DIBOTHROSUCHUS ELAPHROS (in mm.)

VERTEBRA

Vertebral No.	*V.L.	A.H.	A.B.	M.B.	Ht. Az.+C.	Ht. Ns.+C.
I	18.0	14.9	13.0	8.3	22.0	28.6
II	14.5	11.0	13.1	13.5	?21.0	....
III	13.8	13.0	13.6	10.0	?19.0	....

RIB

	L.AB.	L.PB.	D.B.	Pr.B.	D.F.	B.F.
I	14.2	19.0	21.7	13.3	10.0	12.3
II	....	....	....	....	....	....
III	....	....	....	....	....	....

SINGLE RIB

	20.5	....	?20.8	?13.3	12.1	13.8

*V.L.· Ventral length
A.H.: Anterior height
A.B.: Anterior breadth
M.B.: Median breadth
Ht. Az.+C. Height, ant. zygapophysis + centrum
Ht. Ns.+C.: Height, neural spine + centrum

L.AB. Length, ant. border
L.PB.: Length, post. border
D.B.: Dorsal breadth
Pr.B.. Proximal breadth
D.F. Dorsal facet
B.F.: Breadth of facet

A fragment of a triangular rib similar to that of the second sacral is associated with these remains. Its articular facet for the ilium is considerably larger.

Caudal Series (Table 6; fig. 5,E): The postsacral vertebrae are only partially represented. The first six caudals form an articulated series with the sacrals. The more distal vertebrae occur as multiple fragments.

Centra: The first six caudals are quite uniform. The centra are squarely constructed and compressed with broadly rounded and furrowed ventral surfaces; haemapophyses are associated with each. The smaller distal centra are similar in form and presumably amphycoelous. Except for one very distal element, the articulated fragments are transversely broken at the mid-part of the terminal centra.

Neural Spines: The neural spines, while incompletely preserved are clearly directed anteriorly.

Transverse Processes: The processes lie at the center of the vertebrae and project somewhat outward and downward, on the first caudal. They gradually rotate upward and backward in the second–fifth to juxtapose the posterior zygapophyses. A lamella, similar to that noted for the dorsal series, unites the bases of the transverse processes and the posterior zygapophyses in the fourth–sixth caudals

and, in the last, the diapophysis lies under the zygapophysis. The terminal vertebrae lack diapophyses entirely.

Zygapophyses: The anterior zygapophyses become progressively lower and more oblique posteriorly, but project at a low angle beyond the margin of the preceding centrum. From the fourth vertebra posteriorly, the anterior zygapophyses form a costal-neural "articular clump" with the posterior zygapophyses and transverse process of each antecedent vertebra. The posterior zygapophyses are short and widely divergent.

TABLE 6.—MEASUREMENTS OF THE CAUDAL SERIES OF
DIBOTHROSUCHUS ELAPHROS (in mm.)

Position in Series	*V.L.	A.H.	A.B.	M.B.	L. Az-Pz	L.AC.	L.Hem.
			ANTERIOR CAUDAL SERIES				
1	13.3	....	14.6	8.7	18.5	12.7	....
2	12.5	....	11.6	8.0	17.8	12.5	....
3	10.0	....	10.6	7.3	17.2	11.3	....
4	10.0	....	10.9	7.0	17.0	10.2	?18.0
5	12.0	....	9.7	7.4	17.0	9.6	?21.4
6	12.5	....	9.0	...	18.0	8.7	....
			POSTERIOR CAUDAL FRAGMENTS				
1	11.0	10.2	8.4	5.5	15.3	8.0	....
2	12.3	9.1	8.1	6.2	13.0	7.3	....
3	10.0	12.6	9.0	6.9	17.7	?8.2	....
4	10.6	....	....	5.5	17.7	7.4	....
5	10.5	....	8.2	...	16.6	...	....
			POSTERIOR CAUDAL FRAGMENTS				
1	?9.0	7.2	6.0	7.5	13.5	....	....
2	10.0	7.5	6.0	7.7	15.0	....	....
3	10.0	7.5	5.7	3.7	?12.0	....	....

*V.L.: Ventral length   L.Az-Pz.: Length, tip ant. zygapophysis-tip post. zy-
A.H.: Anterior height   gapophysis
A.B.: Anterior breadth   L.AC.: Length, articular 'clump'
M.B.: Median breadth   L.Haem.: Length, hemapophysis

Hemapophyses: Chevron bones are associated with all but the terminal centra; the rami are delicate and fuse distally. These are best preserved between the fourth and fifth, and fifth and sixth vertebrae.

The anterior cervical column of *Dibothrosuchus* is best compared to those of *Hesperosuchus* and *Parringtonia gracilis* Huene (1939a), although these vary somewhat proportionately, and their centra are more compressed and narrowly rounded below. The anterior pre-

sacrals of *Parringtonia* (Huene, 1939a, fig. 5) compare well to the seventh–eighth dorsals of the present form where the neural arch bears costal articulations connected by a common ascending lamella, and erect anterior zygapophyses. The anterior projection of the zygapophysial articulations of the imperfectly preserved dorsal column in *Hesperosuchus* is of the dibothrosuchid-type; the parapophyses and diapophyses are similarly arranged in *Stagonosuchus nyassicus* Huene (1939b) but lack the common lamella. The rather horizontal orientation and length of the posterior zygapophyses of the posterior presacrals is similar to *Parringtonia* and *Hesperosuchus*, but the poorly preserved neural spines lack terminal expansions for the articulation of the dorsal armor in the former (Huene, 1939b, figs. 8, 10) and in *Stagonosuchus* (Ibid, fig. 11). The presacral column cannot be compared further to other ornithosuchia such as *Erpetosuchus* (which has weak costal articulations) which differ markedly also in their skull patterns.

The sacral and caudal vertebrae are flatter and more broadly constructed than those of *Hesperosuchus*, and the latter do not bear ventral longitudinal ridges evidenced in *Parringtonia*.

TABLE 7.—MEASUREMENTS OF THE GIRDLE AND FORELIMBS OF
DIBOTHROSUCHUS ELAPHROS (in mm.)

CORACOID	left	right
Length of:		
base of glenoid fossa to posterior crest....................	29.6	....
dorsal crest..	24.6	....
articular facet for scapula...............................	14.0	....
Breadth of articular facet for scapula.......................	9.0	....
Length of free finished border of coracoid-dorsal.............	10.6	....
Breadth of glenoid region.................................	11.0	....
Depth of glenoid region...................................	9.6	....

HUMERUS		
Length of head to posterior tuberosity (maximum)...........	26.4	25.0
Dorsoventral breadth at crest.............................	11.7	10.2
Breadth (anteroposterior) above crest......................	16.3	15.0
Breadth, neck just above condyles (lateromedial)............	12.0	....
Thickness, neck just above condyles (anteroposterior)........	8.2	....
Breadth of condyles (maximum lateromedial)................	18.3	....
Thickness, lateral condyle.................................	7.6	....
Thickness, medial condyle.................................	7.2	....
Length, intermediate protuberance.........................	11.5	11.0
Length of humerus (allowing 6 mm. for sectioned ends):		
proximal element......................................	48.3	40.0
distal element...	58.0	....
Estimated total length....................................	116.3	....

A

1   2   3

⊢———⊣=10 mm.

B

5   ⊢———⊣=10 mm.

1   2   3   4

10   ⊢———⊣=10mm.

6   7   8   9

28
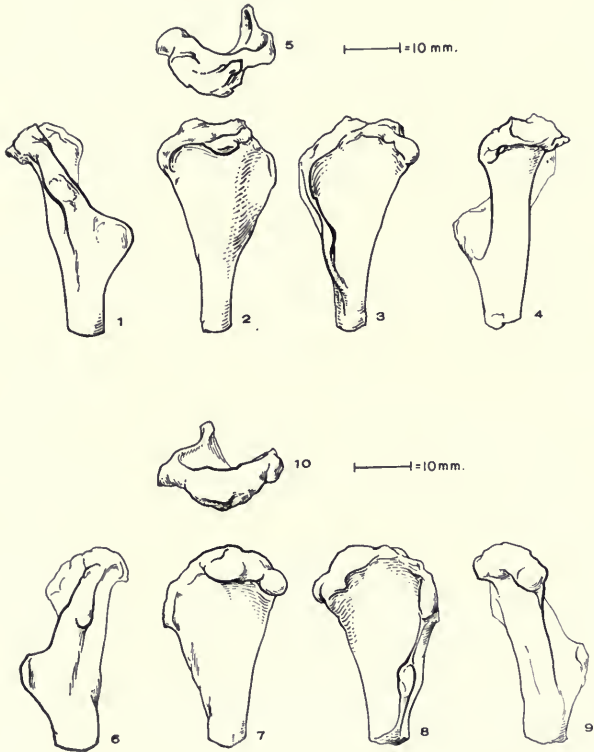
PECTORAL GIRDLE

(Table 7, Fig. 6,A)

The pectoral girdle is known by a left proximal fragment of the coracoid. The bone must have been loosely connected to the scapula since the superior border is finished except for a roughly triangular area in back of the glenoid region, and it rotates inward posteriad (effect of pressure?). The posterior surface is roughened to indicate a cartilaginous cap. The ventral border is finished. The lateral surface is concave and bears an extensive fossa for the *M. supracoracoideus*.

The glenoid fossa formed by the scapula and coracoid is flared laterally and bears a lateral tubercle which probably represents an incipient acromion for the triceps muscle. The glenoid is set off below by a sharp notch and a marked fossa; the bone is narrow and may have been distally elongate.

The inner surface is concave and perforated by a foramen (supracoracoid) which enters at a superior post-glenoid depression and emerges at the level of the acromion in the forward wall of the supra-scapular fossa.

APPENDICULAR SKELETON

(Table 7)

Fragments of the forelimb were segregated from a number of indeterminate limb bones associated with the skull and vertebrae on the basis of their common histologic structure and hesperosuchid-like configuration.

Humerus (fig. 6,B): The humerus is long, slender and proximally expansive; the shaft is bent medially. The head is rounded and positioned at the anterior inferior angle. A large, rather flat, semilunar internal tuberculum lies just posteriad to the head and projects over the crest to the dorsal side. More posteriorly and at approximately right angles, the dorsal crest emanates from the ventromediad wall as a strong ridge and passes distally to the neck of the bone. The ridge is acute above the apex which is swollen and roughened for muscle attachment.

Fig. 6. *Dibothrosuchus elaphros* (gen. et sp. nov.). A, Coracoid, viewed from the medial (1), glenoid (2), and lateral (3) surfaces. B, Humerus, left (1–5) and right (6–10) proximal fragments viewed from the medial (1, 6), dorsal (2, 7), ventral (3, 8), and articular (5 ,10) surfaces. (CUP 2081)

The proximal end of the humerus is dorsoventrally convexoconcave and the deltopectoral crest is set off from the dorsal surface by a narrow sulcus.   The ventral surface becomes flatter distally.

The distal segment of the left humerus (fig. 7,A) curves laterad to give the bone an overall sigmoid configuration.   The condyles are subequal in size; the anterior, or radial, is the longer, rather triangular in cross section, and its articular surface is delimited from above by a Y-system of ridges.   The posterior ulnar condyle is broad and its articular surface is ventrally diposed.   A transverse ridge connects the condyles on the dorsal surface of the bone.   The trochlea is marked by a shallow intermediate depression.

Ulna (fig. 7,B): The ulna is known from a dorsoventrally compressed, moderately expansive proximal fragment which evidences a prominent olecranon process; the medial surface is irregular and asymmetrical.

The surface articulating with the humerus is divided by a moderately elevated ridge occupying the trochlea and is plateaued.   The depression receiving the lateral condyle is the broader and deeper of the two but the arrangement would probably not restrict the rotation of the forearm to any great degree since the elements were undoubtably capped by cartilage.

Radius (fig. 7,B): Only the head of the radius is represented. It is broad and shows a semilunar depression for the articulation with the humerus.   Its shaft is slender and dorsoventrally flattened.

The girdle of the present form is distinguished from other ornithosuchians in that (1) the coracoid and scapula were apparently loosely associated, (2) the glenoid is strongly rotated outward and (3) the subglenoid fossa is acute rather than broad.   The glenoid fossa here has a more open face, but lacks both development in breadth and an accessory lateral process (?acromion) for the triceps muscle.

The pseudosuchian humerus is generally characterized by broadly expansive ends (*Stagonosuchus* and *Erpetosuchus*), but the slenderness of the shaft, position and development of the deltopectoral crest, and condylar inequality in the present form is closest to *Hesperosuchus*.   The coelurosaur *Halticosaurus longotarsus* Huene (1921, pl. IV, fig. 7) also shows rather similar condylar proportions.

The proximal part of the ulna is constructed like that of *Hesperosuchus,* and the olecranon and dorsal oval depression are equally well developed.   The sigmoid notch is, however, less strongly platformed and the humerus-ulnar articulation is simpler in *Hesperosuchus.*   The

peculiar nature of the joint would facilitate a fast running habit, allowing for a strong fore-aft motion with perhaps little rotation of the elements. The animal was probably quadrupedal since the humerus is elongate, and Romer (1956, p. 373) notes that the olecranon (origin of the triceps muscle), little developed in dinosaurs, appears in secondarily quadrupedal forms; its presence is presumably associated with a secondary return to a more flexed position of the forearm.

The osteology of the skull and appendicular skeleton indicates a hesperosuchid-like animal, but the form is slightly larger. The differences in the jaw, skull and vertebral column are conspicuous (the latter approaching *Parringtonia* most closely). The limb structure is perhaps more highly specialized for a cursorial way of life.

<div align="center">

Order **Thecodonta**

Suborder **Pseudosuchia**

Family **Ornithosuchidae**

Genus **Strigosuchus**, gen. nov.

</div>

Diagnosis.—Jaw slender; lower margin straight but sharply upturned at the symphysis. A flat splenial element sheaths the inner wall. The jaw bears only one preserved tooth.

<div align="center">

Strigosuchus licinus, sp. nov.

</div>

Holotype.—A fragment of a left mandible, slender and upturned at the symphysis. Catalog number CUP 2082.

Horizon and locality.—Ta Ti, from the Dark Red Beds of the Lower Lufeng Series.

Diagnosis.—Same as for genus.

<div align="center">

DESCRIPTION

</div>

Jaw (Table 8; fig. 7,C): The mandible is slender and upturned at the snout. Its outer wall is convex although flattened anteriorly; the inner or medial wall is flat in front becoming more concave posteriorly below the alveolar border. The preservation of the material was accompanied by distortion and checkering of the bone, but the sutures are clearly marked. The outer wall of the dentary has been broken away to expose the internal architecture of the jaw, and the articular bones are incomplete.
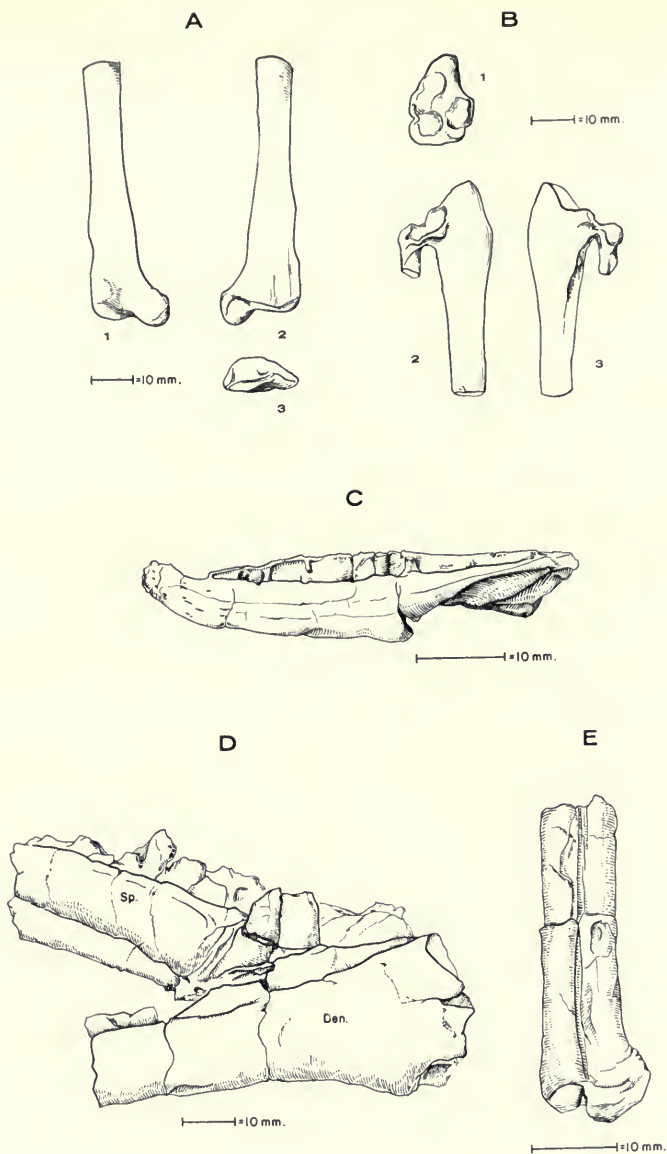
Fig. 7. *Dibothrosuchus elaphros* (gen. et sp. nov.). A, Left humerus, distal fragment viewed from the ventral (1), lateral (2), and articular (3) sides. B, Ulna and radius, proximal fragments in articular (1), medial (2), and lateral (3) aspect (CUP 2081).

Strigosuchus licinus (gen .et sp. nov.). C, Jaw in lateral view. (CUP 2082).

Sinosaurus triassicus Young. D, Jaw fragment posterior to the symphysis. (CUP 2097).

Coelurosaur (CUP 2090). E, Fused metatarsals in dorsal view.

32

TABLE 8.—MEASUREMENTS OF THE JAW OF
STRIGOSUCHUS LICINUS

	mm.
Superior border from broken tip to end of fragment, i.e., lateral fenestration...	49.6
Inferior border from broken tip to posterior fracture of angular....	47.2
Anterior height of jaw at broken tip...........................	7.0
Height of dentary just posterior to preserved tooth............	8.3
Height of jaw at posterior fracture...........................	12.0
Basal length of tooth root....................................	2.7
Height of preserved portion of tooth minus crown.............	2.7
Anteroposterior length of second preserved alveolus...........	2.5

The jaw appeared upon initial examination identical to *Chasmato-saurus yuani* Young (1936). Closer inspection revealed that the surface of the posterior outer fracture was in part finished—evidence that, unlike proterosuchians, the jaw was fenestrated. The mandibles of *Hesperosuchus* and *Dibothrosuchus* are similarly formed, and the symphysis in each bears the greatest concentration of foramina. Further comparison is rather limited for reasons given below.

In the present specimen, a flat spenial bone covers the inner surface of the jaw at the symphysis and contacts the dentary along the inferior margin of the ramus. The posterior portion has been displaced upward and outward by compression during preservation; it encroaches upon the dentigerous border to effect the postmortem loss of the teeth. Forward of the jaw articulation, the splenial wraps about the angular bone.

The meckelian groove passing forward on the inside of the jaw from an oblique nubbin (7.0 mm. long) of the angular bone is limited by a long dorsal prearticular element which pinches out anteriad and disappears below the symphyseal portion of the splenial.

The damage to the dentigerous border incurred by the displacement of the splenial does not allow us a precise knowledge of the dental complement. It is, however, likely that the jaw held 14 to 15 teeth. The single root of a large compressed, somewhat recurved tooth which is most chasmatosaurid-like, lies toward the end of the tooth row and its anteroposterior breadth is equal to the length of the first and second alveolae at the symphysis. Only the first four alveolae are sufficiently well-preserved to indicate the size of the teeth, but it is not known whether these were enlarged like those of *Ornithosuchus* and *Pedeticosaurus leviseuri* van Hoepen (1915; Haughton, 1924). The teeth of *Hesperosuchus* are contrastingly lanceolate, and the jaw is three times as large as that of *Strigosuchus*.

Irrespective of the general chasmatosaurid configuration of the jaw and teeth, the presence of a lateral mandibular fenestra indicates that the present form should be referred to the ornithosuchian pseudosuchians. The specimen is regarded as a new form for which the name *Strigosuchus licinus* (*gen. et sp. nov.*) is proposed.

Order **Thecodonta**

Suborder **Pseudosuchia**

Family **Platyognathidae** (fam. nov.)

Platyognathus hsui Young (1944)

Platyognathus hsui was named by Young (1944) from a jaw fragment, and was assigned to the pseudosuchia. Since then, its ultimate position in the scheme of classification has been speculative at best in view of its fragmentary nature. Young failed to relate it with the well-known primitive South African forms, and stated that it might represent an entirely new family. Huene (private communication; Young, 1951) suggested *Platyognathus* as a forerunner of the Ornithischia since, following the contours of the jaw, the snout was interpreted to be expansive. Romer, earlier (1955), concurred with Young's tentative assignment, but later (1956) referred it to the Notochampsidae (Protosuchidae). Pivateau (1956) suggested a relationship to the pseudosuchian Stagonolepidae.

The type specimen, No. V71, Cenozoic Research Laboratory, National Geologic Survey of China, consisted of the anterior part of a pair of jaws bearing alveolae for 11 and 12 teeth in the left and right sides respectively. The preserved dentition was restricted to a single damaged canine-like tooth on the right side.

Additional Material.—The newly available material includes a partially complete jaw and skull, and armored postcranial elements. All but the sacrum of the vertebral column is represented in part, and the pectoral girdle is complete on both sides. The appendicular skeleton is not represented. Catalog No. CUP 2083.

Horizon and Locality.—Ta Ti, Dark Red Beds, Lower Lufeng Series.

Diagnosis.—Skull V-shaped, low, flat and terminally expansive at the snout; external nares unpaired; symphyseal teeth anteriorly directed, polygonal in cross section. Lumbar and caudal regions of the body completely invested in armor; vertebrae procoelous.

DESCRIPTION

Skull (Table 9; figs. 8,A1–3,D): The skull is complete from the snout to the antorbital fenestra. The dentition is completely represented. Skull low, broad and triangular; snout short, obtuse and laterally expansive; external nares terminal and confluent. The bone is extensively pitted with canals for vascular and nervous elements.

Premaxilla: The premaxilla is expansive and forms the entire lateral wall of the snout and the ventral border of the external nares. The superior margin projects posteriorly about 1.0 cm. between the nasal bones and the anterior portion of the maxilla. There is no evidence of an internasal septum and the nares appear to be confluent; had the septum been cartilaginous, however, it would not have been preserved.

The bone bears four teeth; the first two are anteriorly directed, polygonal, in cross section and subequal in size, the second is the smallest. The third and fourth teeth are recurved. The suture with the maxilla is edentulous where the bone may either have been broken, or was in fact emarginated.

Nasals: The nasal bones are broad and flat, forming the dorsal roof of the skull and external nares. Their median suture is slightly depressed. The bones terminate abruptly at the snout, and it is probable that they projected a short way anteriad. The bones bear many fracture lines due to compression.

Maxillary: While the preservation is generally good, it is difficult to distinguish cracks from sutures. The outer wall is convex, bounded anteriorly and/or dorsally by the posterior tip of the premaxilla and by the nasals. The contact with the premaxilla involves the edentulous region which accommodates a canine-like tooth of the mandible; the skull is constricted at this level. The bone extends about the rounded anterior angle of the antorbital fenestra. Seventeen to 18 finely denticulated (9–10/1.0 mm.) and recurved teeth, the anterior seven of which are largest, lies on this bone.

The bone reveals little about the conformation of the orbit. The remnant of the antorbital fenestra lies relatively high on the skull oriented more or less dorsally due to the convexity of the bone, and it is probable that the orbits were similarly placed. The inferior border of the maxilla is flared medially to form the lateral walls of the choanae. The internal and external borders of the tooth row are equal in height.
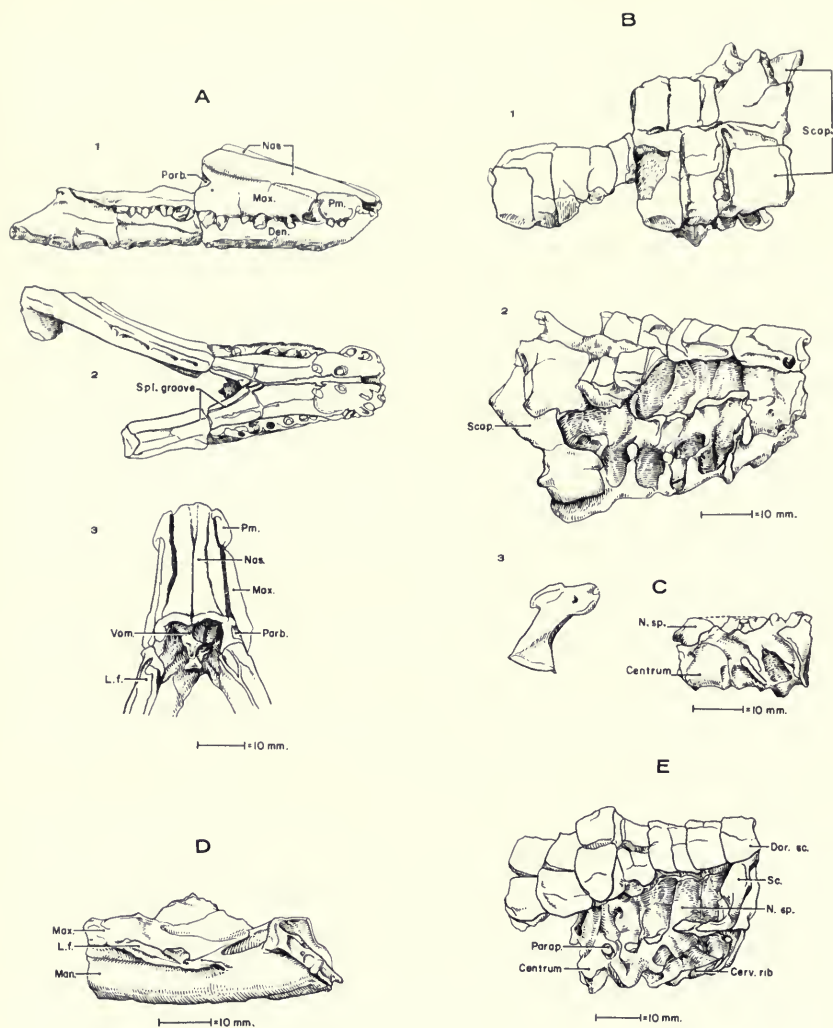
FIG. 8. *Platyognathus hsui* Young. A, Skull and jaws from the right side(1), ventral (2), and dorsal (3) surfaces; (CUP 2083). B, Articulated posterior cervical vertebrae and scutes viewed from the dorsal surface (1), right lateral side showing the scapula (2), and coracoid (3) drawn from the unillustrated ventral surface (CUP 2083). C, Anterior caudal vertebrae viewed from the left side (CUP 2083). D, Jaw fragment showing the inner surface of the orbital region (CUP 2104). E, Posterior cervical vertebrae and scute complex viewed from the right side (CUP 2105).

36

The suborbital region is shown in a maxillary fragment of another specimen of comparable size (CUP 2104); the wall was depressed below the orbit where the bone is particularly thin and not very likely to have been preserved intact. The disposition of the bone might indicate a more forwardly oriented orbit, but it is impossible to say if it was directed more outward or more upward as in the case of later crocodilians. Internally, a deep fossa which may have held a lacrymal gland is formed by an upward extension of the palate. This feature indicates that the antorbital and orbital openings were closely juxtaposed.

Jugal: The jugal replaces the maxilla at the end of the tooth row, and it is probable that it limits the orbit from below.

Palatal Complex (figs. 8,A3,D): The palate is poorly preserved and largely obscured by the long symphysis. The bones have been exposed in cross section at the level of the antorbital fenestra where the skull and jaws have been transversely fractured.

Vomers: The vomers are median-paired, delicate bones (height, 5–6 mm.; thickness, 1–1.5 mm.) which lie just forward of the end of the symphysis and pass upward to divide the choanae. Above, the structure flares to form the palate proper (breadth, 14–15 mm.).

Palate: The palate extends posteriorly and contacts the inner wall of the maxilla. If the terminal epipyterygoid element is included, it is as long as the tooth row; the posterior 14 mm. are free and project downward across the tooth row. As noted above, the palate forms a deep fossa (length, 13.8 mm.; depth, 3.7 mm.) below the orbit (fig. 8,D). The mid-line structures are broken away behin the antorbital fenestra and it is impossible to say whether there was any pterygoid participation. Nevertheless, the development of the vomer has effected at least the rudiments of a secondary palate which can best be described as mesosuchian.

Ectopterygoid: This is a small, narrow element best preserved on the right side. The medial surface is entire and finished, indicating that the associated pterygoid vacuities may have been large.

The snouts of Pseudosuchia are, as a rule, tapered and acute, and bear expanded premaxillae. The primitive crocodilian *Protosuchus* shows comparable expansions and a slight emargination of the suture with the maxilla marking an edentulous or diastemic area. All protosuchians, however—with the exception of *Pedeticosaurus* which has been interpreted as a highly specialized pseudosuchian—lack antorbital fenestrae and the external nares open dorsally. The common suture of the nasal bones, nevertheless, is depressed.

TABLE 9.—MEASUREMENTS OF THE SKULL AND JAWS OF
PLATYOGNATHUS HSUI (in mm.)

		left	right
SKULL			
Length: from the external nares to the antorbital opening		. . . .	35.7
dorsal margin of the premaxilla		21.0	20.0
ventral margin of the maxilla		45.0	50.0
Breadth: at the snout	15.0		
of the external nares	7.0		
premaxilla (maximum)	18.0		
of the nasal bones: anterior, posterior	8.0, 14.0		
of the premaxilla-maxillary junction	16.0		
Height of the maxilla at the antorbital fenestra		12.4	12.2
JAW			
Length of the symphysis	30.5		
Breadth: of the symphysis (maximum)	16.0		
of the submaxillary constriction	13.0		
Length of the rami (preserved length)		57.3	81.4
Height of jaw at posterior end of maxilla		. . . .	14.0

JAW FRAGMENTS	CUP 2083 left	CUP 2104 right
Preserved length	34.0	47.5
Height of maxilla: anterior, posterior	8.7, 3.0	6.0, ...
Height of mandible: anterior, posterior	9.0, 11.0	9.0, 14.0

The prolonged posterior extension of the palate is indicative of a sphenosuchid heritage; the choanae are abbreviated but lie on the anterior part of the skull like *Erpetosuchus,* and the formation of the primitive secondary palate (mesosuchian?) is apparently at the same level of development as that of *Protosuchus.* If the dorsal placement of the nares is a reliable feature, *Protosuchus* was probably more aquatic than *Platyognathus.*

Jaws (fig. 8,A2): The shape of the mandible is particularly diagnostic for *Platyognathus.* The jaw is blunt. Posteriorly, the symphysis gradually expands and then constricts so that the prepremaxilla overlaps the zone of increasing breadth and the diastemic area lies over the expansion. The snout is slightly broader than the jaw. The symphysis is long and deep. The rami are tightly co-ossified and exhibit the shallow troughs noted by Young to either side of the dorsal mid-line. In the present example, the grooves appear at the level of the fifth maxillary tooth where the left and right rami diverge sharply at an angle of about 45°. The ventral surface of the symphysis is flattened and depressed just forward of the constriction

by a shallow transverse groove. Young described a similar groove for the type which lay further forward and masked the individuality of the rami; here, the rami are distinctive throughout.

The dentition is largely obscured by the close apposition of the skull. The jaw lacks a diastema and probably holds some 23–24 teeth which increase in size backwards in the series. The first two project anteriorly and are polygonal in cross section like the maxillary pattern. In contrast to the type, the others are more erect but still caniniform, while the more posterior are slightly recurved. The ventral surface bears round impressions of two sets of large roots, 8.8 mm. and 13.5 mm. from the tip respectively which may be the bases of the third and fourth teeth.

Surangular and Angular: The bones diverge posteriorly and pinch out the dentary at the level of the orbit. The jaw becomes deeper and appears to contain a small lateral fenestra (CUP 2104). The angular displaces the splenial ventromedially which forms the lateral wall of a meckelian fossa.

Splenial: The bone sheaths a medial wall of the dentary and their common suture is well marked. Young misinterpreted the meckelian groove as the point of insertion of a cartilaginous splenial and stated that the bone does not enter into the symphysis. It is here clearly seen to participate in the symphysis if only by a ventral tongue, and its anteriormost limit lies where the lateromedial dimensions of the diverging rami narrow abruptly.

The mandibles are unlike those of any of the pseudosuchia or protosuchia. The disposition of the splenial is sphenosuchid-like, but the relationship of the dentary and splenial is unknown in *Protosuchus;* this is, however, crocodilian in character, particularly in the longer-snouted forms. The symphysis of *Erpetosuchus* is elongate but proportionately shorter relative to the length of the head.

Teeth, Upper Jaw: The premaxilla holds four subequal teeth. The first and second teeth point forward while the third and fourth are gently compressed, sharply pointed and distinctly recurved. The second is needle-like and the smallest. Young described the teeth of the type as octangular in cross-section, but since their geometry in fact varies with the level considered, it might be more precise to describe them as irregularly polygonal. Hence, distal to the tip, the teeth are rather hexagonal in cross-section and only the bases are octagonal.

The post-diastemic teeth are immediately less robust and become progressively smaller backward and more sharply compressed. The

last three–four may be newly erupted. Fine denticulations (9–10/1.0 mm.) appear on both cutting edges.

Teeth, Lower Jaw: The maxillae mask all but the most anterior teeth, but these are patterned after the upper series. The first two teeth are uniformly small, anteriorly projecting, and are followed by larger and more erect teeth. Posteriorly, the teeth are smaller but indistinct.

No pseudosuchian known to the author has been described with polygonal teeth. Moreover, the dental pattern of *Protosuchus*, where the reduction of the maxillary series is nearly immediate, and of *Pediticosaurus* are dissimilar to the present form.

VERTEBRAE

The vertebrae occur as disarticulated and multiple fragments of at least two animals. The cervicals and thoracics bear dorsal and ventral armor plates; the sacrals are missing; the caudals are completely sheathed in armor.

Cervical Vertebrae (Table 10; fig. 8,B,E): Two articulated series of vertebrae, comprising five cervicals (CUP 2105) and five cervicals plus three dorsals, respectively, are known, but they cannot be derived from the same animal since the combined vertebral count would be characteristic of saurischians rather than thecodonts. The latter series is believed to belong with CUP 2083.

Centra short, moderately high, platycoelous–slightly amphicoelous, increasing in length only slightly posteriorly in the series. Ventral surfaces smooth but furrowed. Parapophyses lie anteromediad on the first centrum but move slightly back on the following vertebrae; the trend is accomplished by the typical thecodont rotation of the costal facet outward and upward toward the neurocentral suture.

The neural complex is directed craniad in all but the first vertebra where it is erect. The arches are very high and the spines are terminally expanded to receive the dorsal armor. The transverse processes are stout becoming progressively more obtuse relative to the spine posteriorly. The zygapophyses although poorly preserved, were presumably delicate, high anteriorly becoming more oblique posteriorly.

Dorsal vertebrae: The first three dorsal are in articulation with the cervical series of CUP 2083; only the third is adequately exposed. An armored fragment from the mid-dorsal column shows three additional centra.

TABLE 10.—MEASUREMENTS OF THE VERTEBRAL COLUMN,
PLATYOGNATHUS HSUI (in mm.)

Position in Series	Ventral Length[1]	Maximum Breadth[1]	Height of Neural Complex
		CERVICAL SERIES CUP 2105	
1	...	10.0	12.0
2	6.0	....	10.0
3	6.4	....	11.0
4	6.0	....	?13.3
5	6.5	....	?13.0
6	6.4	....	?13.0
7	...	9.5	....
		CERVICAL SERIES CUP 2083	
1	6.0	9.3	10.0
2	6.9	...	8.4
3	...	...	7.8
4	...	...	10.2
5	...	...	9.2
6	...	...	...
7	...	...	...
		DORSAL SERIES CUP 2083	
1	8.0	7.8	...
2	8.5	7.8	...
3	9.0	7.8	...
4	...	...	...
5	...	...	...
6	?10.0	?	?11.4
		CAUDAL SERIES CUP 2083	
1	?10.0	4.0 W	4.0
		ARMORLESS CAUDALS CUP 2083	
1	6.0	7.0	9.0
2	6.6	?	11.0
3	5.9	7.0	11.0

[1] Centrum

Anterior centra are gently procoelous, compressed, and bear ventral longitudinal ridges which are lost posteriorly as they become deeply furrowed. These are less squat than the cervicals but not immediately more elongate.

In the third vertebra (CUP 2083) the parapophyses have completed their dorsal migration and lie just below the diapophysis.

Posteriorly, the parapophyses lie on or just above the neurocentral suture and subsequently appear to 'fuse' with the diapophyses forming narrow facets for single-headed ribs.

The neural apparatus is high and directed craniad; the spine is elongate, flat, and terminally expansive like the cervicals. The zygapophyses are widely oblique to insure the maximum of lateral motion —a feature of distinct advantage to an aquatic animal.

Caudal Vertebrae (Table 10; fig. 8,C): Anteriormost caudals are completely sheathed in armor. The posterior vertebrae are exposed to permit description.

Centra procoelous, compressed, and anteriorly more elongate than the cervicals which they resemble in other respects. Ventral surfaces smooth, rounded, less deeply furrowed than the dorsals, and bear facets for hemapophyses. The caudal ribs articulate on the neurocentral suture, and above, the zygapophyses show widely oblique facets. The neural spines are low, co-ossified, and form a continuous ridge for the dorsal armor.

Ribs (fig. 8,E): The cervical ribs are plow shaped, approximately 11.0 mm. long and overlapping. The forward projection is longer.

The anterior dorsal ribs are double-headed, acutely bent, and terminate on the sternum. The proximal and vertebral segments appear to be broken at their mid-lengths. The sternal segment bears a ventrolateral triangular flange at the level of the fracture which may have supported some lateral armor plates. The ribs of the mid-dorsal region are long, broadly arched, split sagitally and are apparently single-headed.

The pattern of the vertebral column is protosuchid. The progressive migration of the parapophyses toward the neural arch is essentially completed at the same level by *Erpetosuchus* (eighth–ninth presacral), *Protosuchus* (twelfth presacral) and by the present form (?ninth–tenth presacral). The ninth presacral of *Erpetosuchus* figured by Newton (1894) resembles the cervical of *Platyognathus*, but the protosuchid type is uniformly amphicoelous. The procoelous centra of *Platyognathus* is a much more advanced feature of crocodilian evolution.

PECTORAL GIRDLE

The bones are nearly complete bilaterally, and lie on the cervical series (CUP 2083). The dorsal blades of the scapulae are damaged in part. The left carocoid is complete, but the right retains only a proximal fragment.

Scapula (fig. 8,B2): The bone is elongate and the dorsal and ventral blades are broadly expanded. The glenoid region is rotated slightly outward and bears a strong acromion tuberosity above. The dorsal portion tapers gradually to form a strong inferomedial constriction; the expansion of the ventral blade is immediate thereafter and the anterior portion is prolonged.

Coracoid (fig. 8,B3): The coracoid is elongate, expanded proximally, and suturally united to the scapula where it participates in the glenoid. The dorsal surface is concave and pierced by an anteromedial foramen.

TABLE 11.—MEASUREMENTS OF SCAPULA AND SCAPULOCORACOID
OF *PLATYOGNATHUS HSUI* (in mm.)

	left	right	Breadth left	Breadth right	Thickness left	Thickness right
SCAPULA						
Preserved maximum length....	38.3	?33.3				
Level of:						
dorsal blade...............			?21.4	?23.3	...	1.0
inferomedial constriction.....			....	6.2	...	3.0
sutural union of scapula						
and scapulocoracoid.......			....	8.2	...	6.0
acromion.................			15.6	16.6	...	...
SCAPULOCORACOID						
Length of scapulocoracoid......	21.1	....				
Dorsal blade (maximum)......			15.0	13.2	7.0	...
Medial constriction...........			....	5.1	...	5.1
Ventral blade...............			....	11.1	...	...

Sternum: A thin and unsegmented bowed plate of bone lying to the left of the ventral cervical scutes (21.5 mm. long) is interpreted as the sternum.

The features of the pectoral girdle are those of primitive protocrocodilians and of two relatively advanced suborders of the Crocodilia. The scapula is reminiscent of Broom's reconstruction of the ventral blade of *Sphenosuchus* and of that of *Notochampsa* Broom (1904, Haughton, 1924), while the coracoid is modeled upon that of the eosuchian *Alligator* redrawn by Colbert and Mook (1951). The ratio, coracoid length/scapular length, is 0.52 for *Protosuchus, circa* 0.96 for *Alligator,* and 0.60(?) for *Platyognathus;* the latter figure should probably be lower since the dorsal blade of the scapula is incomplete and would then approximate that for *Protosuchus* although the configuration of the coracoid is quite different.

SCUTES

The postcranial skeleton is variably sheathed with ornamented scutes. Dorsal armor occurs uniformly on all regions of the body as a double row of transverse scutes. The postsacral region bears smaller and more numerous unpaired lateral scutes which form a transverse series with the ventral armor, paralleling the dorsal series in distribution. Rounded pits and a pattern of radial rugosities ornament the dorsal series; the lateral and ventral plates are randomly pitted.

Dorsal Series (figs. 8,B,E; 9,A): The plates form a broadly rectangular overlapping series corresponding in number and position to the underlying vertebrae. These are broader than long, the ratios (length/breadth) being 0.63, 0.51 and 0.73 for the cervical, dorsal, and anterior caudal regions respectively. The width of the plates, then, increases posteriorly and the ratio may approach unity in the last postsacral plates. The lateral margins are slightly rounded, and each scute bears a lateral longitudinal keel becoming more prominent toward the posterior margin. The outermost surfaces are depressed below this axis.

Lateral Series: The lateral plates form a tightly overlapping series which is apparently restricted to the caudal region, and are keeled in like-fashion to the dorsals. The length/breadth ratio increases posteriorly, i.e., 0.58–0.75 in the anterior caudal and posterior caudal regions. A single pair of convex scutes (fig. 8,E) oriented obliquely and outward to the dorsal series is associated with an anterior vertebra of cervical series (CUP 2105); these contact the cervical ribs of the centrum immediately in front and may indiacte that the entire neck was armored.

Ventral Series: The ventral scutes are paired and distributed like the dorsals although only the right series has been preserved in cervical series (CUP 2083). The fragment of the dorsal vertebrae (fig. 9,B) is covered ventrally by eight paired rows of four scutes each, but there are only two scutes in each transverse row in the caudal region. The plates lack lateral keels, are irregularly quadrate and suturally united but overlap somewhat in the posteriormost caudal region. The length/breadth ratio is rather uniform in all regions of the body, i.e., cervical, 1.0; dorsal, 0.75; caudal, 1.0.

The configuration of the scutes in *Platyognathus* is similar to *Protosuchus* although the ventral deflection of the border lateral to the keel is less acute and the ornamentations are dissimilar. The cervical scutes in *Erpetosuchus* differ in that they are longer than broad,
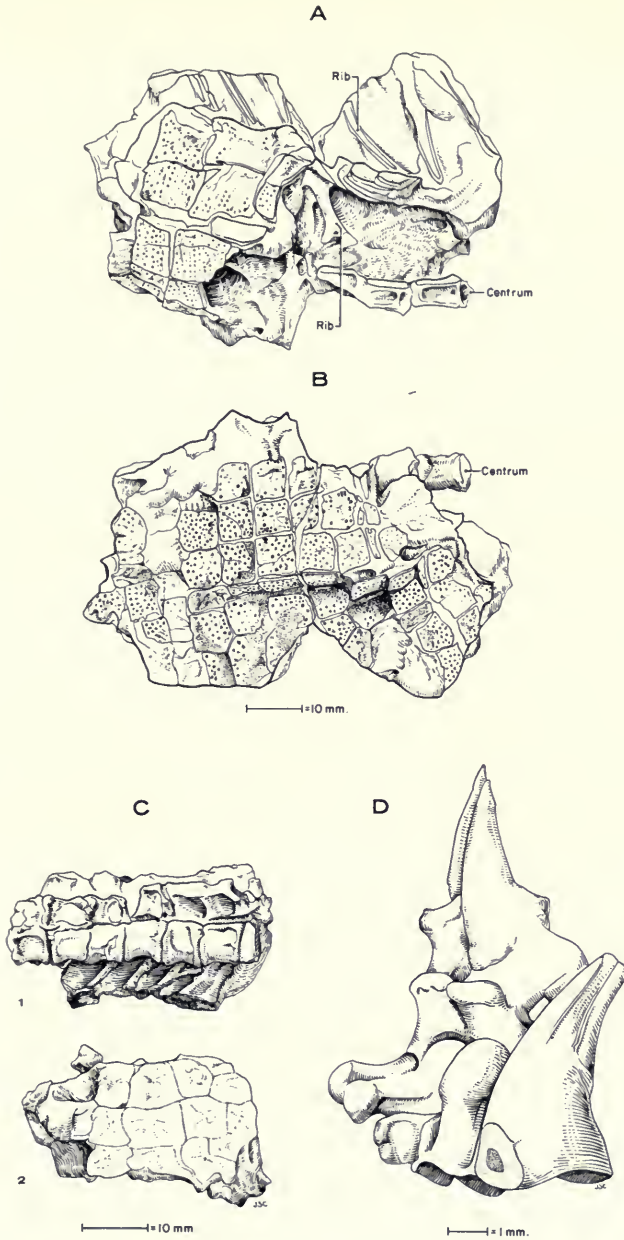
FIG. 9. *Platyognathus hsui* Young. A, Presacral vertebrae and scutes viewed from above (CUP 2083). B, Ventral aspect of presacral scutes (CUP 2083).

Microchampas scutata Young. C, Vertebrae and ribs viewed obliquely from below (1) and the ventral scutes (2); (CUP 2085). D, Hand with claws, metacarpals and phalanges (CUP 2086).

45

but the dorsal transverse series is similarly ornamented. The ventral scutes are apparently developed here more extensively than in *Protosuchus* where armor is preserved only from the lumbar region posteriorly. *In toto*, the armor pattern is somewhat reminiscent of aetosaurus-like pseudosuchians.

CHARACTERS INDICATING A THECODONT HERITAGE

The short skull and elements about the terminal confluent nares are patterned after *Sphenosuchus*. The armor images the rather specialized pseudosuchians although *Sphenosuchus* is itself without armor. Antorbital fenestrae are almost exclusively limited to the thecodonts although the exceptional protosuchian *Pedeticosaurus* presents a similar structure. The centra of the vertebrae lack hemapophyses.

CHARACTERS INDICATING A CROCODILIAN AFFINITY

A flat snout, an edentulous and emarginated premaxillary-maxillary suture, dorsally oriented orbits, a primitive 'mesosuchian' palate and ventro-lateral choanae are characters to be found in primitive crocodilian groups. Confluent external nares are common to many mesosuchians and eosuchians.

The symphysis of the mandible is elongate and includes the splenial.

Eosuchian-like procoelous vertebrae compose the presacral vertebral column. The parapophyses migrate upward onto the neural arch and fuse with the diapophyses to form wide lateral processes.

The coracoid is elongate and intermediate in length between the protosuchian and crocodilian pattern with respect to the scapula.

The features of the skull make it valid to assume that *Platyognathus* was most probably derived from a sphenosuchid-like pseudosuchian. The line of descent of the crocodiles was evidently very plastic, and in three areas of the world, i.e., North America (*Protosuchus*), South Africa (*Sphenosuchus*) and China, the pseudosuchia and protosuchia were developing along a quite definite crocodilian plan. F. von Huene (1925a) and Broom (1927) have outlined several schemes depicting the steps in the development of the crocodiles from a generalized sphenosuchid-like ancestor. Broom's scheme appears to be the more reasonable interpretation, since he removes rather specialized forms such as *Pedeticosaurus, Aetosaurus* and *Erpetosuchus* from the line of direct descent toward *Notochampsa* (*Erythro-*

champsa); in accordance, therefore, *Platyognathus* may be interpreted to have been independently developed in the same fashion as *Pedeticosaurus* which, as Colbert and Mook point out, is so different from other South African protosuchians that it had better be considered a pseudosuchian.

The suite of characters which define *Platyognathus* bespeak a taxonomic position intermediate between the Pseudosuchia and Protosuchia. If, however, the greater emphasis is placed upon the more conservative features of the skull rather than upon the progressive nature of the postcranial skeleton, and these are considered to be specialized responses to an aquatic habitat, *Platyognathus* will properly be seen to be a pseudosuchian.

It is recommended that the present form be placed in a new family of pseudosuchia, the Platyognathidae (fam. nov.) which has the following characters: Skull: triangular with a short, broad snout; confluent terminal nares; orbit upwardly placed; a small antorbital fenestra; a secondary palate of a mesosuchian type; a long symphysis. Vertebrae: dorsal and caudal series procoelous. Pectoral Girdle: coracoid very elongate. Armor: scutes broader than long.

<div align="center">

Order **Thecodonta**

Suborder **Pseudosuchia**

Family **Incerta sedis**

</div>

Holotype.—A fragment of the right ilium and proximal end of the femur. Catalog No. CUP 2084.

Horizon and Locality.—Ta Ti, Dark Red Beds, Lower Lufeng Series.

<div align="center">

DESCRIPTION (Table 12, Fig. 10,A1–2)

</div>

Ilium: The crest is straight, narrow, and prolonged anteriorly; the bone is fractured just back of the ischial process but if a posterior extension were also developed, it would most probably have been modest. The roof of the acetabulum is expansive anteriorly to provide a broad, deep, articular surface for the head of the femur.

The lateral surface bears an oblique ridge which passes anteroventrally to the acute and somewhat upturned border of the supra-acetabular buttress. The buttress is strongly developed anteriorly, but gradually merges with the bone above the ischial process. The ischial process limits the acetabulum posteriorly (fig. 10,A), projects downward and outward, and bears a demilunar facet.

TABLE 12.—MEASUREMENTS OF THE PSEUDOSUCHIAN, CUP 2084

(in mm.)

ILIUM

Length of the crest...	37.0
Height of the crest above the mid-acetabulum.................	13.0
Height of the ilium at the ischial process......................	30.7
Breadth of the acetabulum, from the tip of the ischial process to the lip of the supra-acetabular buttress..................	20.0
Height of the acetabulum above the obturator................	15.0
Facet of the ischial process: length, breadth...................	11.0, 6.0

FEMUR

Head: proximal dorsoventral breadth........................	14.0
Anterior-posterior breadth of the proximal articular suface......	22.3
Breadth of the proximal articular surface behind the head.......	10.6
Neck: anteroposterior, dorsoventral..........................	11.0, 12.0
Ridge systems: proximal breadth of the posterior, ventral........	11.4, 12.0

The medial surface features a pair of broad crescentic depressions above the ischial and pubic processes. These are separated by about 7.0 mm. above the obturator which is open and presents a finished surface.

Femur (fig. 10,A3–5): The femur was displaced during preservation, and made contact with the posterior part of the iliac crest. The head is large and divided by a slight dorsal constriction 17–18 mm. backward, appearing then biconvex; the proximal anterior surface is gently concave. A pair of ridges, the posterior ridge and the proximal anterior branch of the ventral ridge are separated by a strong intertrochanteric fossa, and pass diagonally downward and anteriad across the ventral surface of the shaft. The bone is hollow and thin-walled.

The taxonomic position of the fragments is indefinite. The configuration of the ilium does not approach that of either the Proterosuchia or of the ornithosuchian pseudosuchians where the primitive triradiate pelvis is a solid plate-like structure having a continuous ventral symphysis. The obturator in the present form is acute and finished indicating that the space was not filled with cartilage. The overall proportions of the ilium of the stagonolepid *Typothorax meadei* Sawin (1947) are comparable to the present form, and the bone shows a prominent supra-acetabular buttress, an incipient subacetabular foramen and downturned ischial processes. The development of the proximal biconvexity and of the ridge systems in the femur is intermediate between *Typothorax* and *Episcoposaurus horridus* Cope (Huene, 1915), although the incompleteness of the remains limits comparison. A more definitive analysis of the relationships of

CUP 2084 to the stagonolepid group might be possible if the distal shaft were known for, in these, the proximal and distal condyles are perpendicular to each other.

It is probable that the remains are not those of the poorly known parasuchian *Pachysuchus imperfectus* Young (1951). Even though the ilia of other phytosaurs are low and prolonged anteriorly, the pubo-ischiatic suture is incompletely ossified and filled with cartilage. The nature of the femur affords a more likely comparison to the stagonolepid group.

Order **Crocodilia**

Suborder **Protosuchia**

Microchampsa scutata Young (1951)

Microchampsa scutata Young (1951)

Holotype.—An articulated fragment of eleven vertebrae and ribs covered by three longitudinal rows of dermal armor.

Horizon and Locality.—Dark Red Beds, Lower Lufeng Series, Huangchiatien, Lufeng, Yunnan.

Diagnosis (Young, 1951, p. 31).—"Thecodontia with a single row of dorsal scutes closely arranged on each row of the lateral scutes. Presence of ventral scutes doubtful but probable. Dorsal vertebrae short and stout, becoming slightly elongated and constricted posteriorly. Ribs are double headed, only slightly curved. Size very small, being about one-half that of *Erythrochampsa longipes* Br."

DESCRIPTION

The dorsals are amphiplatyan, stout and short (1.1–2.0 mm.) anteriad becoming slightly longer and constricted posteriad (2.1–3.0 mm.). The parapophyses are small and become indistinct by the fifth centrum. Four of the seven ribs exposed on the left side had distinct capitula and tubercula which tended to lie closer together backward along the column. The last centrum was cited as a lumbar. The ribs are short and only slightly curved.

The dermal scutes become shorter posteriorly and correspond in number to the vertebrae. A single median dorsal row, which lacks pittings and other ornamental rugosities, is similarly constructed and adjoins broader unpaired rows of dorsolateral scutes at almost right angles. The fragment measures about 21.0 mm. long, 11.0 mm. high, and 7.0 mm. broad at the middle part.

ADDITIONAL MATERIAL

Material.—A fragment of seven consecutive vertebrae and five ribs with dermal armor, Catalog No. CUP 2085. Bones and claws of the hand, Catalog No. CUP 2086.

Horizon and Locality.—Ta Ti, Dark Red Beds, Lower Lufeng Series, Lufeng, Yunnan.

Amended Diagnosis: An armored reptile. Three rows of scale-like dorsal scutes—a single median dorsal row adjoining unpaired bilateral series. Ventral scutes present. Thoracic vertebrae short, becoming elongate and sharply compressed posteriorly; anteriormost ribs doubly headed, free and slightly curved, becoming fused to the lateral armor in the lumbar region and articulating with broad transverse processes.

DESCRIPTION

Vertebrae and Scutes, CUP 2085 (fig. 9,C1–2): The fragment appears to be from the lumbar region and is twice as large as the type, V87 (length, 39.0–40.0 mm.; height, 17.0–18.0 mm.; breadth, 18.0 mm. at midlength). Ventral armor plates arch over the left side of the vertebral column and cover the median dorsal and left lateral scutes.

The specimen must have turned 180° during preservation. The right side was denuded of protective armor and covered with an indurated, whitish waxy material of a color and texture approximating that of the underlying bone which was difficult to prepare—perhaps due to the surface solubility under pressure tending to fuse and thereby obscure the boundaries of the elements. The better preserved features of the left side were rather easily prepared from a soft reddish matrix.

Lumbar Vertebrae, CUP 2085 (Table 13): The column is arched. The centra are amphiplatyan, ventrally furrowed and deeply incised posteriorly in the series. The costal articulations of the right side are fused, broad, dorsoventrally convexoconcave and lie on the neural arch.

The neural spines are broad, flat and terminally expanded to accommodate the median dorsal row of scutes. Measurements of the height (Table 13) are only approximate due to crushing. The zygapophyseal articulations are obscured by the crowding of the vertebrae along the curvature of the column, but they are probably rather flat as in other proto-crocodilians.

TABLE 13.—MEASUREMENTS OF *MICROCHAMPSA SCUTATA*
(in mm.)

LUMBAR VERTEBRA

Specimen No.	Position in Series	Ventral Length	Right Side				
			*A.H.	L.Tp.	B.Tp.	H.	H.Ns.
CUP 2085	1	. . .	. . .	. . .	. . .	. . . .	. . .
	2	3.7	5.0	4.0	5.5	17.0	6.0
	3	3.5	5.9	4.0	5.2	16.7	6.0
	4	4.2	5.5	4.6	5.0	16.0	?4.7
	5	4.8	5.6	4.6	5.5	16.7	5.5
	6	?4.2	5.6	4.0	6.4	?15.0	?4.2
	7	?4.5	5.6	?3.6	5.1	?	. . .

CAUDAL VERTEBRA

Specimen No.	Position in Series	Distance between the tips of the Transverse Processes
CUP 2087	1–2	. . .
	2–3	?2.0
	3–4	2.5

* Anterior height
  Transverse process length
  Transverse process breadth
  Height of the vertebra
  Height of the neural spine

Caudal Vertebrae, CUP 2087: The fragment consists of the neural arches and scutes of five vertebrae. The transverse processes are short and narrow, and contact the edges of the median dorsal scutes. The posterior zygapophyses are rather obliquely oriented (fourth vertebra).

Ribs, CUP 2085: The dorsal ribs of the type were double headed and free. The proximal shafts of the lumbar ribs apparently fuse to the anterior margin of the lateral scutes, and the heads persist as linear exostoses converging to form the shaft 2–3 mm. from the outer border of the armor; the tubercular relief is the higher. The features are best seen in the third and fourth ribs in the series. The shafts clearly extended beyond the end of the scutes but become structurally weaker posteriorly.

Ventral Armor, CUP 2085 (Table 14): Young's speculation that *Microchampsa* had ventral armor is confirmed. Four transverse rows of four scutes each overlap the mid-dorsal and lateral series, but are only unilaterally represented. The plates which would have contacted the midline are broken while the outermost plates have been displaced and overlap slightly. These are rather squarely fashioned (6.0 mm.^{2}), but the lateral borders of the outermost plates are rounded

anteriorly and finished, indicating that the armor ended at this point and did not extend over the sides of the body.

Dorsal Armor, CUP 2087 (Table 14): Four scutes from the mid-dorsal and right lateral series are exposed on a caudal fragment. The laterals contact the under surface of the dorsals at an oblique angle, and are broader anteriorly than posteriorly in the thoracic column; in the caudal region, the dorsals are the broader (dorsals, 6.2 mm.; laterals, 3.0–4.0 mm.) and become shorter and more closely fitting posteriorly.   The dermal armor is simply pitted and has ornamental rugosities.

TABLE 14.—MEASUREMENTS OF THE DERMAL ARMOR OF
MICROCHAMPSA SCUTATA (in mm.)

Specimen No.	Position Along Column	Mid-Dorsal Series		Lateral Series			
				left		right	
		L.[1]	B.[2]	L.	B.	L.	B.
CUP 2087	1	?2.0	?5.4	...	...	2.9	3.3
	2	2.2	5.6	...	...	2.7	5.4
	3	2.5	6.1	...	...	2.0	3.5
	4	2.4	1.3	...	...	...	...

[1]L.=Anteroposterior length
[2]B.=Lateromedial breadth

APPENDICULAR SKELETON

Hand, CUP 2085 (fig. 9,D): The association of the specimen with the vertebral fragment and its small size figure importantly in the tentative assignment of the complex to *Microchampsa*.   The fragment consists of two gently curving claws subequal in length, sharply tipped and grooved to receive the horn, and rather elongate, slender phalanges of equal length which have large condyles—probably the third and fourth or the fourth and fifth digits.

The absence of skull materials limits the definition of *Microchampsa* since the dermal armor pattern is most atypical with respect to the stem reptiles.   The rectangular scutes are of a protosuchid type, but the dorsal plates of the Notochampsidae are paired and there is no indication that the microchampsid pattern originated by the simple fusion of plates to either side of the midline—absence of lateral keels.   Moreover, the dorsal armor in *Notochampsa istedana* (Haughton, 1924) gradually becomes quadrangular posteriorly while the rectangular configuration in *Microchampsa* is retained in the caudal region and it is to be expected that the obscured lumbars were similarly fashioned.   The pattern approaches most nearly the poste-

rior caudal scutes of *Protosuchus* and *Pedeticosaurus* which are quadrate or become even slightly longer than broad; the number of plates in each transverse ventral row also decrease toward the sacrum. Supernumerary ventral plates relative to the dorsals, however, distinguish other protosuchians (2:1) from *Microchampsa* (1:1) although the caudal regions are similarly encased in dermal armor; the development, while not as great as that of the more specialized pseudosuchians such as *Aetosaurus*, surpasses that of the more conservative thecodont group.

The vertebral structure is most crocodilian; the centra resemble *Protosuchus* and related forms. The expansive spines are particularly like those of *Pedeticosaurus* and there is a tendency for the fusion and establishment of the costal articulations on broad, flat, transverse processes in the lumbar region of the body. The protosuchian rib pattern is virtually unknown, however, the doubly flanged shafts of the thoracic ribs of *Protosuchus* are not found in either *Microchampsa* or in modern crocodilia where only anterior flanges persist. It is possible, nonetheless, that the lumbar ribs and scutes of *Microchampsa* were flanged and free in young animals, i.e., in the type, but became fused during ontogeny.

The available structures are insufficient to establish the systematic position with any certainty, but the most reasonable assignment appears to be to the Protosuchia, recognizing that it apparently represents a new type of primitive crocodilian.

<div align="center">

Order **Saurischia**

Suborder **Theropoda**

Infraorder **Coelurosauria**

Family **Podokesauridae**

Lukousaurus yini Young (1948b, 1951)

</div>

Original Diagnosis.—"Skull rather small. Nasal opening small and anteriorly situated. Preorbital opening triangular and high. Orbits well rounded. Muzzle looks slender. Lower jaw slender with the lower margin straight. Premaxilla bears five teeth and maxilla about ten teeth. All the teeth are sharply compressed and pointed backward. Posterior side with fine and short serrations."

Lukousaurus is the only carnosaur known from eastern Asia and the only small saurischian of the Lufeng assemblage. The original

diagnosis of the genus was based on materials from the Dark Red Beds at Huangchiatien—the anterior part of a skull and jaws (V23), a tooth (V263) and the proximal part of a right humerus (V261). Recently (Young, 1951), three additional fragments from the Dull Purplish Beds at Shawan (V77) were referred to this genus, the distal part of a right humerus and an upper middle part of a co-ossified tibia and fibula.

The present collection includes an additional and similarly pre-served skull fragment with a more complete jaw than the type (V23).

Additional Material.—An anterior fragment of a skull and jaws with teeth.   Catalog No. CUP 2092.

Horizon and Locality. Hei Koa Peng, Dark Red Beds, Lower Lufeng Series.

Diagnosis.—Same as for the Type V23 (Young, 1948b).

DESCRIPTION (Table 15)

The skull is badly damaged.   A fragment of the left premaxilla lies at the snout while the nasal bones are displaced to the right side. Posteriorly the roofing bones are limited to a small fragment of a sus-pect prefrontal.   The left wall shows the anterior angle of the pre-orbital fenestra; the position of the external nares is only indicated since the borders are crushed and the orbits are ill-defined.   The outer wall of the left maxilla is broken away.

A short anterior fragment of the left jaw bears the roots of two teeth.   The right mandible is transversely fractured and crushed pos-teriorly, but indicates the presence of a small, high, lateral fenestra; its internal architecture is exposed medially by the loss of the splenial which is intact only at the symphysis.   The prearticular is seen to project anteriorly.   The surangular-angular contact is indistinct due to the checkering of the bone.   The angular is a large element which overlaps the smaller superior surangular and wraps about the infe-rior surface of the jaw.

The tips of the second–fifth teeth of the left maxilla are imbedded in the matrix of the lower jaw; the fifth is completely exposed (11.0 mm.).   The sixth and seventh exist as hemi-root fragments adhering to the inner wall of the maxilla.   Roots of the eighth and ninth, with perhaps the crowns of their replacement teeth, are simi-larly contained while two large, badly checkered fragments—(?)lowers —lie above them.   A series of four small teeth (terminals) occur just forward of the orbit.

On the right side, a single premaxillary tooth (?fifth) lies internal to the space marking the suture with the maxilla, and is followed by the first maxillary tooth with its replacement. The first–third maxillary teeth lack crowns and the root of the second lies at the alveolar margin. The sixth–eighth and ?twelfth teeth become progressively smaller. As noted by Young, the jaw could not have supported more than 12 teeth.

The tight apposition of the right maxilla masks the mandibular dentition. The short fragment of the left mandible exhibits the roots of three teeth mediad to the fourth maxillary tooth.

TABLE 15.—MEASUREMENTS OF THE SKULL AND JAWS OF
LUKOUSAURUS YINI (in mm.)

	left	right
Preserved length of the skull: upper	29.0	51.6
lower	56.0	51.6
Preserved length of the jaw	63.0	19.4
Anterior height of the skull (excluding nasals)	10.6	13.0
Posterior height of the skull fragment	17.0	17.0
Length of the tooth row	37.0	56.6
Preserved length of the premaxilla	....	8.0

Remains Referrable to the Podokesauridae

Catalog No. CUP 2089

Material.—An articulated fragment of a left femur, tibia and fibula with isolated fragments of metacarpals and phalanges.

The bones were associated with the skeleton of *Dibothrosuchus*, but are quite distinct from other known pseudosuchia. Moreover, on the basis of the proportions of the appendicular skeleton among the Ornithosuchidae, where the acquisition of bipedalism parallels the reduction of the forelimb relative to the more massive hindlimb, the femur is as slender and equally as long as the humerus of *Dibothrosuchus*. The histologic structure of these bones is similar and at apparently the same level of maturation, but morphologically identical fine structure is common among unrelated groups during their ontogeny.

DESCRIPTION (Fig. 10,B1–4; table 16)

Femur: The shaft is long and curved; the dorsal and ventral surfaces are normally angular in places, perhaps indicating the origins and insertions of the extensor and adductor muscles. The distal con-

dylar area is triangularly expansive and bent backward; the correspondingly formed intercondylar fossa is very deep and broad for the insertion of an apparently powerful *M. quadriceps* to extend the thigh, while the popliteal space is smooth, shallow and longitudinally cleft. The surface of the lateral condyle is smooth; the medial condyle is bifurcated. The bone is hollow and thin-walled.

The rectangular articular surface and straight, slender shaft compare favorably to *Coelophysis longicollis* Cope (1887; Huene, 1906, 1915). The shortness of the condyles approaches the condition in *Podokesaurus holyokensis* Talbot (1911) but their ventral disposition is here less prominent. Small condyles are also reported for *Halticosaurus longotarsus* Huene (1932), but this bone was not figured.

Tibia: The proximal articular surface is roughly triangular and divided by a shallow groove. The convex, dorsal, extensor surface bears a triangularly broad and low cnemial crest for the insertion of the extensor muscle below the anterior femoral condyle. The shaft is broad anteroposteriorly and moderately concave ventrally.

TABLE 16.—MEASUREMENTS OF THE APPENDICULAR SKELETON
OF CUP 2089 (in mm.)

FEMUR

Preserved distal length (lateral, medial)........................55.6, 56.4
Maximum condylar breadth (lateromedial)........................... 21.0
Maximum breadth above the condyles (lateromedial)................ 15.0
Maximum breadth at the most proximal end (lateromedial, antero-
    posterior)..7.4, 8.3
Depth of condyles (anteroposterior):
    anterior condyle (fibula)....................................... 13.3
    posterior condyle (tibial)...................................... ?16.7
Depth above the condyles (anteroposterior):
    anterior condyles (fibula)...................................... 13.0
    posterior condyles (tibial).....................................   9.0
Depth of the intercondylar fossa (lateral border, medial border)......6.6, 5.4
Proximal-distal height of the posterior condyle.................... 10.0

TIBIA

Preserved proximodistal length (medial, lateral)..................33.7, 31.6
Breadth of the proximal articular surface........................... 18.7
Maximum depth... 13.0
Distal width (lateromedial)...   8.0
Distal thickness (anteroposterior).................................   6.0

FIBULA

Preserved proximodistal length (medial)............................ 30.0
Proximal breadth (lateromedial).................................... 14.0
Proximal depth (anteroposterior)...................................   5.0
Breadth of the neck (lateromedial).................................   8.0
Depth of the neck..   6.0

Tibias of Triassic coelurosaurs are poorly known. A straight, narrow shaft is reported for *Dolichosuchus cristatus* Huene (1932) and *Podokesaurus;* the first is twice as large as the present form and develops a strong pair of dorsal ridges (cnemial crest), but their mid-length cross sectional areas are comparable. While the tibia of *Coelophysis* has a small head, its shaft bears a low, lateral tuberosity.

Fibula: The fibula is very slender, subcircular in cross section and the head is sharply set-off from the shaft by a constriction.

Fibulae of coelurosaurs, while little known and poorly preserved, are commonly thin, and may be straight (*Podokesaurus*) or curved (*Saltopus elginensis* Huene, 1910). The expansion of the head is a distinctive feature, but weak in *Coelophysis*.

Hand (metacarpals and phalanges): The metacarpals are long and slender. The elements of the proximal and distal fragments are straight, round in cross section, and widely spaced although the condyles are contiguous. The phalanges are known from a small joint fragment.

The hands of coelurosaurs are incompletely known as well. The bones of *Procompsognathus* (Huene, 1921) are a third smaller, lie closer together and are more heavily constructed. The apparent large size of the hand in the present specimen may be similar to *Podokesaurus;* the elongation and slenderness of the metacarpals and the reduced size of the phalanges (?claws) may have been of advantage to a form purportedly adapted for grasping like that of *Coelophysis*.

Catalog No. CUP 2090

Material.—The proximal fragments of two cojoined metatarsals.

The bones were associated with the remains of *Dibothrosuchus*, but in view of their slenderness, a like-assignment is unwarranted. Moreover, these were not modeled upon the Hesperosuchid-type.

Horizon and Locality.—Ta Ti, Dark Red Beds, Lower Lufeng Series.

DESCRIPTION

The fragments are entirely fused (fig. 7,E). The free condylar border of the larger bone (length, 42.4 mm.) is sharp. The breadth of the proximal and distal ends of the cojoined elements is 16.4 mm. and 11.0 mm., respectively.

Metatarsals are rarely preserved in coelurosaurs. *Avipes dill-stedtianus* Huene (1932) is known solely from these bones which are
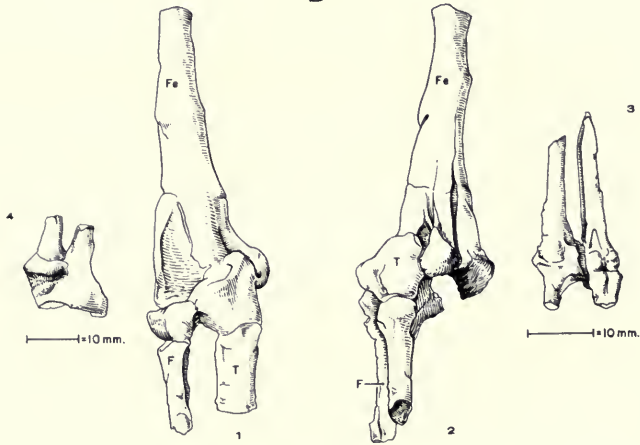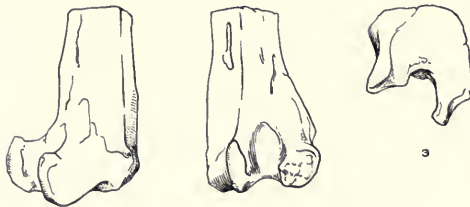
A

1   2

⊢——⊣ = 10 mm.

3   4   5

⊢——⊣ = 10 mm.

B

Fe   Fe   3

4

⊢——⊣ = 10 mm.   T   T

F   F

1   T   2   ⊢——⊣ = 10 mm.

⊢——⊣ = 10 mm.

C

1   2   3

⊢——⊣ = 10 mm.

proximally fused for at least half their length and bear acute con-crescent edges, but it is not known if they similarly diverged distally in the present example.   Fusion of bones is doubtful in *Podokesaurus* and *Saltopus*, but entirely lacking in *Procompsognathus* and *Hallopus*.

Catalog No. CUP 2091

Material.—The distal end of a right femur.

Horizon and Locality.—Ta Ti, Dark Red Beds, Lower Lufeng Series.

DESCRIPTION

The shaft is rather triangular in cross section above the distal condyles and is preserved for a short distance (fig. 10,C).   The condyles are subequal and strongly rotated to the ventral side; the lateral articular process for the fibula is upturned at its apex and is the longer and more massive; the shorter medial condyle for the tibia is downturned.   The narrow superior crest of the lateral condyle is continued as a ridge on the shaft while the bone is broadly rounded above the median condyle.   The ventral intercondylar space is tri-angular and sharply depressed, but viewed from below it appears narrow and shallow.   The dorsal and inferior surfaces of the frag-ment are relatively flat and smooth and lie at right angles.

The fragment appears closer in nearly every respect to the simi-larly preserved *Walgettosuchus woodwardi* Huene (1932) from the lower Cretaceous, New South Wales, Australia, than to any of the carnosaurs or prosauropods I know of where condylar inequality is less marked and the intercondylar sulcus is deeper, i.e., *Gresslyo-saurus ingens, Plateosaurus gracilis, P. plieningeri* Huene (1932).

The proportions of *Gresslyosaurus ingens* are similar to the pres-ent form, but *in toto*, these forms are more massive.

Conclusions.—The hind limb (CUP 2089), femur (CUP 2091) and foot bones (CUP 2090) rather clearly demonstrate coelurosaurian affinities, and particularly to the common upper Triassic family, the Podokesauridae.   Generic identity has not been accorded these speci-

---

Fig. 10.   Pseudosuchian (CUP 2084).   A, Ilium, medial (1) and lateral (2) sides.   Femur, proximal fragment viewed from the ventral (3), dorsal (4) and articular surfaces (5).

Coelurosaur (CUP 2089).   B, Femur, distal fragment articulating with prox-imal fragments of the tibia and fibula (1, 2).   3, phalanges.   4, metacarpals.

Coelurosaur (CUP 2091).   C, Femur, distal condyles viewed from the medial (1), ventral (2), and articular (3) surfaces.

mens since it is felt that additional finds might be of more satisfactory diagnostic value. It is hoped that future collections from the Lufeng Basin will disclose more complete forms with which these fragments can be associated.

TABLE 17.—MEASUREMENTS OF THE FEMUR OF CUP 2091
(in mm.)

Lateromedial breadth at the condylar surfaces	21.0
Transverse cross section length at the break	13.7
Sagittal cross sectional length at the break	12.4
Sagittal thickness of the lateral condyle	23.4
Transverse thickness of the lateral condyle	8.2
Sagittal thickness of the medial condyle	15.0
Maximum separation between the condyles	12.0
Lateral length of the fragment	34.3
Medial length of the fragment	33.4

Suborder **Prosauropoda**

Gyposaurus sinensis Young (1941a, 1948a, 1951)

Original Diagnosis.—"Small Prosauropoda, about the size of *Gyposaurus capensis*. Teeth of general *Thecodontosaurus*-type with anterior and posterior coarse serrations. Vertebrae number probably: neck 10, dorsal 15, sacrum 3, and tail ?. Anterior limb extremely short, scapula vigorously bending at the base of the shaft. Pelvic girdle rather slender with the ilium high. Both hand and foot with distinct lateral reduction."

The collection made by Young represents about 14 individuals of which the majority are unquestionably identified. V45 and V46 from Huangchiatien were perhaps considered immature individuals of *Lukousaurus* or *Gyposaurus* since they demonstrated some anatomical differences from known comparative materials.

Remains Referred to G. sinensis *Young*

LOCALITY	CATALOG No. CUP	ELEMENT
Unknown	2021	Third–fourth cervical vertebral centrum.
Hei Koa Peng	2027	Neural apparatus, anterior dorsal vertebra.
Hei Koa Peng	2028	Cojoined mandible and maxillary.
Hei Koa Peng	2029	Scapula, distal end.
Hei Koa Peng	2026	Maxillary fragment, left.
Ta Ti	2006	Mandibular symphysis and ramus including teeth; a premaxillary fragment with teeth; cojoined upper and lower jaw fragment with teeth.

Ta Ti	2007	Neural spine of a cervical vertebra.
Ta Ti	2008	Fourth metatarsal.
Ta Ti	2009	Left ulna and radius, proximal end
Ta Ti	2010	Vertebral centra, sacrals I and II.
Ta Ti	2011	Left pubis, proximal end.
Ta Ti	2012	Right humerus, distal end.
Ta Ti	2013	Left femur, distal end of a juvenile.
Ta Ti	2014	Right radius, proximal end.
Ta Ti	2015	Right pubis, distal end.
Ta Ti	2016	?Pubis, distal end of a juvenile.
Ta Ti	2017	Fourth metatarsal, proximal end.
Ta Ti	2018	Right ulna, proximal end.
Ta Ti	2019	Left ulna, proximal end.
Ta Ti	2020 and 2023	Neural apparatus, cervical vertebra. Vertebral centra, sacral ?I.
Ta Ti	2024	Left fibula, proximal end.
Ta Ti	2025	Right fibula, distal end.

Lufengosaurus hueni Young (1941b, 1947b, 1951)

Original Diagnosis.—"From large to gigantic size Plateosauridae, Prosauropoda. Skull small. Teeth with short crown and long, strong root. They are weakly spatulated and with coarse anterior and posterior serrations. Vertebrae number: neck 10, dorsal 14?; sacrum 3, and caudal 45 or more. Pectoral girdle with well-ossified sternum. Pubes weakly constructed. Tibia comparatively short. Mt. III is rather long. Anterior limbs are very short. Hand and foot with the first claw are especially strong."

Remains Referred to L. hueni *Young*

LOCALITY	CATALOG No. CUP	ELEMENT
Yang Tsao Ti (Loc. No. 3)	2071	Claw
Hei Koa Peng	2062	Claw, proximal end.
Hei Koa Peng	2063	Claw, proximal end.
Hei Koa Peng	2064	Right and left maxillary fragments, with the ?premaxilla.
Hei Koa Peng	2065	Tibia and Tibiale, distal end.
Hei Koa Peng	2066 2067	Haemal arches.
Hei Koa Peng	2068	Basisphenoid.
Hei Koa Peng	2069	Right anterior maxillary fragment with teeth.
Hei Koa Peng	2070	Right mandibular ramus with teeth.
Ta Ti	2059	Jaw fragment with teeth, left.
Ta Ti	2060	Tibia and tibiale, distal end.
Ta Ti	2061	Neural apparatus, dorsal vertebra.

Lufengosaurus magnus Young (1947b, 1951)

Original Diagnosis.—"Size one third larger than *L. hueni*, Vertebrae robust, Centrum large and short. Scapula strongly bented. Humerus-radius extremely short and massive. Hand short. Pelvic girdle massive, ilium long, Ischium comparatively weakly built. Pubis long and slender with thickened distal end. Tibia relatively long as compared with the femur. Mt. III one half of the length of the tibia. Both the hand and the foot are built in the same way as in the case of *L. hueni*. Anterior leg is much shorter as compared with the whole posterior leg."

Remains Referred to L. magnus *Young*

LOCALITY	CATALOG No. CUP	ELEMENT
Unknown	2052	Jaw fragment with teeth.
Unknown	2053	Jaw fragment with teeth.
Hei Koa Peng	2054	Left fibula, proximal end.
Hei Koa Peng	2055	Jaw fragment with teeth.
Hei Koa Peng	2107	Proximal end of right ulna.
Ta Ti	2056	Crown of tooth.
Ta Ti	2057	Neural spine, caudal vertebra.
Ta Ti	2058	Jaw fragment.

Remains Referrable to Lufengosaurus sp.

LOCALITY	CATALOG No. CUP	ELEMENT
Yang Tsao Ti	2072	Haemal arch.
Hei Koa Peng	2073	Tibiale.
Hei Koa Peng	2074	Jaw fragment with teeth.
Hei Koa Peng	2075	Jaw fragment lacking teeth.
Hei Koa Peng	2076	Premaxillary fragment, right.
Ta Ti	2077	Premaxilla, right.
Ta Ti	2078	Haemal arch.
Ta Ti	2079	Centrum, caudal vertebra.
Ta Ti	2080	Two metatarsals.

Yunnanosaurus sp. Young (1942, 1951)

Original Diagnosis.—"From the middle to rather large sized Prosauropoda with the skull proportionately rather long, more than 3.5 the length of the anterior caudal vertebrae, *ca.* 4. Nasal opening small, anterior orbital opening rather large. Orbit rounded and rep-

resents the largest opening of the skull. Upper temporal opening is bean-shaped and can be seen mostly from the lateral aspect of the skull. Lower jaw slender with small dental foramen. Teeth with long pointed crown, distinctly spatulated in primitive Sauropod fashion. Serrations are poorly developed. Vertebrae robust. Scapula is strongly bending above the proximal expansion. Sternum is ossified and elongated. Humerus robust and shorter than the scapula. Hand with strong lateral reduction. Ilium small with the iliac border low. Ischium slender. Pubis rather thin. Femur and tibia massive, the latter is only somewhat shorter than the former. Fibula rather straight. Foot similarly built as that of *Gyposaurus*."

Remains Referrable to Y. huangi *Young* (Young, 1942, 1951)

LOCALITY	CATALOG No. CUP	ELEMENT
Unknown	2039	Six or seventh cervical vertebra.
Hei Koa Peng	2030	First metacarpal, left.
Hei Koa Peng	2031	left femur, proximal end.
Hei Koa Peng	2032	Left fibula, proximal end.
Ta Ti	2033	Left femur, distal end.
Ta Ti	2034	Third and fifth metacarpals.
Ta Ti	2035	Right fibula, proximal end.
Ta Ti	2101	Distal ends of two fibulae.
Ta Ti	2036	Two centra, caudal vertebrae.
Ta Ti	2037	Skull and jaws, nearly complete, juvenile.
Ta Ti	2038	Maxillary and mandibular fragments.

Remains Referrable to Y. robustus *Young* (1951)

LOCALITY	CATALOG No. CUP	ELEMENT
Unknown	2040	?18th caudal vertebral centrum.
Ta Ti	2041	Two dorsal vertebrae (seven and eight?)
Ta Ti	2042	Left maxillary.
Ta Ti	2043	Right maxillary.
Ta Ti	2102	Ilium.
Hei Koa Peng	2046	Vertebral centrum.
Hei Koa Peng	2047	Tooth fragments.
Hei Koa Peng	2048	Claw fragment.
Hei Koa Peng	2049	Centrum, sixth or seventh dorsal vertebra.
Hei Koa Peng	2044 and 2045	Caudal vertebrae (2).

Remains Referrable to Yunnanosaurus sp.

Hei Koa Peng	2050	Tooth fragment.
Ta Ti	2099	Ilium fragment.
Ta Ti	2100	Ilium fragment.
Unknown	2051	Two teeth.

Infraorder **Carnosauria**

Family **Teratosauridae**

Sinosaurus triassicus Young (1948b, 1951)

Original Diagnosis.—"Carnosauria of gigantic size, Maxilla high. Teeth with long massive root, compressed sharply pointed and curving backwards. Both the anterior and posterior edges are marked by fine serrations."

A number of articulated neck, dorsal, sacral and caudal vertebrae strongly built but comparatively slender to *Lufengosaurus magnus;* part of the anterior and posterior limbs massively constructed but the proportions of the appendicular skeleton are similar to *Yunnanosaurus sp.* Hand short and broad.

Additional Remains Referred to Sinosaurus triassicus *Young*

Catalog No. CUP 2097

Material.—A fragment of the anterior part of the jaws with teeth; two isolated teeth.

Horizon and Locality.—Ta Ti, Dark Red Beds, Lower Lufeng Series.

DESCRIPTION

The rami have been transversely fractured behind the symphysis and disoriented during preservation (fig. 7,D). The alveolar border is acute and forms a narrow ledge above a rather thick but flat, lateral wall. The right jaw fragment is the shorter.

The splenial sheaths the inner surface of the jaw at the symphysis and the dentigerous border, and limits the meckelian groove which passes forward below and internal to it.

The left jaw holds eight–nine teeth which lack crowns. The right, in addition, possesses two large and recurved, narrowly compressed broad teeth which are finely denticulated on their back edges. The isolated teeth are flattened with longitudinal median depressions (ref. V35, V48– Young, 1948b).

The referral of the jaw and teeth to *S. triassicus* is problematical since similar materials are unknown for the type. The teeth vary from known specimens in their greater compression and lack of serrations on the anterior trenchant edges.

Remains Referrable to S. triassicus

LOCALITY	CATALOG NO. CUP	ELEMENT
Unknown	2095	?Centrum; ?third dorsal vertebra.
Unknown	2096	Tooth fragments (3).
Hei Koa Peng	2001	Teeth (24).
Hei Koa Peng	2002	Teeth (2).
Hei Koa Peng	2003	?Centrum; ?third dorsal.
Ta Ti	2004	Teeth (4).
Ta Ti	2005	Teeth (3).
Ta Ti	2098	Centra; one cervical, two dorsals.

Order **Ornithischia**

Suborder **Ornithopoda**

Infraorder **Hypsilophodontidae**

Diagnosis.—An ornithischian of small size. Mandible low anteriorly, slender and tapered; anterior ventral border bends medially toward the symphysis; jaw higher and more convex posteriorly. Teeth thecodont, overlapping, relatively simple and increasing in size from front to rear. Dentary-predentary junction edentulous.

Tatisaurus oehleri sp. nov.

Holotype.—A fragment of a left mandible with teeth. Catalog No. CUP 2088.

Horizon and Locality.—Ta Ti (Locality No. 8) from the Dark Red Beds of the Lower Lufeng Series.

Diagnosis.—Same as for genus.

DESCRIPTION (fig. 11,A,B,C)

The ramus is low anteriorly, of slender proportions and broken in front and in back of the tooth row. Viewed from above, it is slightly sigmoid; from below, the inferior border is acute and bends anteromedially toward the symphysis. All sutural contacts have been obliterated by the extensive checkering of the bone.
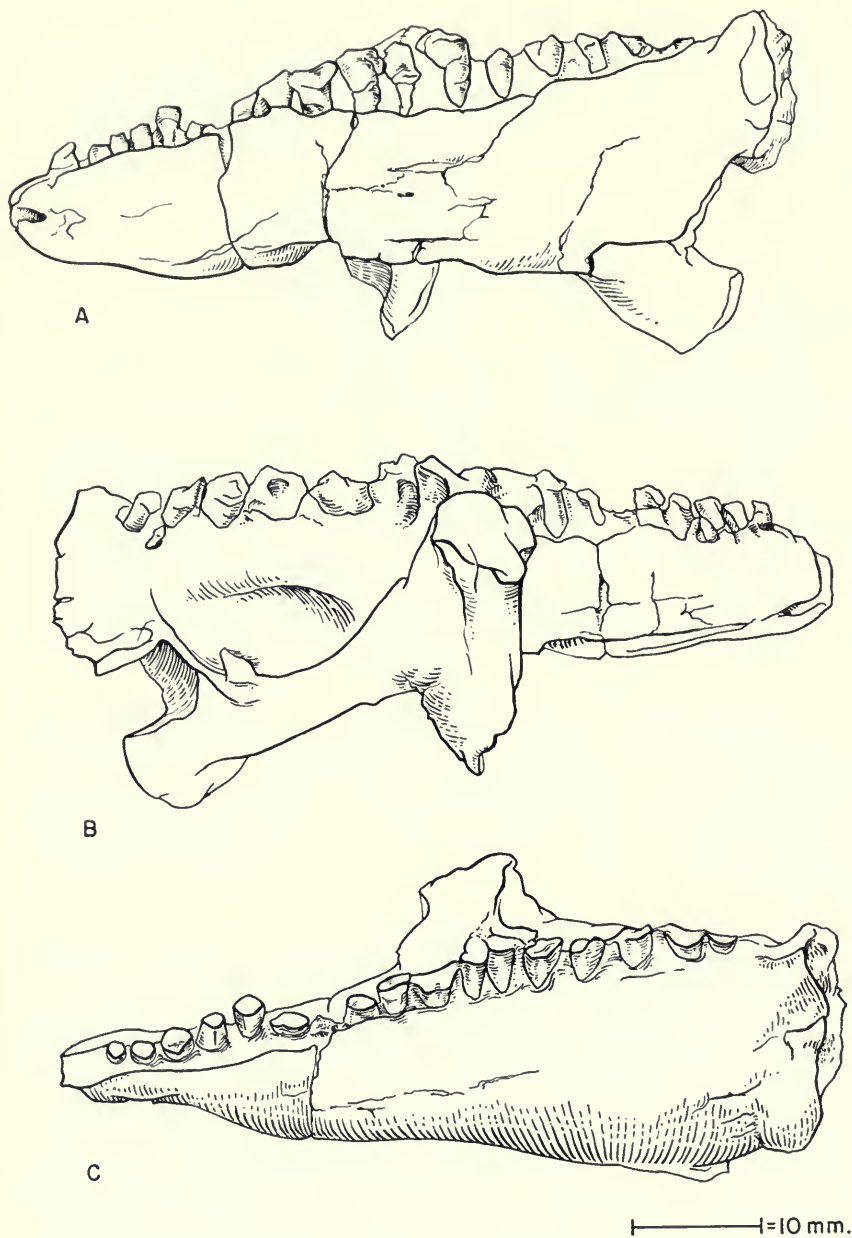
FIG. 11. *Tatisaurus oehleri* (gen. et ep. nov.). Jaw viewed from the lateral (A), medial (B) and dorsal (C) surfaces in association with the head of a rib (B). (CUP 2088).

The jaw is biconvex, but the early oblique displacement of the dental series from the midline exaggerates the lateral curvature, while the alveolar border follows the conformation of the median wall, i.e., moderately S-shaped and laterally concave. The outer wall is weakly constricted at the level of the eighth-ninth teeth below which the curvature of the bone becomes sharper. Posteriorly, the curvature is greatly exaggerated and effects a plateau or shelf lateral to the teeth. The apex of curvature appears as a well-defined but low ridge which then becomes confluent with the shelf. The greatest breadth of the "shelf" is about 7.0 mm. and it perhaps indicates the life-presence of a cheek pouch.

The dentary becomes progressively deeper posteriad, but the superior and inferior borders are parallel from the eighth or ninth-thirteenth teeth. The profile of the superior border is sharply elevated behind the tooth row but it is doubtful that it terminated in a coronoid process since the lateral ridge (definitive in all ornithischia possessing the element) is reduced and disappears at the cheek pouch. It is not known whether the postcoronoidal region is as short as in the more advanced ornithischia.

It is difficult to distinguish the tiny foramina for nervous and/or vascular elements which are scattered over the extensively fractured and pitted outer surface. Foramina oppose the fifth and twelfth-fourteenth teeth, and with the exception of the first, penetrate the bone at right angles. A group of at least five foramina lies above the "ridge" at the lateral constriction and the fifth is the largest.

The splenial sheaths the inner wall, but its sutural union with the more posterior jaw elements, if present, cannot be discerned. It covers the anteriormost limit of the large meckelian fenestra and groove which extends to the predentary.

Like the saurischian dinosaurs, the dentigerous border is higher externally, but has a sigmoid configuration. The dentary holds 18 thecodont teeth which become larger posteriorly and are arranged in a uniformly overlapping series. Anteriorly, the dentary-predentary junction is edentulous. The functional teeth are worn and lack crowns. Unworn replacement teeth (five) lie on the inner surface.

The dentition exhibits a slight degree of heterodonty. The roots are generally subcircular or slightly constricted lateromedially, but may manifest an inner swelling suggestive of a triangular cross section. The crown-root junction of the smaller anterior teeth is variably constricted or expansive.

The crowns of the functional teeth are low, rather symetrically triangular with gently curved or evenly bevelled, smooth polished surfaces. The trenchant edges of the replacement teeth are coarsely denticulated, but unlike most ornithischians, the lateromedial surfaces are not fluted. The anterior edge is the steeper; the apical denticle is pointed slightly backward and bordered by three-four marginal denticles (some with accessory cusps). An anterior replacement tooth appears adenticulate, perhaps due to incipient wear since the mature teeth are small. The crown-root junctions are frequently swollen, probably in response to wear but none of the replacement teeth have definitive cingula.

TABLE 18.—MEASUREMENTS OF THE JAW OF
TATISAURUS OEHLERI (in mm.)

	height	breadth
Estimated length of the jaw (postcoronoid=one-third total length).. 78.6		
Length of the alveolar border..................... 52.4		
Anterior end of the dentary...............................	4.0	3.6
Level of: 8th–9th tooth.....................................	13.0	12.4
constricted lateral wall...........................	....	8.1
13th tooth...	13.4	12.5
18th tooth...	?18.6	11.4
?coronoid process.................................	?15.6	....
Maximum breadth of the cheek pouch (lateromedial).........	....	14.4

Discussion and Relationships.—Since *Tatisaurus* is the temporal equivalent of the earliest known ornithischian derived from upper Triassic Rhaetic Beds in South Africa, it is considered that the relationships of the form can be drawn to the best advantage by a systematic survey of the groups which appear to be related to it.

HYPSILOPHODONTIDAE

The fragmentary *Geranosaurus atavus* Broom (1908; Haughton, 1924) from the Stormberg Series is the earliest representative, but differs importantly from *Tatisaurus* in details of size and large, chisellike teeth. The jaws of *Hypsilophodon foxii* Huxley (1870; Hulke 1882; Nopsca, 1905) and *Thescelosaurus edmontonensis* Sternberg (1940) are fashioned like *Tatisaurus* but taper forward only slightly and decrease markedly in height at the dentary-predentary contact. The coronoid process, indistinct in *Tatisaurus* is prominent in *T. edmontonensis* and blunt in *H. foxii*. While their tooth structures are dissimilar, they are arranged in an overlapping series which arches inward, but the pattern is reversed from the fifth–eighth tooth in

H. foxii.   Similar to the progressive Nodosaurids, however, a splenial element occludes much of the meckelian groove.

IGUANODONTIDAE

The jaw construction, while hypsilophodontid (spout-like predentary-dentary contact and a short symphysis) shows a more prominent coronoid process and a flatter symphysis than *Tatisaurus*.   The meckelian groove passes forward to approximately the same level, but an obtuse prominent ridge marks the outer surface of the jaw of *Iguanodon foxii* Owen (1874) which is correspondingly thickest where it is penetrated by a series of five foramina.   The overlapping tooth row of *Iguanodon* is nevertheless not sigmoid but simply curved to effect the lateral concavity and the teeth are elaborately fluted.

ANKYLOSAURIA

The diagnostic features of *Tatisaurus* were initially interpreted as ankylosaurian.   These forms, however, are strictly upper Cretaceous and of relatively larger proportions.   The recognized Chinese ornithosuchians are Ornithopoda (Young, 1944) and include no ankylosaurs.   The Asian ankylosaurs (from Mongolia) are all referrable to the Nodosauridae.[1]

NODOSAURIDAE

Unlike *Tatisaurus*, the jaws of nodosaurs are generally massive and invested in dermal bone which obscures the elements.   Those of *Edmontonia rugosidens* Gilmore (Russell, 1940) and *E. longiceps* are more or less rectangular.   Except for *Pinacosaurus grangeri* Gilmore (1933) where the dermal bone is reduced, a splenial element covers the meckelian groove (as in the Hypsilophodontiae) and the dentigerous border lies at the posterior two-thirds of the dentary after its

---

[1] Since this paper went to press, Crompton and Charig (1962, Nature, **196,** pp. 1074–1077) have published a preliminary description of a newly discovered ornithischian, *Heterodontosaurus tucki*, from the transitional beds of the Upper Triassic Cave Sandstones, South Africa.   Compared with *Tatisaurus*, the jaw of *H. tucki* has a well-defined coronoid process and the dentition includes an anterior recurved caniniform tooth.   While the general morphology of the cheek teeth (concave crowns) is quite different from that of *Tatisaurus*, the teeth in both specimens importantly lack cingula.   *Heterodontosaurus* appears to be more closely related to the Hypsilophodontidae than *Tatisaurus*, but both seem to show interesting similarities to Upper Cretaceous forms.   This further indicates that the main radiation of Ornithischia probably occurred prior to the Upper Triassic (Huene, 1948).

maximum depth has been attained. The slenderest jaws obtain in the Canadian *Dyoplosaurus acutosquameous* Parks (1924) and in *Anadontosaurus lambei* Sternberg (1928b), however, commensurate with the ornithopods, the decrease in height at the predentary-dentary contact is precipitous rather than gradual. Considerable intergroup variability exists both with respect to (1) the inferior border of the mandible—keeled (*Edmontonia longiceps* Sternberg, 1928a), acute (*Panoplosaurus mirus* Lambe, 1919) or flanged (*Europlocephalus tutus* Lambe Gilmore, 1923)—and (2) the predentary relationships— forms a yoke between the rami (*P. mirus*), merely caps the symphysis (*Edmontonia* spp., *Paleoscincus* sp.), or makes a minimal ingression between the cojoined rami (*P. grangeri*). The inward curvature of the dentary anteriorly is as strong in the cited forms as in *Tatisaurus*, but the incompleteness of preservation vitiates comparison. The coronoid element and postero-lateral ridge when present are pronounced in all but *Ankylosaurus magniventris* Brown (1908) and *Panoplosaurus*, while these features are only suggested in *Tarisaurus*.

The dentigerous border of nodosaurs is rather simply curved and not sigmoid, but the displacement from the midline may be so extreme (*E. longiceps*) that it overhangs the infero-internal border at its midlength. While the number of teeth may vary from 11 (*E. rugosidens*) to 17–21 (*E. tutus*), they occupy a space roughly comparable to that of the plateaued ninth–eighteenth teeth of *Tatisaurus*. The teeth are grossly similar in outline, but they are elaborately fluted as in the ornithopods and bear more or less well-developed median ridges; those of *P. grangeri* alone lack the features of foldings and definitive cingula which are conspicuous in its Asian relative *P. ninghsiensis* Young (1935).

ACANTHOPHOLIDAE

Tatisaurus is favorably compared to this group which shows a sigmoid alveolar border; this feature, while not exclusively ankylosaurian, occurs in the more massive stegosaurs and ceratopsians (*Microceratops gobiensis* Bohlin, 1953), but it delimits the present form from the groups already considered. Two European genera have been selected for comparison, *Acanthopholis horridus* Huxley (1867), *Struthiosaurus transylvanicus* Seeley (1881) and *S. austriacus* Nopsca (1929). The nature of the teeth and jaw fragments of *Hylaeosaurus* Owen (1872) preclude any affinity to *Tatisaurus*.

Acanthopholis horridus shows a sigmoid alveolar border and the absence of an outer ridge, i.e., no coronoid process, irrespective of

the folded enamel surfaces of its teeth (Nopsca, 1923). To my knowledge, the mandible has never been figured and the original description was largely based on post-cranial materials.

Drawings of the fragments of the mandibular rami and teeth of *Struthiosaurus sp.* show that the alveolar border is sigmoid but that it approaches the extreme mediad displacement observed for the nodosaur *Edmontonia*. Accordingly, the internal wall of the mandible is concave in height while that of *Tatisaurus* is moderately convex, but in length, the convexity of the jaws is quite comparable. The meckelian groove is considerably larger in *Struthiosaurus*, but it terminates anteriorly at approximately the same level. *S. austriacus* apparently has a weak predentary element forming a yoke between the rami, but the preservation of *Tatisaurus* does not permit comparison on this point. While *Struthiosaurus* lacks a coronoid element, the lateral side of the jaw is convex and sharply ridged. The morphology of *Tatisaurus* is, then, somewhat intermediate between it and *Acanthopholis*—the ridge is low and restricted largely to the midlength of the ramus. A series of four large foramina occupy an essentially similar position on the outer wall of *Struthiosaurus* and might have resulted from the coalescence of several smaller perforations. The jaw of *S. trannsylvanicus* is less tapered than *Tatisaurus*.

Similarities in dental architecture, including patterns of wear (Nopsca, 1929, fig. 5) form the greatest point of comparison. The teeth of *S. austriacus* are graded from small to large anteroposteriorly. In early use, the functional teeth first lose their denticulations, and additional impairment produces a low median ridge and reduces the cingulum (*S. trannsylvanicus*) to a cinguloid swelling. The ultimate picture is a symmetrical, compressed crown with adenticulate trenchant edges and a low median rib. It is not known if the teeth were oriented into an overlapping row. In *S. trannsylvanicus*, the dental series numbers at least 20, but only 13 occupy a length commensurate with the total complement (18) of *Tatisaurus*.

Summary.—The specimen is significant in that it represents the third find of ornithischia in the Triassic; *Geranosaurus* of the South African upper Triassic-lower Jurassic was the first recorded and placed into the primitive hypsilophodont family. In *Tatisaurus*, the precoronoid part of the dentary and the relationship of its elements is morphologically like the Jurassic-Cretaceous iguanodonts, particularly *Iguanodon foxii*, rather than the most primitive ornithopods such as *Hypsilophodon* and *Thescelosaurus* where the splenial element masks the forward course of the meckelian groove. It is, moreover,

a good deal more slender than any of the cited forms and tapers more gradually toward the symphysis. The placement of the foramina, however, is entirely comparable to these early appearing ornithopods.

The detailed structure of the jaw differs importantly from the forms cited above; the apparent reduction or complete lack of a coronoid element and the distinctly sigmoid character of the dentigerous border and tooth row resembles most closely the Upper Cretaceous ankylosaur group, particularly the Acanthopholidae. The form of the teeth and the pattern of wear especially is remarkably similar to that of *Struthiosaurus austriacus*. Since, however, this particular character occurs only in this form, it is likely that we are dealing with a particularly conservative rather than a progressive feature and *Struthiosaurus* may therefore retain the traces of its heritage.

Evolutionary Considerations of Tatisaurus

By their expansive premaxillae and armor, it seems feasible to seek the ancestors of the Ornithischia among the Pseudosuchia (Romer, 1956). Yet, no pseudosuchian is known which expresses the ornithischian tetraradiate pelvis, toothless premaxilla or specialized dentition. Huene's suggestion (Young, 1951) that *Platyognathus*, with its polygonal teeth and anterior jaw expansion, might serve as the forerunner is vitiated by the knowledge of its crocodilian-like postcranial skeleton. Nopsca (1923) notes that certain camptosaurs (ex. *Rhabdodon*) have teeth with tapered and elongated roots with feebly polygonal cross sections. This suggests that the iguanodonts, to which *Tatisaurus* appears most closely related on the basis of the precoronoid portion of the jaw, as well as *Platyognathus*, perhaps arose from a generalized sphenosuchid line which was sufficiently plastic to be the predecessor of other evolutionary lineages such as the crocodiles.

When ornithischians first appear in the Upper Triassic, they seem already diversified. The jaw of the South African *Geranosaurus* from the Stormberg Series has a concave upper surface which indicates that the premaxilla was toothed. A toothed anterior jaw in *Tatisaurus* is probably obviated by the narrowness of the bone, but the dentition was specialized to conform to one of the more advanced ornithischian families.

The Triassic materials are heterogeneous, and incorporated both primitive and advanced characters. It is considered that the osteologic affinities of *Tatisaurus* are to these primitive hypsilophodonts, although the dentition is particularized as ankylosaurid, and that it

represents an early offshoot from the line of which *Scelidosaurus* Owen (1861) is the base. So little is known about the pre-Cretaceous evolution of the group that the suite of characters which seem to ally the jaw with the advanced ankylosaurs may really be primitive rather than diagnostic (Romer, 1959).

STRATIGRAPHIC AND PALEOECOLOGIC CONSIDERATIONS

Continental Triassic beds are widespread in northern China, but occur less well developed in the south where the facies are chiefly marine. Depositional basins in southwest Sinkiang, southeast and southwest Shansi and in Yunnan—the Lufeng Basin—have yielded vertebrate fossils, but the temporal sequence of these Triassic sediments is discontinuous. In order to determine the age of these beds more precisely, Young (1946) compared the vertebrate assemblages from these localities to other faunas in the world during the Triassic and noted their relative developments. Preliminary to a consideration of the fauna from Lufeng which is rather homogeneous in all the four fossiliferous horizons, it may be useful to visualize a chart comparing the Triassic continental stratigraphic divisions pertinent to the following discussion based upon the work of Young, Huene (1940) and Reeside *et al* (1957). The physical character of the rocks is discussed in this section, but the vertebrates have proven to be the more sensitive indices of age.

Lower Triassic.—In Sinkiang (Chitai), Lower Triassic sediments are well developed by the Tunghunshan and Shoufangkou Series. The older has yielded three genera which appear in the South African Lower Triassic Lystrosaurus Zone. Although *Lystrosaurus* and *Dicynodon* are the principal anomodonts of the South African Karroo as well, the Chinese area is relatively impoverished in terms of diversity.

<div align="center">

No. of species

Genera	S. Africa	Sinkiang
Dicyndon	3	1 (Young, 1939a)
Chasmatosaurus	1	1 (Young, 1936)
Lystrosaurus	19	1 (Yuan and Young, 1934)

</div>

At the type section in Sinkiang, taken at Fuyuan, the Triassic lies conformably on the Upper Permian; the Tunghunshan fauna includes a fragmentary specimen of a probable eosuchian, *Santaisaurus*

yuani Koh (1940) which is apparently related (Romer, 1956) to the Paliguanidae from the Karroo, Cistacephalus Zone. An additional eosuchian fragment (Efremov, cited by Huene, 1940) has also been described from the Upper Permian Rhophalodon Horizon (Zone 1) of Russia. The anomodont character of the Chinese assemblage and the diagnostic genus *Lystrosaurus* are, nevertheless, strong arguments for a lower Triassic age. The genus is also recognized from the Triassic Panchet Beds of India and from the *Capitosaurus* Level (Zone VI) in Russia. Eosuchians are known as well from the Karroo *Lystrosaurus* Zone.

Middle Triassic.—Three determinable genera have been recorded from the Shansi Beds: *Chasmatosaurus* and *Lystrosaurus* (Young, 1958) from the lower levels (Lutzeyu, Wuhsiang) and *Sinokannemeyeria pearsoni* Young (1937)—osteologically very similar to *Kannemeyeria spp.* from the Karroo Upper Beaufort *Cynognathus* Zone —in the middle level. The *Cynognathus* Zone has variously been regarded as Lower Triassic (Watson, 1942), Middle Triassic (Huene, 1940), or Upper Triassic (Broom, 1932). In Shansi, as in Sinkiang, the Permian and Triassic sediments are entirely conformable and relatively unfossiliferous, but Young (1946) reasoned that owing to the high level at which *Sinokannemeyeria* was found and since the horizon is apparently overlain elsewhere by a coal-bearing series of Rhaetic age, the beds were deposited not earlier than the uppermost part of the Middle Triassic and not later than the lowermost part of the Upper Triassic. The finds of *Chasmatosaurus* and *Lystrosaurus* connect the Lower-Middle (Chitai) and Middle (Wuhsiang) Triassic faunas in China.

Upper Triassic.—In Sinkiang, the Upper Triassic is questionably developed as the Kankou Series, and in Shansi the *Sinokannemeyeria* Beds have been divided between the upper part of the Middle Triassic and the lower part of the Upper Triassic. Upper Triassic–Lower Jurassic vertebrate-bearing beds are represented in a structural basin in Lufeng, Yunnan, where the age determinations were similarly based upon the character of the representative vertebrates.

The sediments everywhere appear to have undergone typical red bed development: (1) alternating red sandstone and shales—Tunghunshan Series, Sinkiang; (2) dark red shales, clays and sandstones for the Lower Triassic and green sandstones with red sandy clays for the Upper Triassic-Shansi. The character of the Lower Lufeng Series is entirely like the Upper Triassic beds in Shansi. While physical correspondence alone is inconclusive evidence of contemporaneity

since the vertebrates are individually exclusive, it may nevertheless demonstrate somewhat equivalent conditions of deposition.

The predominately silty deposits of the Upper Triassic Moenkopi and Chinle Formations of North America are fine textured like the fossiliferous clays, shales and sandstones of the Lower Lufeng Series; but otherwise, they feature lenticular and conglomeratic members, etc.—particularly evident in the Chinle, lower Red Member—and
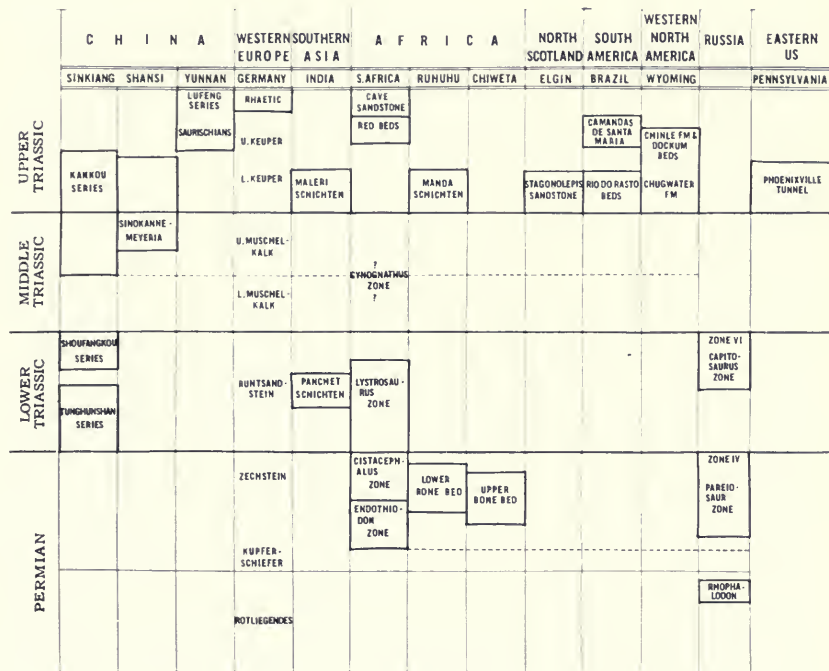

	CHINA			WESTERN EUROPE	SOUTHERN ASIA	AFRICA			NORTH SCOTLAND	SOUTH AMERICA	WESTERN NORTH AMERICA	RUSSIA	EASTERN US
	SINKIANG	SHANSI	YUNNAN	GERMANY	INDIA	S.AFRICA	RUHUHU	CHIWETA	ELGIN	BRAZIL	WYOMING		PENNSYLVANIA
UPPER TRIASSIC	KANKOU SERIES		LUFENG SERIES / SAURISCHIANS	RHAETIC / U.KEUPER / L.KEUPER	MALERI SCHICHTEN	CAVE SANDSTONE / RED BEDS	MANDA SCHICHTEN		STAGONOLEPIS SANDSTONE	CAMANDAS DE SANTA MARIA / RIO DO RASTO BEDS	CHINLE FM & DOCKUM BEDS / CHUGWATER FM		PHOENIXVILLE TUNNEL
MIDDLE TRIASSIC		SINOKANNE-MEYERIA		U.MUSCHEL-KALK / L.MUSCHEL-KALK		CYNOGNATHUS ZONE							
LOWER TRIASSIC	SHOUFANGKOU SERIES / TUNGHUNSHAN SERIES			BUNTSAND-STEIN	PANCHET SCHICHTEN	LYSTROSAURUS ZONE						ZONE VI CAPITOSAURUS ZONE	
PERMIAN				ZECHSTEIN / KUPFER-SCHIEFER / ROTLIEGENDES		CISTACEPHALUS ZONE / ENDOTHIODON ZONE	LOWER BONE BED	UPPER BONE BED				ZONE IV PAREIOSAUR ZONE / RHOPHALODON	

FIG. 12. A chart showing the world distribution of vertebrate bearing horizons during the late Paleozoic and early Mesozoic comparable in time to the Chinese section.

the gypsiferous and ripple marked, cross-bedded sands wanting in the Lower Lufeng Series (Akers *et al*, 1958). The Triassic-Jurassic Kayenta Formation, from which Lewis secured a *Tritylodon*-like reptile (Reeside *et al*, 1957), is typically silty, grading to sandstone to the south-east; the sediments from southwest Utah and that part of northern Arizona demonstrate a reddish siltstone and mudstones with ripple marks and mudstone pellets characteristic of shallow

water deposition which are somewhat grossly similar to the Upper Lufeng Series, but the beds at Lufeng become somewhat more cal- careous toward the top of the section.

The German Upper Keuper, from which sauropods comparable to those at Lufeng have been found, has been characterized as a lagoonal, saliferous formation containing variegated marls, anhy- drates and plant bearing sandstones and porous dolomitic limestones (Gignoux, 1955). To the east in Upper Silesia and Poland, unioid- bearing fresh water limestones occur which perhaps are attributable to a facies change concomitant with isolation from the Alpine Sea. While marly layers are developed much more extensively elsewhere than in Lufeng during the Triassic, some poorly preserved plant re- mains have been found (Chang, 1947), but it is doubtful that these are Equisitales like those from the German Keuper (Gignoux, 1955). Although the sediments of the Lufeng Series were deposited under terrestrial conditions in an area isolated from the Triassic Sea enter- ing Yunnan from the south, unioid-bearing marl-like rocks do occur in the Upper Series.

In Tanganyika (German E. Africa), the Manda-Schichten upper bone beds, K8 (Krenkel, 1939), consist of rose feldspathic sandstone and marl, and iron containing calcareous concretions. A prosauro- pod, *Thecodontosaurus*, comparable with the Lufeng *Yunnanosaurus* is derived from these strata which are, as in Lufeng, disconformably separated from the lower bone beds (K6) by a sandstone. The sec- tions are, however, not entirely comparable in detail. The mineral- ogy of the Lufeng sediments is unknown, but iron-bearing rocks with calcareous concretions are common to both. The lower bone beds contain *Dicynodon* species like the lower Triassic Sinkiang sediments.

Perhaps the depositional history of the upper Triassic Red Beds of the South African Stormberg Series parallels that of the Lufeng section most closely. These consist of well-layered friable, red violet clay marls penetrated by carbonate and red and green sandstones. In many places, silicified woody stems of over ½ m. thick are found, and their presence has been taken to indicate that moist conditions prevailed, or even an alteration of rainy periods (Huene, 1925b). Haughton (1924) has considered a semi-arid climate for this time, since evaporites such as salt and gypsum are absent. While the sedi- ments are largely bedded, many red marl complexes are discordant denoting active periodic erosion. Huene believes that the fine-tex- tured marls represent lagoonal environments from which fish and crustaceans have been collected, while the coarser sediments resulted

from flooding. The overlying Cave Sandstone (Triassic–Jurassic) purported to be aeolian in origin, indicate that there was a slow increase in aridity, concomitant with which the residual lagoons and pools with their faunas became covered over with sand derived from the desiccated uplands to the south. Organic remains are found in the lowest levels. The evolution of the faunas progressed from large saurischians (*Plateosaurus*, etc.) and smaller and lightly built forms in the red beds to smaller and fewer saurischians, an ornithischian and the more primitive crocodilian-like creatures in the Cave Sandstones. A degree of faunal overlap does occur nevertheless, due perhaps to the passing back and forth from the marshes to the highlands at certain times of the year (Huene, 1925b).

The detail to which the regularity of the bedding corresponds to that in Lufeng cannot be determined from the descriptions of the section in the literature. Earlier it was noted that the Lower Series is highly variegated perhaps due to the inclusion of plant remains which would have had the effect of differentially reducing the iron contained in the rocks. Rather moist conditions would certainly have catalyzed the process and from the scattered nature of the fossil record and the alternating sequence of lithologies, it might be concluded that the basin was crossed by streams of varying competencies and that even periodic flooding occurred. It is rare that completely articulated skeletons were found; rather, the bones occur predominately as scattered nodular elements indicating transport rather than scavenger action—the epiphyseal regions of the long bones are intact and have not been gnawed. In his excellent survey of red bed development, van Houton (1948) states that nodules of concretionary iron oxide and calcium carbonate may be formed about fossil bones during or shortly after deposition. In section, only some of the smaller bones were impregnated with red color throughout. His thesis is that red bed formation is optimum where environmental conditions lie between the extremes of moderate rainfall and semi-aridity under relatively high temperatures and that rapidity of deposition is most favorable for the preservation of color in detrital sediments from original red bed source areas. The uppermost beds of the Lufeng Series and the dull-purplish beds of the Lower Lufeng Series contain evaporites and calcareous concretions respectively which are attributed by van Houten to ground water action in warm, humid climates marked by intense dry seasons. Intermittent aridity might have produced the relatively thin sandstone dividing the first and second fossiliferous

horizons and that serving as a basal marker for the Upper Series, although these are described as merely massive and otherwise fea- tureless except for rock fragments in the former (fluvial?).

Toward the top of the Lower Lufeng section, Young's records show an increase in the number of individuals at his principal col- lecting sites: Shawan, 24; Tachung, 30; Heilungtan, 45. These fig- ures, however, probably lack ecologic significance and reflect rather a sampling bias.

It is evident that a true estimate of the living population cannot be inferred from the fossilized accumulations. Of the nearly 100 indi- viduals reported, more than 85 per cent are the larger prosauropods. The concentration of fossils and their extreme degree of disarticula- tion makes it probable that the majority were upland forms carried in during periods of flooding. The poor record of Triassic ornithis- chians has been explained on the same basis (Huene, 1950). The few rare articulated skeletons, in addition to the coprolitic nature of some materials, may infer little transport and imply that some of the forms may have moved back and forth onto the flood plain proper. Pseudosuchians, i.e., *Platyognathus sp.* and the prosauropod, *Lufen- gosaurus*, may be cited as animals which possibly ascribed to this latter category.

The fish and crustacean yielding variegated beds of the Upper Lufeng Series signify a change in the environmental situation which has been considered in the initial sections of this paper. A facies shift is indicated by the fauna peculiar to pond environments. The Shihmen Sandstone (Jura–Cretaceous) forming the uppermost levels of the Lufeng Section, but disconformable with it, differs from the Cave Sandstone in being current-crossbedded. Moreover, it con- tains a basal lenticular pebble to massive boulder conglomerate; the sandstone demonstrates shaley intercalations toward the top (Bien, 1941). The calcareous features of the fossiliferous zones and their faunas (turtles, pelecypods, etc.) are probably good indicators of shallow water environments with the development of temporary lakes fed by streams bearing dissolved calcium salts which at times pro- duce the strongly indurated limestone bands of the upper middle part.

Most of the Lower Lufeng vertebrates show close affinities to the Stormberg fauna and there is the same general trend of faunal evolu- tion with the increasing youthfulness of the sediments. In view of the apparent flood plain environment interpreted for these sediments, however, and the sharp faunal break above which no vertebrates (save fish and turtles) appear, the progression may be entirely arti-

ficial. The paucity of articulated skeletons is, nevertheless, evidence that some upland forms did frequent the basin lands.

Studies of parallel patterns of sedimentation in geographically distant sites have little dependency *per se* as determiners of the time element. The most definitive proof of contemporaneity is faunal identity, and reference to the constitution of the assemblages was unavoidable in the paragraphs above. By means of the rocks, the Lower Lufeng Series at best can be determined to be Upper Triassic while those of the Upper Series can only be said to transgress the Triassic-Jurassic boundary.

ZOOGEOGRAPHICAL AND PALEOGEOGRAPHIC CONSIDERATIONS

Young's contributions (1946, 1951) established the basis for the interpretations accorded the new fossil evidences. The taxonomic work seemed to indicate that there was either a particular correspondence to Triassic-Jurassic forms, especially in South Africa, or that the larger taxonomic units (coelurosaurs, carnosaurs, etc.) were represented in like-proportions in faunas when the direct comparison of forms was not feasible.

His earlier paleogeographic assessment was reinforced only by the generic identity of the Lower (Sinkiang) and Middle (Shansi) Triassic assemblages—about 60 per cent of the forms—rather than by the Upper Triassic Lufeng fauna where only one-ninth of the elements (9 genera, 14 species) were similarly involved—notably by the single form, *Gyposaurus*. The problem of interpreting close faunal ties for the Lufeng assemblage upon such slight evidence was, however, made less precarious by the common paucity of the pseudosuchia and carnosaurs. The exceptional therapsid *Bienotherium* is cited as an equivalent of the South African and North American *Tritylodon* and tritylodon-like form respectively.

Table 19, a compilation of comparative forms, serves as a resume pointing out other refractions noted by Young in his considerations of the faunal relationships and those noted by the findings reported in this paper.

THECODONTS

Pseudosuchia.—With the exception of two North American forms occurring where the Triassic-Jurassic stratigraphic boundaries are in

TABLE 19.—ZOOGEOGRAPHY OF THE LUFENG NON-THERAPSIDS

Lufeng	South Africa	North America	Europe	Scotland
Thecodonts				
Platyognathus hsui	Sphenosuchus	Protosuchus*		Ornithosuchus*
Dibothrosuchus elaphros	Parringtonia*	Hesperosuchus		
Strigosuchus licinus				
CUP 2084				
		?Typothorax		
		?Episcopothorax		
Parasuchia				
Pachysuchus imperfecta		Rutiodon	Mystriosuchus	
Coelurosauria				
Lukousaurus yini	Gryponyx*	Ammosaurus*		Saltopus*
		Podokesaurus*		
CUP 2089		Coelophysis		
CUP 2091			Aripes	
Carnosauria				
Sinosaurus triassicus	Orosaurus**		Teratosaurus	
Prosauropoda				
Lufengosaurus hueni				
Lufengosaurus magnus			Plateosaurus	
Yunnanosaurus huangi				
Yunnanosaurus robustus	Massospondylus			
Gyposaurus sinensis	Gyposaurus			
Ornithischia				
Tatisaurus oehleri	Geranosaurus**		Iguanodon	

* Indirect comparison
** Faunal equivalent

doubt, pseudosuchia are limited to Upper Triassic sediments. The Lufeng fauna as described by Young included one barely determinable animal, *Platyognathus hsui* from Huangchiatien (second fossiliferous horizon). The present collection has yielded a diverse array of forms derived essentially from the same horizon (Ta Ti and Hei Koa Peng) which have been compared to South African and North American types; none has yet been found above or below the sediments just bordering the Upper Series. The levels at which related thecodonts are found have been tabulated in Table 20. All but *Dibothrosuchus* and CUP 2084 resemble elements in the Stormberg Series.

Dibothrosuchus is similar to *Ornithosuchus* in the shape of its skull, but resembles *Hesperosuchus* and *Parringtonia* in most other respects. The jaw of *Strigosuchus* is hesperosuchid-like. The forms, then, cannot be older than the lowest part of the Upper Triassic, but their upper limit in time is ill-defined as Upper Triassic–Lower Jurassic.

The sphenosuchid-like appearance of the skull of *Platyognathus* indicates an age not later than the Upper Triassic, but the complete investiture of the body by scutes in primitive crocodilian fashion is like the North American *Protosuchus* (Orange Red Sand, Moenhave Formation, Dinosaur Canyon sandstone member) which, like *Hesperosuchus*, enjoys a questionable stratigraphic position. Reeside *et al* (1957) considers the Moenhave to be Upper Triassic; Harshbarger *et al* (1958) considers the orange red sand the lower Member of the Moenhave (the basal formation of the Glen Canyon Group) not younger than the Middle Jurassic (Carmel Formation), and interprets it like Colbert and Mook (1951) as both Triassic and Lower Jurassic. The decision for *Platyognathus* depends on whether emphasis is placed upon the more conservative general character of the skull or upon the suite of apparently independently evolved, highly adaptive characters of the postcranial skeleton.

Pelvic girdle and femoral fragments of the indeterminate pseudosuchian CUP 2984 bear some resemblance to *Typothorax* from the Texas Dockum Group and the New Mexican Chinle Formation. The Stagonolepidae as a whole are of Middle Triassic age in Europe and of Upper Triassic age in North America.

Parasuchia (Phytosaurs).—Incomplete skull and jaw fragments of *Pachysuchus imperfecta* Young (1951) derive from the upper fossiliferous horizons of the Lower Lufeng Series. Phytosaurs are major components of European and North American assemblages and appear to be an exclusive development of the Triassic. In America,

TABLE 20.—FAMILIAL ASSOCIATIONS OF THE LUFENG THECODONTS

Family	Time	Geographic Position	Horizon	Genus
Ornithosuchidae	Lower-Middle Triassic	S. America	Upper Rio do Raso	*Procerosuchus* *Prestosuchus* *Rauisuchus* *Rhadinosuchus*
	Lowest part of Upper Triassic	N. Scotland	Stagonolepis SS.	*Erpetosuchus* *Ornithosuchus*
		Tanganyika	Manda Schichten, upper Bone Bed	*Parringtonia* *Stagonosuchus*
	Upper Triassic	India	Maleri-Schichten	2 ?*Pseudosuchia*
		S. America	Camandas de Santa Maria	*Ceratosaurus*
		E. Asia	Lower Lufeng Series	*Dibothrosuchus* *Strigosuchus*
	Upper Triassic–Lower Jurassic	N. America	Chinle-Petrified Forest Member	*Hesperosuchus*
Sphenosuchidae	Upper Triassic	S. Africa	Red Beds-Karroo Fm.	*Sphenosuchus*
Platyognathideae	Upper Triassic	E. Asia	Lower Lufeng Series	*Platyognathus*
Incerta sedis	Upper Triassic	E. Asia	Lower Lufeng Series	CUP 2084

they are known from the Dockum, Chugwater and Cumnock Formations. The Indian genus *Brachysuchus* is reported from the Maleri Schichten with two other poorly known forms, and perhaps from North America as well; it emphasizes the paucity of like forms from Asia. That the South African group is devoid of phytosaurs is of particular interest to this discussion. *Pachysuchus* has been compared to *Mystriosuchus planirostris* (Germany) and to *Rutiodon carolinensis* (North America).

SAURISCHIANS

The saurischian remains are of limited time diagnostic value. Prosauropods, known mostly from isolated fragments, are the dominant forms and appear to be typically Upper Triassic forms; *Lufensaurus hueni* is the most complete specimen. "Structurally, the position of the skull to the vertebral column, the primitive features of the teeth, presence of abdominal ribs, the absence of the foot-like expansion of the pubis and the relative length of the femur, exceeding that of the tibia and fibula and five digits of the hand and foot are all primitive characters which are rarely or never found in the Saurischia of later age (Young, 1939a)."

Coelurosaurs.—These are known from the second fossiliferous horizon of the Lower Lufeng Series. They are so imperfectly realized that it was considered expedient to refer them (*Lukousaurus*, CUP 2089, 2090, 2091) to the general Upper Triassic family, the Podokesauridae. Only *Lukousaurus* is known by cranial materials.

Lukousaurus and other Podokesauridae occur in Europe and North America in the Upper Triassic sediments. CUP 2089 has been related to the North American *Coelophysis*. The only comparison afforded the femur CUP 2091 was to an Australian Upper Cretaceous form. No coelurosaurs are recognized from the African assemblage, but Young listed *Gryponyx* as the faunal equivalent of *Lukousaurus*.

Carnosaurs.—Remains of the sole Lufeng carnosaur, *Sinosaurus triassicus* are ubiquitous in the saurischian facies, and Young (1946) compared it to the German *Teratosaurus suevicus*. It has also been cited as the faunal counterpart of the South African Upper Triassic *Orosaurus;* while these are not closely compared, it is striking that both assemblages are characterized by individual specimens of the Teratosauridae. Elsewhere, the family ranges from the Middle-Upper Triassic of Europe (3 genera) and North America (1 genus).

The jaw (CUP 2097) tentatively identified as that of *S. triassicus* may actually represent a second carnosaur.

Among the carnosaurs, the range of generically identical forms is very broad. An advanced megalosaurid, *Antrodemus*, has been tentatively identified from east Asia, North America and east Africa. Similarly, the North American tyrannosaurid, *Aublysodon*, is reported from east Asia. It may be considered that carnosaurs, therefore, as indicators of faunal relationships, need relate only to familial associations. The contribution of *Sinosaurus* to the faunal complex is in this way directly comparable to that of the South African genus.

Prosauropods.—Saurischia comparable to the Lufeng prosauropods occur in Triassic beds world-wide in distribution.

Age	Geographic position	Site
Lower–Upper Triassic	North America	Phoenixville Tunnel, Pa.
Upper Triassic	Tanganyika	Manda-Schichten, upper bone bed.
	India	Maleri-Schichten.
	Germany	Keuper.
	South Africa	Red Beds.
"Rhaetic (?)"	South Africa	Cave Sandstone.

The massive *Lufengosaurus* resembles the Knollenmergel *Plateosaurus fraasianus* of Germany more closely than the correspondent South African species; *Yunnanosaurus spp.* however have been compared to *Massospondylus* of the Red Beds and Cave Sandstones, although the genus is also known from India and east Africa. The referral of the most common and rather completely known animal, *Gypsosaurus sinensis*, to the South African genus from the Cave Sandstone (*G. capensis*) is particularly significant.

ORNITHISCHIA

The new find of *Tatisaurus oehleri* in the second fossiliferous horizon evidencing both primitive and relatively advanced characters is particularly pertinent both to the considerations of the time element, and to the faunal relationships. The geographic distribution of the first recorded ornithischians is scattered discontinuously—in South Africa and North America. Although incomplete, *Tatisaurus* is more favorably compared to younger European forms which are not older than Upper Jurassic rather than to *Geranosaurus* but it nevertheless contributes to the Lufeng assemblage in like proportions.

Ornithischians are rare in Upper Triassic sediments. *Geranosaurus* is derived from the Cave Sandstone, South Africa and is Rhaetic in age. The progressive ornithischian characters of *Tatisaurus* which resemble the Upper Cretaceous ankylosaur *Struthiosaurus* have been considered conservative features which are not indicative of a direct lineage. It is interesting that the earliest ornithischians are a heterogeneous group, but are mutually associated with forms of a more or less late Triassic age.

THERIODONTS

Although outside the scope of this paper, it should be mentioned that the Lufeng sediments have yielded mammal-like reptiles, the cynodont *Kunminia minina* Young (1947a) and the ictiodosaur *Bienotherium* Young (1940a). Cynodonts appear generally throughout the Upper Permian to the Upper Middle–Lower Upper Triassic Karroo sediments and their range elsewhere in the world is essentially the same.

Time	South Africa (zone)	Time equivalent strata	Geographic location
Permian	Endothiodon-Cistacephalus Zone	Ruhuhu-Gebiet: lower Bone Bed.	Tanganyika
	Cistacephalus Zone	Chiweta: upper Bone Bed.	Nyassaland
		Pareiosaur Zone, Zone IV	Russia
Upper–Middle Triassic Lower–Upper Triassic		Upper Rio do Rasto	South America
	Cynognathus Zone	Manda-Schichten: upper Bone Bed.	Tanganyika

Kunminia is too poorly known to afford direct comparison with any of the forms representative of the localities cited above; it occurs at Huangchiatien just below the purported Triassic–Jurassic boundary.

Ictidosaurs range into the red beds and Cave Sandstones of the Karroo Upper Triassic to the Jurassic boundary and are known (*Archaeodon*) from the Stormberg Series in southwest Africa and from the Kayenta Formation of Arizona (Averett *er al*, 1955). The group is evidenced in Jurassic sediments, *Trityodon* being closely compared to *Bienotherium*.

Oehler's collection of therapsids, now under study by Drs. E. C. Olson and J. Hopson from the University of Chicago, have yielded a wealth of new *Bienotherium* materials which demonstrate a more complex structure than hitherto recognized for the genus.   The form ranges throughout the Lower Lufeng Series.[1]

SUMMARY

The fauna of the Lower Lufeng Series is best described as cosmopolitan.   Relative to the standard section of the Triassic (Germany), the sediments should probably be classified Upper Triassic, equivalent in time to the Upper Keuper, Knollenmergel facies.   Support for this correlation is based upon the generalized structure of the saurischian fauna, but there are many instances of forms morphologically related to animals derived from Rhaetic, Jurassic and even younger beds.   For example, *Platyognathus* is similar to *Protosuchus* (Upper Triassic–Lower Jurassic) and to *Sphenosuchus* (Upper Triassic Red Beds, Stormberg Series).   Prosauropods are typically Upper Triassic forms, yet it is possible to infer a somewhat younger age from the numerous examples of *Gyposaurus* (and the theriodonts). In reference to the North American section, a tritylodont has been found in the uppermost level of the Kayenta Formation bearing likeness to *Bienotherium* and to *Tritylodon* from the Red Beds and Cave Sandstones (?Rhaetic) of South Africa.   The opinion has been expressed (Reeside, *et al*, 1957) that the Kayenta may be Upper Triassic in time, but the dinosaur *Megalosaurus weatherilli*, more comparable to the Middle-Late Jurassic megalosaurids of Europe than to the Late Triassic forms in its proportions, derives from a lower level than *Tritylodon*.

The theriodont evidence speaks for a Rhaetic or Lower Jurassic age at the earliest.   The ictidosaurs, while a highly advanced specialized group may also be a relatively small and possibly conservative aggregation among themselves and one might not expect them to be a particularly definitive index of stratigraphic contemporaneity. *Bienotherium* has been compared (Watson, 1942) to the Upper– Middle Triassic cynodont *Diademodon* (*Compsognathus* Zone).   For the present, it is probably safer to place the greatest reliance upon the more profuse suarian elements of the Lufeng fauna and to de-

[1] Patterson and Olson (1961, Internat. Evol. Mammals, Kon. Vlaamse Acad. Wetensch. Lett. Sch. Kunsten Belgie, Brussels, pp. 129–191) have recently published a description of a triconodontid mammal from Hei Koa Peng of Upper Triassic age.

emphasize the importance of the mammal-like reptiles where stratigraphic problems are the principal concern.

The relationships of the Lufeng non-therapsids is predominately to European, South African and North American forms. The Pseudosuchia relate directly to North American and South African elements. Coelurosaurs, with which the Lufeng fauna now appears to be richly endowed, have no South African components. There is, however, an essential correspondence in the contribution of carnosaurs, prosauropods, and ornithischians to the faunas of Lufeng and South Africa during this same approximate geologic time, notwithstanding the more specific relations of some of the prosauropods to European forms.

The non-therapsids have an old world flavor despite the apparent overlap in some groups to the North American elements. Importantly, the prosauropod contribution is large and for the most part lacking in Triassic new world assemblages (other than *Paleosaurus*). Instances in which the vertebrates as a group or as individuals fail to correspond to South African forms are rather exceptional. Young's interpretation of the cosmopolitanism of the fauna and their essentially African flavor is supported by the therapsid evidence and by the important discovery of the early ornithischian.

Equal emphasis has not been accorded to all parts of the Lufeng Basin where the fauna is known almost entirely from the Lower Series. However, even here, the general mode of collecting, i.e., from surface nodules, by two individuals with different habits has yielded different results. The present collection has brought to light several new forms and it is most probable that the diversity of life of the Lufeng Basin is greater than now known. Re-exploration of the beds is decidedly warranted and additional fossil evidence will clarify the existing uncertainties as to the time factor.

REFERENCES

AKERS, J. P., M. E. COOLEY and C. A. REPENNING
  1958. Moenkopi and Chinle formations of Black Mesa and adjacent areas. *In* New Mex. Geol. Soc. Guidebook for 9th Field Conf., *edited by* R. Y. Anderson and J. W. Harshberger.

AVERITT, P. J., J. S. DETTERMAN, J. W. HARSHBERGER, C. A. REPENNING and R. F. WILSON
  1955. Revisions in Corrleation and Nomenclature of Triassic and Jurassic Formations in Southwestern Utah and Northern Arizona. Bull. Amer. Ass. Petrol. Geol., **39**, pp. 2515–2524.

BIEN, M. N.
  1941. "Red Beds" of Yunnan. Geol Soc. China **21**, pp. 159–198.

BOHLIN, B.
  1953. Fossil Reptiles from Mongolia and Kansu. Sino-Swedish Expedition Publication 37, **6**, pp. 1–113.

BROOM, R.
  1904. On a new Crocodilian Genus (*Notochampsa*) from the upper Stormberg beds of South Africa. Geol. Mag., **1**, pp. 582–584.
  1908. On the Dinosaurs of the Stormberg, South Africa. Ann. S. Afr. Mus., **12**, pp. 291–308.
  1927. On *Sphenosuches,* and the Origin of the Crocodiles. Proc Zool. Soc. London, **1927**, pp. 395–370.
  1932. On some South African Pseudosuchians. Ann. Natal. Mus., **7,**, pp. 55–59.

BROWN, B.
  1908. The Ankylosauridae, the new family of Armored Dinosaurs from the upper Cretaceous. Bull. Amer. Mus. nat .Hist., **24**, pp. 187–201.

BYSTROW, A. P.
  1947. Hydrophilous and Xerophilous Labyrinthodonts. Acta Zool., **28**, pp. 137–164.

CHANG, C. H.
  1947. The Triassic Paleogeography and Stratigraphy of Yunnan. Bull. Geol. Soc. China, **27**, pp. 193–204.

COLBERT, E. H.
  1952. A pseudosuchian reptile from Arizona. Bull. Amer. Mus. Nat. Hist., **99**, pp. 565–592.

COLBERT, E. H. and C. C. MOOK
  1951. The Ancestral Crocodilian *Protosuchus.* Bull. Amer. Mus. Nat. Hist., **97**, pp. 147–182.

COPE, E. D.
  1887. A contribution to the History of the Vertebrata of the Trias of North America. Proc. Amer. Phil. Soc. **24**, pp. 209–228.

GIGNOUX, M.
  1955. Stratigraphic Geology. (English translation from 4th ed., 1950, by G. G. Woodford) San Francisco.

GILMORE, C. W.
  1923. A new species of *Corythosaurus* with notes on other Belly River Dinosauria. Canad. Field Nat.,**37,** pp. 47–52.
  1933. Two new Dinosaurian reptiles from Mongolia with notes on some fragmentary specimens. Amer. Mus. Nov. no. 679.

HARSHBERGER, J. W., C. A. REPENNING and J. H. IRWIN.
  1958. Stratigraphy of the uppermost Triassic and the Jurassic rocks of the Navajo country. *In* New Mex. Geol. Soc Guidebook for 9th Field Conf., *edited by* R. Y. Anderson and J. W. Harshberger., pp. 98–114.

HAUGHTON, S. H.
  1915. Investigations in South African Fossil Reptiles and Amphibians. Ann. S. Afr. Mus., **12,** part 9, pp. 98–105.
  1924. Fauna and Stratigraphy of the Stormberg Series. Ann. S. Afr. Mus., **12,** pp. 323–437.

HULKE, J. W.
  1882. An attempt at a complete osteology of *Hypsilophodon foxii:* a British Wealdon Dinosaur. Trans. Roy. Soc. London, **173,** pp. 1035–1062.

HUXLEY, T. H.
  1867. On *Acanthopholis horridus,* a new reptile from the chalk-marl. Geol. Mag. **4,** pp. 65–67.
  1870. On *Hypsilophodon foxii;* a new dinosaurian from the Wealdon of the Isle of Wight. Quart. Journ. Geol. Soc., **26,** pp. 3–12.

KOH, T.
  1940. *Santaisaurus yuani* gen. et sp. nov., ein neues Reptil aus den unteren Trias von China. Bull. Geol. Soc. China, **20,** pp. 73–92.

KRENKEL, E.
  1939. Geologie der Deutschen Kolonien in Afrika. Berlin.

LAMBE, L. M.
  1919. Description of a new genus and species (*Panoplosaurus mirus*) of an armored dinosaur from the Belly River Beds of Alberta. Trans. Roy. Soc. Canada, sect. IV, ser. III, pp. 39–50.

LEIDY, J.
  1960. Extinct vertebrata from the Judith River and great lignite formations of Nebraska. Trans. Amer. Phil. Soc., **11,** pp. 139–154.

MISCH, P.
  1945. Remarks on the Tectonic History of Yunnan, with special reference to its relations to the Type of the young orogenic deformation. Bull. Geol. Soc. China., **25,** pp. 47–153.

MOOK, C. C.
  1933. A skull of *Crocodilus clavis* Cope, in the United States National Museum. Amer. Mus. Nov., no. 678, pp. 1–7.

NEWTON, E. T.
  1894. Reptiles from the Elgin Sandstone. Description of two new genera. Phil. Trans. Roy. Soc. London, ser. B, **185,** pp. 573–607.

NOPSCA, F. BARON
  1905. Notes on British Dinosaurs. Part I. *Hypsilophodon*. Geol. Mag. **2**, pp. 203–208.
  1923. Notes on British Dinosaurs. Part VI. *Acanthopholis*. Geol. Mag., **60**, pp. 193–199.
  1929. Dinosaurerreste aus Siebenbürgen. V. Geol. Hung. Tomus I, facs. 4, pp. 1–76.

OWEN, R.
  1861. A monograph of the Fossil Reptilia of the Liassic Formations. Part I. *Scelidosaurus harrisonii*. Palaeontogr. Soc. (Monog.), **1e**, pp. 1–13.
  1872. Suppl. no. IV. to the Monograph on the Fossil Reptilia of the Wealdon Formation. Palaeontogr. Soc. (Monog.),pp. 1–15.
  1874. Suppl. no. V. to the Monograph on the Fossil Reptilia of the Wealdon and Purbeck Formations (*Iguanodon*). Palaeontogr. Soc. (Monog.), pp. 3–16.

PARKS, W. A.
  1924. *Dyoplosaurus acutosquameus*, a new genus and species of Armored dinosaur. Notes on a skeleton of Prosaurolophus maximus. Uni. of Toronto Studies, Geol. Ser., III, **18**, pp. 1–35.

PIVATEAU, J.
  1956. Traite de Paleontologie, **5**, Paris.

PRICE, L. I.
  1946. Sobre Um Novo Pseudosuquio Do Triassico Superior Do Rio Grande Do Sul. Departmento Nacional de Producao Mineral, Divisao Di Geologie Mineralogie. pp. 7–39.

REESIDE, J. B., chairman., et al
  1957. Correlation of the Triassic Formations of North America exclusive of Canada. Bull. Geol. Soc. Amer., **68**, pp. 1451–1541.

ROMER, A. S.
  1955. Vertebrate Paleontology. Chicago
  1956. The Osteology of the Reptiles. Chicago.

RUSSELL, L. S.
  1940. *Edmontonia rugosidens* (Gilmore) an armored dinosaur from the Belly River Series of Alberta. Univ. of Toronto Studies, Geol. Ser., no. 43, pp. 3–28.

SAWIN, H. J.
  1947. The pseudosuchian reptile *Typothorax meadei*. Journ. Paleontol. **21**, pp. 201–238.

SEELEY, H. G.
  1881. The reptile fauna of the Gasau formation preserved in the geological museum of the University of Vienna. Quart. Journ. Geol. Soc., **37**, pp. 620–707.

STERNBERG, C. M.
  1928a. A new armored dinosaur from the Edmonton Formation of Alberta. Trans. Roy. Soc. Canad. (ser. 3), **22**, sec, pp. 93–106.
  1928b. A toothless armored dinosaur from the upper Cretaceous of Alberta Nat. Mus. Canada, Bull. **54**, pp. 28–33.
  1940. *Thescelosaurus edmontonensis*, n. sp., and classification of the Hypsilophodonotidae. Journ. Paleontol., **14**, pp. 481–494.

TALBOT, M.
  1911. *Podokesaurus holyokensis* a new dinosaur from the Triassic of the Connecticut Valley. Amer. Journ. Sci., **31**, pp. 469–479.

VAN HOEPEN, E. C. N.

    1915. Contributions to the knowledge of the reptiles of the Karroo Formation 4, A new pseudosuchian from the Orange Free State. Ann. Transvaal Mus., **5**, pp. 83–87.

VAN HOUTEN, F. B.

    1948. Origin of Red-Banded Early Cenozoic Deposits in Rocky Mountain Region. Bull. Amer. Ass. Petrol. Geol., **32**, pp. 2083–2126.

VON HUENE, F.

    1906. Über die Dinosaurier der Aussereuropäischen Trias. Geol. palaont. Abh., **8**, pp. 19–22.

    1910. Ein primitiver Dinosaurier aus der mittleren Trias von Elgin. Geol. palaont. Abh., **8**, pp. 317–322.

    1914–1915. Beiträge zur Kenntnis und Verteilung der Pseudosuchier. Geol. palaont. Abh., **13**, pp. 1–82.

    1915. On Reptiles of the New Mexican Triassic in the Cope Collection. Bull. Amer. Mus. Nat. Hist., **34**, pp. 485–507.

    1921. Neue Pseudosuchier und Coelurosaurier aus dem Württembergischen Keuper. Acta. Zool., **2**, pp. 329–403.

    1925a. Die Bedeutung der Sphenosuchus-Gruppen für den Ursprung der Krokodile. Z. indukt. Abstamm.-u. VererbLehre, **38**, pp. 307–320

    1925b. Die südafrikanische Karroo-Formation als geologisches und faunistisches Lebensbild. Berlin.

    1932. Die Fossils Reptil-Ordnung Saurischia, ihre Entwicklung und Geschlichte. Leipzig.

    1936. Die Altersbeziehungen der Südamerikanischen Gondwana-Fauna. Physis (Rev. Soc. Argentina Cienc. Nat.), **14**, pp. 289–497.

    1939a. Ein kleiner Pseudosuchier und ein Saurischier aus den ostafrikanischen Mandashichten. Neus. Jb. Miner., Mh., Abt. B., pp. 61–69.

    1939b. Ein grosser Stagonolepide aus der jüngeren Trias Ostafrikas. Neues Jb. Miner., Mh., Beilage-Band Abt. B. **80**, pp. 264–278.

    1940. Die Saurier de Karroo-. Gondwan-, und verwandten Ablagerungen in faunistischer, biologischer, und phylogenetischer Hinsicht. Neues Jb. Miner., Mh., Beilage-Band Abt. B, **83**, pp. 246–437.

    1948. Short Review of the Lower Tetrapods. Roy. Soc. S. Afr. Spec. Publ., Robert Broom Comm. Vol., pp. 65–106.

    1950 Die Entstehung der Ornithischia schon früh in der Trias. Neus. Jb. Geol., **0**, pp. 53–58.

WATSON, D. M. S.

    1942. On Permian and Triassic Tetrapods. Geol. Mag., **79**, pp. 81–116.

WELLES, S. P.

    1954. New Jurassic Dinosaur from the Kayenta Formation of Arizona. Bull. Geol. Soc. Amer., **65**, pp. 591–598.

YOUNG, C. C.

    1935. On a new Nodosaurid from Ninghsia. Palaeont. sinica, (ser. C), fasc. 1, **11**, pp. 1–34.

    1936. On a new *Chasmatosaurus* from Sinkiang. Bull. Geol. Soc. China, **15**, pp. 291–320.

    1937. On the Triassic Dicynodonts from Shansi. Bull. Geol. Soc. China, **17**, pp. 393–412.

    1939a. Preliminary notes on the Lugeng saurischian remains. 40th Anniversary Paper. Nat. Univ. Peking, pp. 111–114.

    1939b. Additional Dicynodontia remains from Sinkiang. Bull. Geol. Soc. China, **19**, pp. 279–315.

1940a. Preliminary note on the Mesozoic mammals of Lufeng, Yunnan, China, Bull. Geol. Soc. China, **20**, pp. 93–111.

1940b. Preliminary note on the Lufeng vertebrate fossils. Bull. Geol. Soc. China, **20**, pp. 235–239.

1941a. *Gyposaurus sinensis* Young (gen. et sp. nov.), a new Prosauropoda from the Red Beds at Lufeng, Yunnan. Bull. Geol. China, **21**, pp. 205–252.

1941b. A complete osteology of *Lufengosaurus hueni* Young (gen. et sp. nov.), from Lufeng, Yunnan, China. Palaeont. sinica, (ser. C), **7**, pp. 1–53.

1942. *Yunnanosaurus huangi* Young (gen. et st. nov.), a new Prosauropoda from the Red Beds at Lufeng, Yunnan. Bull. Geol. Soc. China, **22**, pp. 63–104.

1944. On a supposed new pseudosuchian from Upper Triassic Saurischian-bearing beds of Lufeng, Yunnan, China. Amer. Mus. Nov., no. 1264, pp. 1–4.

1946. The Triassic vertebrate remains of China. Amer. Mus. Nov., no. 1234, pp. 1–14.

1947a. Mammal-like reptiles from Lufeng, Yunnan, China. Proc. Zool. Soc. London, **117**, pp. 537–597.

1947b. On *Lufengosaurus magnus* Young (sp. nov.) and additional finds of Lufengosaurus hueni Young. Palaeont. sinica, **12**, pp. 1–53.

1948a. Further notes on *Gyposaurus sinensis* Young. Bull. Geol. Soc. China, **28**, pp. 91–103.

1948b. On two new Saurischians from Lufeng, Yunnan. Bull. Geol. Soc. China, **29**, pp. 75–90.

1951. The Lufeng saurischian fauna in China. Palaeont. sinica, (ser. C), **13**, pp. 19–96.

1958 On the occurrance of *Chasmatosaurus* from Wuhsiang, Shansi. Vertebrata Palasiatica, **2**, pp. 251–262.

YUAN, P. L. and C. C. YOUNG
    1934. On the occurrance of *Lystrosaurus* in Sinkiang. Bull. Geol. Soc. China, **13**, no. 4, pp. 575–580.