# A PRIMITIVE PARASUCHID (PHYTOSAUR) REPTILE FROM THE UPPER TRIASSIC MALERI FORMATION OF INDIA

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ABSTRACT. Two nearly complete and articulated parasuchian (phytosaur) skeletons, recently discovered from the Upper Triassic Maleri Formation of India, allow a detailed osteological description and restoration of the species *Parasuchus hislopi* Lydekker, 1885. The skull shows almost all of the archaic characters of parasuchians listed by Gregory (1962). The well-preserved braincase permits a reconstruction of the brain from a latex-rubber cast of the brain cavity. The tooth-replacement cycle of an individual tooth has been worked out from serial sections of a premaxilla. The parasuchian tarsus, hitherto poorly known, shows the basic crocodilian pattern of ankle joint. The mode of life of this carnivorous reptile is considered.

The extremely close relationship between *Parasuchus* and *Paleorhinus* from the early Upper Triassic of North America, indicates generic identity; the latter becomes a subjective junior synonym of the former. The family group name Parasuchidae Lydekker, 1885 is herein reinstated. *Parasuchus* also permits a more accurate dating of the Maleri Formation; the suggested age ranges from Late Carnian to Early Norian. Possible evolutionary trends within the family are outlined, and phenetic and phylogenetic relationships are suggested.

THE parasuchians (phytosaurs) are long-snouted, carnivorous reptiles of Late Triassic age superficially resembling the modern crocodiles in size, proportions, and inferred activities. However, certain anatomical differences separate these two related groups into two different orders. The parasuchians are most abundantly recorded from Europe, India, and North America. Their remains from North Africa, China, and Madagascar are insufficiently known at present. Rapid structural modifications during a brief geological period, combined with fairly wide geographical distribution, make them potentially very useful for a palaeontological subdivision of the Late Trias.

The Indian parasuchian, *Parasuchus hislopi*, was first described by Lydekker (1885, p. 22, pl. 3) from a number of fragmentary specimens from the Maleri Formation of the Pranhita-Godavari Valley. Lydekker also mentioned the occurrence of a parasuchian from the Tiki Formation of the Son-Mahanadi Valley, without any formal designation. Further surface collections of parasuchian material from the Maleri and Tiki Formations were acquired by the Geological Survey of India from time to time, and the material was reviewed by von Huene (1940) and Colbert (1958).

Gregory (1962), while critically evaluating the parasuchian genera of the world, commented that the available Indian parasuchian material was too incomplete for diagnostic value. This deficiency was remedied by the discovery, during the winter of 1965/1966, of two nearly complete and articulated parasuchian skeletons from the Maleri Formation (Chatterjee 1967). These are the most complete skeletons of parasuchians to be discovered anywhere in the world. In the previous year, a parasuchian skull was found by Mr. T. S. Kutty in the Tiki Formation. Two more skulls of parasuchians were subsequently collected from the Maleri rocks in 1973–1974.

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The new material described below considerably amplifies our knowledge of *Parasuchus* and permits reconsideration of this parasuchian's affinities and its stratigraphic significance. This paper is a projected series of studies of the Gondwana vertebrates of the Pranhita-Godavari Valley by the Geological Studies Unit of the Indian Statistical Institute.

*Parasuchus* is found in two closely related formations of Gondwana sediments—namely the Maleri Formation of the Pranhita-Godavari Valley, and the Tiki Formation of the Son-Mahanadi Valley; both are Late Triassic in age. In India, Gondwana sediments occur as relatively restricted strips and patches in several river valleys. In the Pranhita-Godavari Valley, these deposits crop out in a narrow elongated basin covering parts of Andhra Pradesh and Maharashtra, extending NNW from near the coast for about 220 miles length with an average width of 25 miles, and following the general trend of the present river valley. The Gondwana sediments within the basin are flanked on either side by Precambrian rocks. The Maleri is a red-bed formation consisting mainly of red clays with subordinate sandstones and lime-pellet rocks. The Triassic sequence in the Pranhita-Godavari Valley is shown in Table 1.

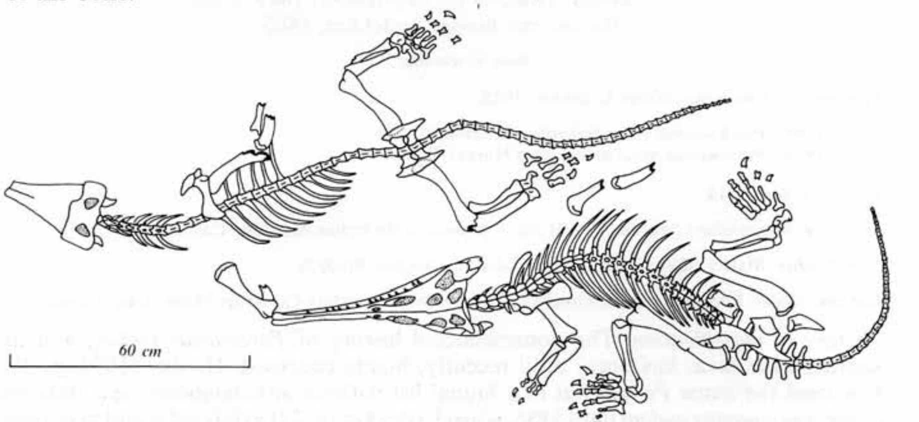
TABLE 1

| Formation | Main lithologies | Characteristic fossils | Age |
|---|---|---|---|
| Dharmaram | Sandstones with red clays | Plateosaur, thecodontosaur | Late Upper Trias (Upper Norian and Rhaetian) |
| Maleri | Sandstones, red clays and lime-pellet rocks | Dipnoi, metoposaur, rhynchosaur, parasuchian, aetosaur, coelurosaur, thecodontosaur, traversodont | Early Upper Trias (Carnian through Early Norian) |
| Bhimaram Sandstone | Sandstone with intercalated red clays | Fragmentary remains, indeterminate | (?Ladinian) |
| Yerrapalli | Red clays and sandstones | Capitosaur, ?brachyopid, dicynodonts, erythrosuchid, trirachodont cynodont, rhynchosaur | Middle Triassic (Anisian) |

The Tiki Formation, so far, the only representative of the Triassic sequence in the Son-Mahanadi Valley, can be equated with the Maleri Formation by its lithology and fossil content. Good skull material of parasuchians, metoposaurs, and aetosaurs has been discovered recently from the Tiki Formation and will be described soon.

## MATERIAL AND METHODS

The new and associated parasuchian material from the Maleri Formation was found in red clay very near to the surface in the vicinity of Mutapuram village (lat. 19° 8′ N., long. 79° 40′ E.) of Adilabad District, Andhra Pradesh. Some fragments were scattered on the surface and a series of associated vertebrae were showing through the clay. After careful removal of the clay, two complete parasuchian skeletons were exposed. Both the animals were roughly 8 ft in length, lying on their ventral surface side by side (text-fig. 1). The right individual, as seen from the rear, lies a little ahead of the left. The skull of the left individual is better preserved; much of the right skull has been washed away. The body shows the general curvature and a life-like pose. Almost all of the bones were found in position, including the scutes. The two skeletons were taken out as they lay, articulated in a single block of clay of 10 × 8 × 1 ft. The block was gradually encased in a crate made of wooden beams and planks screwed and bolted together. Crate and specimen, when finished and lifted, weighed about 2 tons. The bones were cracked in some places but held together by cementation and are otherwise well preserved. The preparation has been done mechanically using pin vice and brush. Acetic acid was occasionally used for removing the calcareous coating of the bone.



TEXT-FIG. 1. *Parasuchus hislopi* Lyd. (× 0·08). Two associated skeletons, as found in Mutapuram village, Dt. Adilabad, A.P., India; *top*, specimens ISI R 43; *bottom*, ISI R 42.

A couple of miles north of this site, two more parasuchian skulls were recovered near the Venkatapur village in an excellently preserved condition. The solitary skull from the Tiki Formation was found in a loose boulder of hard calcareous sandstones, about 4 miles west of Tiki village (lat. 23° 56′ N., long. 81° 22′ E.) of Shadol District, Madhya Pradesh. Except for the snout and the squamosal, the skull is otherwise complete and well preserved. Acid preparation was found ineffective. Small cold chisels and a light hammer were employed for removing the hard matrix. A vibro-tool was safely used very close to the bone as this lent itself to much finer control.

The material used in the following description comprises the following specimens.

*Indian Museum Collection, Calcutta.* GSI H20/11: the lectotype specimen; part of the premaxillary snout, from Maleri.

*Geology Museum, Indian Statistical Institute, Calcutta.* ISI R 42: left individual of the articulated parasuchian from the Maleri, as seen from the rear; ISI R 43: right individual of the articulated parasuchian from the Maleri, as seen from the rear; ISI R 44: skull, from Tiki; ISI R 45: isolated basioccipital from Maleri; ISI R 46: isolated conjoined basioccipital/basisphenoid from Maleri; ISI R 47: isolated conjoined basioccipital/basisphenoid from Maleri; ISI R 160: an isolated skull, from Maleri; ISI R 161: part of the skull and postcranial, from Maleri.

## SYSTEMATIC PALAEONTOLOGY

### Order THECODONTIA
### Suborder PARASUCHIA Huxley, 1875
### Family PARASUCHIDAE Lydekker, 1885
### Subfamily PARASUCHINAE Lydekker, 1885
### Genus PARASUCHUS Lydekker, 1885
### *Parasuchus hislopi* Lydekker, 1885

Plate 8; text-figs. 1-15

*Type species. Parasuchus hislopi* Lydekker, 1885.

1940 *Brachysuchus* (?) *maleriensis*; von Huene, p. 6.
1958 *Phytosaurus maleriensis*; (von Huene) Colbert, p. 75.

*Diagnosis*. See p. 114.

*Lectotype*. Premaxillary rostrum, GSI H 20/11, housed in the Indian Museum, Calcutta.

*Type locality*. Maleri village in the Adilabad district, Andhra Pradesh.

*Horizon*. Maleri Formation of the Gondwana Group in the Pranhita-Godavari Valley, Late Triassic.

*History of classification*. The nomenclatural history of *Parasuchus hislopi*, and its supraspecific taxa, has been, until recently, highly confused. Huxley (1870, p. 49) first used the name *Parasuchus* in a faunal list without any diagnosis, and thus his name was a *nomen nudum* until 1885, when Lydekker (p. 22) validated it and proposed a formal family group name Parasuchidae. Unfortunately, the type species of *Parasuchus*, *P. hislopi* Lydekker, 1885, has as syntype material a rhynchosaurian basicranium mixed with parasuchian bones, scutes, and teeth. Von Huene (1940, p. 6) identified the basicranium as belonging to the rhynchosaur *Paradapedon huxleyi* (Lydekker) 1881; thus he attempted to suppress the name *Parasuchus hislopi* and coined a specific name 'aff. *Brachysuchus*' *maleriensis* for the Maleri parasuchian. Later Colbert (1958, p. 75) designated all the Indian parasuchian material as *Phytosaurus maleriensis*. Gregory (1962) thought that the Indian parasuchian material lacked the critical portions for comparisons and was too incomplete for diagnostic value; he provisionally accepted Colbert's proposition.

The new and fairly complete specimens clearly show that the Indian parasuchian is rather primitive and distinctive, and is not generically identical with either *Brachysuchus* Case, 1929 (= *Angistorhinus* Mehl, 1913) or *Phytosaurus* Jaeger, 1828 (= *Nicrosaurus* Fraas, 1886).

Since the rhynchosaur basicranium is neither the holotype of *Parasuchus hislopi*, nor the lectotype of *Paradapedon huxleyi*, the suppression of *Parasuchus hislopi* can be avoided to preserve the stability of nomenclature, and to meet Lydekker's original intention (that is, that the name should apply to a parasuchian). Chatterjee (1974) validated the name *P. hislopi* for the Indian parasuchian after carefully selecting a premaxillary rostrum as the lectotype from the original syntypes of Lydekker.

Once the name *P. hislopi* is established on a sound basis, there is a strong case for using names based on *Parasuchus* for higher categories as they are still available. The name Parasuchia was coined by Huxley (1875, p. 427) as a subordinal taxon for parasuchian genera (including aetosaurs, as then understood). Lydekker (1885, p. 22) first proposed the family group name Parasuchidae based on the nominal genus *Parasuchus*. Later, he (1888) erected a second family Phytosauridae to include *Phytosaurus* Jaeger, 1828. McGregor (1906, p. 91) raised the Parasuchia to ordinal rank, containing two suborders Phytosauria and Aetosauria. He included all the known long-snouted parasuchian genera within a single family Phytosauridae. Later von Huene (1915, p. 492) established a new family Mystriosuchidae to include all the parasuchian genera except *Phytosaurus* which he regarded as the sole member of the Phytosauridae. In a subsequent revision, he (1922) referred Parasuchia as a suborder. Since then the name Parasuchia continued in general use for the suborder (Romer 1956, p. 597; Charig 1967, p. 709). Camp (1930) and Gregory (1962) accepted a single family group name Phytosauridae containing all parasuchian genera.

It appears from this discussion that three family names were proposed for the parasuchian genera from time to time: Parasuchidae Lydekker, 1885, Phytosauridae Lydekker, 1888, and Mystriosuchidae von Huene, 1915. According to code of zoological nomenclature, a family group name formed by the union of two or more taxa of that group takes the oldest valid name (Stoll *et al.* 1964, Article 23 (d) (1)). Thus Parasuchidae Lydekker, 1885 has a clear priority over Phytosauridae Lydekker, 1888, and Mystriosuchidae Huene, 1915. In addition, *Phytosaurus* is now regarded as indeterminable (Gregory and Westphal 1969). It is also a singularly inappropriate name for a carnivore. Parasuchidae Lydekker, 1885 is re-established herein as the sole family group name for all parasuchian genera of a distinctive suborder Parasuchia of the Order Thecodontia.

The Indian genus *Parasuchus* and the North American primitive form *Paleorhinus* are so similar in structure, as discussed in a later section, that it is difficult to differentiate between them at a generic level. *Paleorhinus* Williston, 1904 is considered here as a subjective junior synonym of *Parasuchus* Lydekker, 1885. Recognizing *Parasuchus* and *Paleorhinus* as subgenera seems to be a useful compromise which permits expression of close relationship between two geographically separated populations.

Gregory (1962), on the other hand, suggested that the German form *Francosuchus* Kuhn, 1932 is congeneric with *Paleorhinus* Williston, 1904. However, *Francosuchus* appears to be more divergent phylogenetically than *Paleorhinus* and it would seem logical to regard it as a genus in its own right. There are good arguments in favour of a subfamilial dichotomy, the branches of which may be labelled as Parasuchinae and Mystriosuchinae (see discussion in a later section). The subfamily Parasuchinae (*nom. transl. ex* Parasuchidae Lydekker, 1885) includes *Parasuchus*, *Angistorhinus*, *Nicrosaurus*, and *Rutiodon*. The subfamily Mystriosuchinae (*nom. transl. ex* Mystriosuchidae von Huene, 1915) includes *Francosuchus* and *Mystriosuchus*.

There is no evidence that the Indian parasuchian material now in the Maleri and

Tiki Collections, represents more than one species. The slight variability encountered may result from differences in sex and age.

*Description of* Parasuchus hislopi: *Skull.* Specimens ISI R 42, ISI R 44, ISI R 160, and ISI R 161 were used as a basis for the study of the skull. The specimens are undistorted and well preserved. ISI R 42 is fairly complete and is the basis for restoration. ISI R 44 displays the endocranial structure in great detail.

A table of the main measurements in millimetres of *Parasuchus* specimen ISI R 42 is as follows:

TABLE 2

| | | | |
|---|---|---|---|
| Skull length | 585 | Humerus length | 182 |
| Skull width | 182 | Humerus, least diameter of the shaft | 22 |
| Skull height | 105 | Radius length | 122 |
| Prenarial length | 305 | Radius, least diameter of the shaft | 12 |
| (measured from anterior border of the | | Ulna length | 135 |
| nares) | | Ulna, least diameter of the shaft | 17 |
| Postnarial length | 280 | Manus length | 120 |
| Distance from rear of naris to front of orbit | 110 | Ilium, crest length | 126 |
| Interorbital width | 30 | Ilium, breadth of neck | 62 |
| Preorbital length | 453 | Ilium height | 105 |
| (measured from anterior border of the | | Ischium height | 125 |
| orbit) | | Pubis height | 105 |
| Postorbital length | 132 | Total length of the puboischiadic plate | 200 |
| Total length of the mandible | 622 | Femur length | 240 |
| Length of the symphysis of the mandible | 327 | Femur, least diameter of the shaft | 26 |
| | | Tibia length | 153 |
| Presacral column length | 900 | Tibia, least diameter of the shaft | 18 |
| Scapulocoracoid height | 195 | Fibula length | 158 |
| Breadth apex of scapula | 60 | Fibula, least diameter of the shaft | 14 |
| Coracoid breadth | 110 | Pes length including tarsus | 212 |
| Clavicle length | 117 | Estimated total length | 2700 |
| Interclavicle length | 200 | | |

*Dermal bones of the skull roof* (text-figs. 2–4; Pl. 8). The septomaxillae are small forming a bar between the nares. In specimen ISI R 42, the nasals are elevated into narrow rims around the nares, whereas in specimens ISI R 44 and ISI R 161, the nasals are flat. The presence or absence of elevated rims around the nares is regarded by Camp (1930) as a sexual character—according to him, the former is the female, the latter the male.

The lachrymal extends anteriorly as a narrow depressed rim bordering the antorbital fenestra postero-dorsally and receives a similar rim of the maxilla on the opposite side of the fenestra. The supratemporal fenestrae are small, triangular, and lie at the level of the skull roof. The infratemporal fenestrae are fairly large. Inside each of the supratemporal fenestrae, a flange of the parietal turns downwards to meet the

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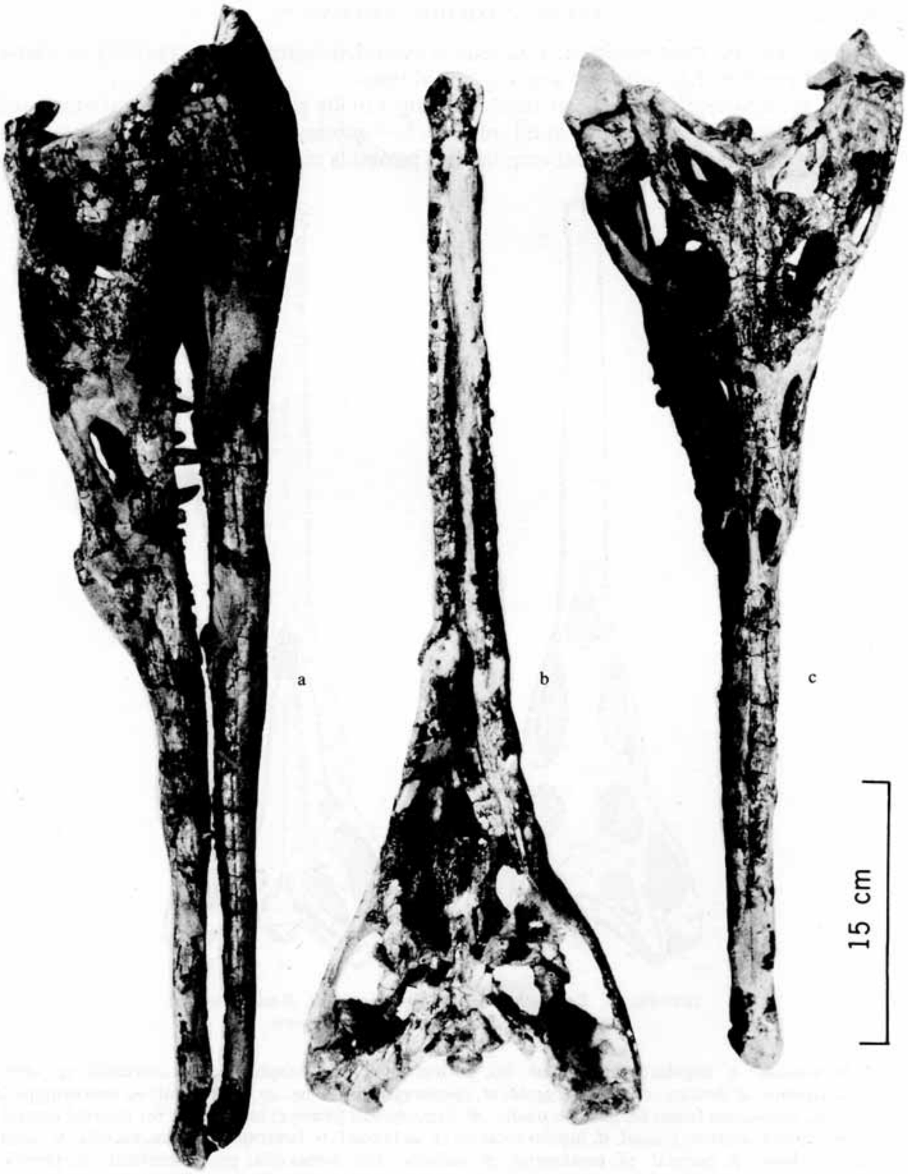
EXPLANATION OF PLATE 8

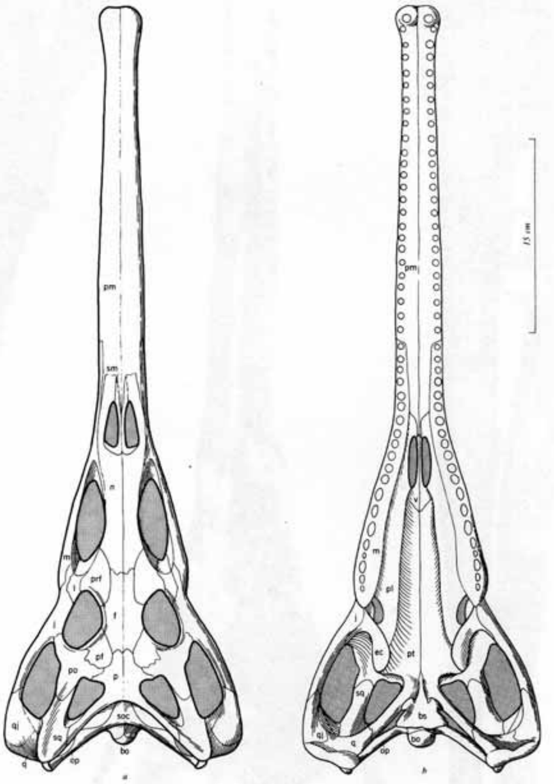
*Parasuchus hislopi* Lyd. (×0·3). Specimen ISI R 42, Skull. *a*, left lateral view; *b*, ventral view; *c*, dorsal view.



CHATTERJEE, Indian reptile *Parasuchus*

laterosphenoid. Posteriorly each parietal is extended laterally and ventrally as a lens-shaped process that joins the supraoccipital below.

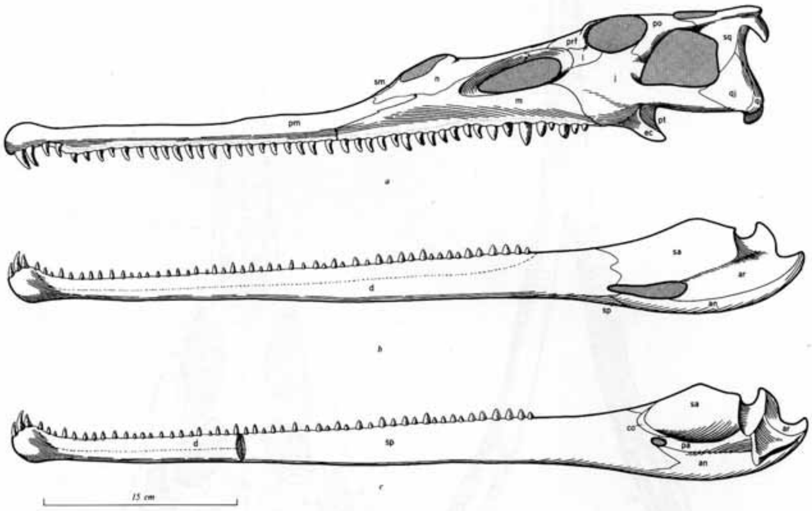
No interparietals have been found. Camp (1930) recognized interparietals and tabulars only in a juvenile skull of *Machaeroprosopus* (= *Rutiodon*); these are probably fused with the supraoccipital and parietals respectively in the adult form.



TEXT-FIG. 2. *Parasuchus hislopi* Lyd. (×0·20). Restoration of the skull; *a*, dorsal view; *b*, ventral view.

Abbreviations: a, angular; ar, articular; bo, basioccipital; bs, basisphenoid; c, coronoid; cp, crista paroccipitalis; d, dentary; ec, ectopterygoid; ef, epipterygoid foramen; eo, exoccipital; es, endolymphatic sac; euf, eustachian fossa; fo, fenestra ovalis; hf, hypophyseal fenestra; ic, foramen for internal carotid; is, interorbital septum; j, jugal; jf, jugular foramen; l, lachrymal; ls, laterosphenoid; m, maxilla; n, nasal; op, opisthotic; p, parietal; pf, postfrontal; pl, palatine; pm, premaxilla; po, postorbital; pr, prootic; pra, prearticular; prf, prefrontal; prs, presphenoid; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sf, stapedial fossa; soc, supraoccipital; sm, septomaxilla; sp, splenial; sq, squamosal; st, supratemporal; v, vomer; vc, vestibular cavity. Foramina for cranial nerves in Roman numerals.

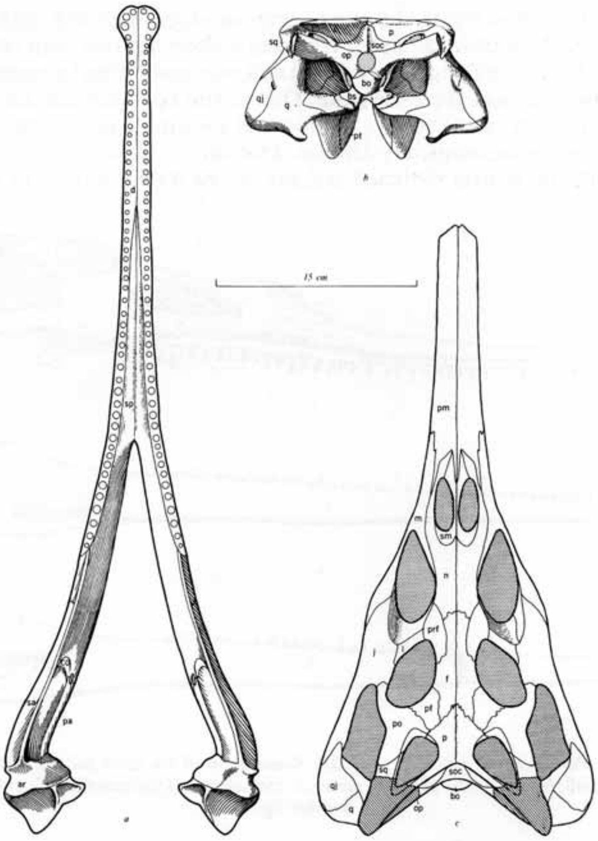
The quadrate is held rigidly by the squamosal dorso-laterally and by the quadratojugal anteriorly. Below the head, it makes a short contact with the paroccipital process. Mesially a deep flange is produced as a pterygoid wing to receive the overlap of the quadrate ramus of the pterygoid. The ventral condylar surface is of uniform width, slants mesially, and shows a double keel for articulation with the lower jaw. The epipterygoid is incompletely known. Dorsally it fits into a pit of the laterosphenoid, while the ventral flattened end sits on the dorsal surface of the pterygoid.



TEXT-FIG. 3. *Parasuchus hislopi* Lyd. (×0·20). Restoration of the skull and mandible. *a*, lateral view of the skull; *b*, lateral view of the mandible; *c*, medial view of the mandible. For abbreviations, see text-fig. 2.

*Palate* (text-fig. 2). The palate is primitive with large palatal fenestrae, and is somewhat vaulted. Almost parallel with and in the vicinity of the mesial edge of the palatine, a low, rounded ridge is visible. Camp (1930) suggested that these ridges on either side were probably connected in life by a membranous sheath to form an incipient secondary palate. This soft palate would help in bringing a separate air passage well back along the palate. Dorsally the palatine, with the pterygoid behind, forms the floor of the orbit.

The choanae are placed slightly behind the external nares. The palatal ramus of the pterygoid extends considerably forward almost close to the choana. Posteriorly the transverse flange of the pterygoid curves ventro-laterally and is supported by the epipterygoid. The basipterygoid articulation consists of a smooth glenoid surface facing upwards and backwards, which curl around the basipterygoid process. The deep quadrate ramus is a thin sheet of bone and has a wing-like extension on either side to brace the medial surface of the quadrate.



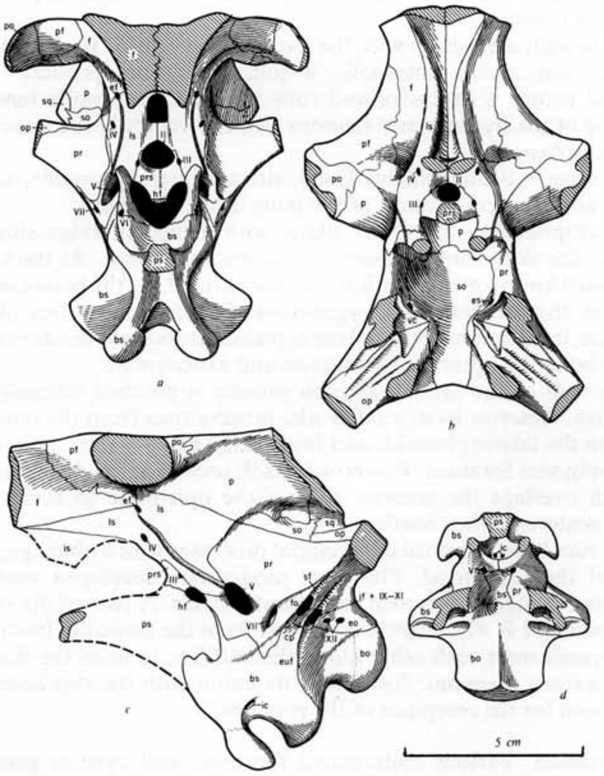
TEXT-FIG. 4. *Parasuchus hislopi* Lyd. (×0·20). Restoration of the skull and mandible. *a*, dorsal view of the mandible; *b*, occipital view of the skull; *c*, dorsal view of the skull (specimen ISI R 44 ♂). For abbreviations, see text-fig. 2.

*Braincase* (text-fig. 5). Six specimens display portions of the braincase of which ISI R 42, ISI R 44, and ISI R 160 are fairly complete and important for interpreting the detailed structure. An isolated basioccipital is represented by ISI R 45. The remaining two specimens are in the form of conjoined basioccipital-basisphenoid. A slight variability between the two sexes is observed.

The basioccipital shows a pair of basal knobs which abut against the basal tubera of the basisphenoid almost in a vertical plane. The knobs are connected by a small growth of bone which is usually concealed by the parasphenoid. Dorsally, the articular surfaces for the exoccipitals are rugose and slant ventro-laterally on either side of the mid-line.

The basal tubera of the basisphenoid are separated by a median notch and exhibit rugose muscle scars on the posterior faces. Anteriorly the basipterygoid processes are more slender than the tubera, and diverge as they descend from the anterior end. Each process shows a strong lateral facet for articulation with the palatal structure. Dorsally the basisphenoid exhibits the pituitary fossa or sella turcica behind which rises the dorsum sellae to join the pillars of the prootic on either side of the hypophyseal foramen. The long, sinuous dorso-lateral edge of the basisphenoid is capped by the prootic. Behind the dorsum sellae, a large basin-like depression is formed dorsally by the basioccipital and basisphenoid, lodging part of the mid-brain. Anteriorly and ventrally the basisphenoid supports the expanded base of the parasphenoid.

The parasphenoid is partly preserved as an extensive ventral ossification, sheathing



TEXT-FIG. 5. *Parasuchus hislopi* Lyd. (×0·56). Restoration of the braincase. *a*, anterior view; *b*, ventral view of upper portion; *c*, lateral view; *d*, dorsal view of the conjoined basioccipital-basisphenoid; specimen ISI R 44. For abbreviations, see text-fig. 2.

the conjoined basioccipital-basisphenoid. The base of the cultriform process is broken; anteriorly it extends as an elongated blade and slips into the interpterygoid vacuity. The presphenoid is represented by a tiny V-shaped bone hanging postero-ventrally from either side of the laterosphenoids. It separates the optic fissure from the hypophyseal foramen. The ventral stem is missing in the available specimens.

The laterosphenoids are large paired elements; each has two well-marked divisions —a mesial branch extending considerably forward below the skull roof, and a lateral branch curving downwards and backwards. The mesial branch encloses much of the olfactory tract. Ventrally the two sides meet each other and form the upper edge of the optic fissure. The interorbital septum is not represented in any specimens. Dorsally each branch articulates broadly with the frontal and barely touches the postfrontal by a serrate suture. Below the postfrontal, a pit is seen facing laterally for the reception of the epipterygoid. From this pit runs a longitudinal groove leading postero-ventrally into the prootic fenestra.

The lateral branch articulates with the parietal and prootic by dorsal and postero-ventral edges respectively. Internally it joins the supraoccipital. The prootic/laterosphenoid suture is extensive and runs between the prootic fenestra and the lateral opening of the hypophyseal fenestra. Antero-ventrally the bone supports the wing of the presphenoid.

The epiotics are indistinguishably fused with the laterosphenoids, supraoccipital, and prootics, and the demarcation of the bone is not possible.

The supraoccipital is a triangular plate, with a median ridge sloping postero-ventrally from the skull roof to cover the foramen magnum. At the summit of the plate is a rounded knob for articulation with the parietal. As the bone extends laterally it is sheathed by the parietal and the squamosal. On the inner surface of the side wall of the braincase, its junctions with the laterosphenoids and prootics are more extensive. Ventrally the bone lies upon the opisthotics and exoccipitals.

In the side wall of the braincase, each prootic is notched laterally by the large prootic fenestra. Anterior to it, a pillar-like process rises from the dorsum sella and is inserted into the laterosphenoid, and bridges the gap between the prootic fenestra and the hypophyseal foramen. Posteriorly each prootic is produced into a tapering process which overlaps the anterior part of the opisthotic to form the tympanic groove at its postero-ventral border.

The opisthotics have powerful paroccipital processes which abut against the downward hook of the squamosal. There are moderately developed ventral processes which separate the jugular foramen and fenestra ovale. A part of the stapes is found in one specimen (ISI R 47), slightly dislodged from the stapedial fossa.

The exoccipitals meet each other along the mid-line to form the floor and lateral wall of the foramen magnum. Just below its union with the supraoccipital a small projection is seen for the reception of the proatlas.

*Braincase foramina.* Various endocranial foramina and cavities preserved in our specimens give some information about the topography of the enclosed soft parts. The foramina provide passage for several important cranial nerves, and their positions and relationships can be ascertained when compared with those of closely related living reptiles.

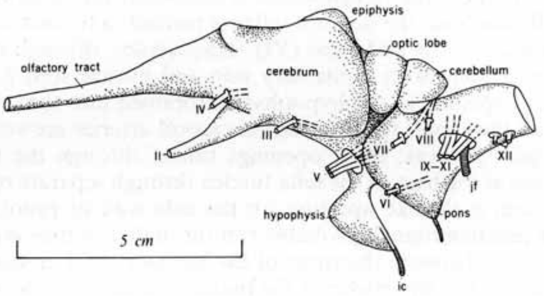
In front of the braincase, the large optic fissure is the exit of the optic nerve (II). Below this fissure, a pair of small pits conveyed the occulomotor (III), while above it lie a pair of small foramina for trochlearis (IV). The trigeminal (V) left the brain cavity through the prootic fenestra. A narrow longitudinal groove running upwards from the mouth of the prootic fenestra, indicates the course of the ramus opthalmicus. In the mid-line, just below the presphenoid, a narrow hypophyseal foramen can be seen. Below this foramen, the basisphenoid is excavated into a large pituitary fossa or sella turcica. Behind this, the dorsum sellae is pierced in the dorso-lateral parts by the external openings of the abducens (VI). Transversely through the sella turcica, the abducens nerve along with a pituitary vein and muscle slips possibly emerged through the lateral opening of the hypophyseal foramen into the orbit.

The openings of the canals for the internal carotid arteries are visible at the roots of the basipterygoid process; these openings tunnel through the bone in normal fashion and emerge at the base of the sella turcica through separate openings. Behind the prootic fenestra, a slit-like aperture on the side wall of prootic conveyed the facialis (VII); its palatine branch probably ran through a ventral groove and would take a forward course between the roots of the basipterygoid process. The foramen for the acousticus (VIII) is not visible in the Indian specimens, although Camp (1930) recognized it in *Machaeroprosopus* (= *Rutiodon*), in the suture between the prootic and paroccipital. The thin ridge-like crista paroccipitalis separates the fenestra ovalis from the jugular foramen. The jugular foramen lies between the otic capsule and the exoccipital; it probably transmitted nerves IX–XI, and a posterior branch of the jugular vein. The paired foramina at the base of each exoccipital are the outlets for the hypoglossal (XII).

*Inner ear*. The bony labyrinth (text-fig. 5) lodging the inner ear is enclosed within the prootic, opisthotic, and part of the supraoccipital bones. It comprises a large central vestibular cavity, encircled by three interconnected semicircular canals. The vestiblar cavity is rather triangular, mesially flattened, with its apices lying dorsally, anteriorly, and posteriorly respectively. It is mainly formed by the prootic and opisthotic. Proximate to its dorsal apex lies a small pit at the junction of supraoccipital and prootic for the endolymphatic sac.

The shape of the utriculus and sacculus cannot be judged with certainty from the bony contour of the vestibular cavity. The utriculus is likely to have been irregular triradiate structure as revealed from the triangular shape of the cavity. The sacculus may have been a rounded structure as is inferred from living reptiles. Below the vestibular cavity, the dorsal suture of the basioccipital/basisphenoid is excavated into a pair of pockets—the cochlear recesses for the reception of the lagenae. The close proximity of the fenestra ovalis to its cochlear recess indicates that the lagena was not elongate. Below the jugular foramen, the deep embayment on the basioccipital indicates the eustachian fossa, through which the eustachian tube connected the middle ear with the pharynx. In the middle-ear cavity, a low ridge separates the stapedial fossa from the tympanic fossa. The latter leads into a small tympanic foramen near the vestibular cavity.

*Brain*. Although the internal architecture of the fossil brains cannot be ascertained, it is possible to draw a number of conclusions from the cast of the brain cavity. The brain cavity of *Parasuchus* is extremely well preserved in specimen ISI R 44, permitting a partial reconstruction of the soft parts enclosed in the cavity. The brain of *Machaeroprosopus* (= *Rutiodon*), restored by Camp (1930), shows a slightly different flexure from this model. A cast in latex rubber of the brain cavity has been made and the major features are outlined here (text-fig. 6).



TEXT-FIG. 6. *Parasuchus hislopi* Lyd. (×0·7). Restoration of the brain, drawn mainly from a latex rubber cast of the cranial cavity; specimen ISI R 44.

Camp noticed that in *Alligator* the internal contours of the brain cavity reflect fairly closely the general topography of the brain, except in the region of the medulla oblongata which is considerably smaller in cross-section than the foramen magnum. This fact has been taken into account, and the medulla, in this reconstruction, is shown slimmer than the actual cavity.

Anterior to the medulla is a large ventrally projecting swelling, the pons varioli, uncommon in reptiles. The development of the pons, as interpreted by Camp, is due to heavy jaw muscles in parasuchians. The nerves innervating these jaw muscles have their centres in the pons. Farther forward, a second downward-dipping projection is the hypophysis which sinks vertically into the well-marked sella turcica.

The dorsal outgrowths of the cerebellum, optic lobes, and the cerebral hemispheres cannot be differentiated from the bony contours; their shapes and sizes shown in the model are conjectural, and are made from comparisons with *Alligator* (Romer 1956, fig. 14). The cerebral hemispheres lie in a position a little behind the orbit, and are connected to the olfactory bulbs by a slender isthmus of olfactory tract. The olfactory bulbs lie in an anterior position immediately behind the olfactory cavity. Below the olfactory tract, the optic nerve (II) runs forward almost parallel to it.

Although the pineal foramen is not present, the undersurface of the parietal in this region is hollowed out, presumably to accommodate the large epiphysis or pineal organ lying postero-dorsal to the cerebral hemispheres.

*Mandible* (text-figs. 3, 4). Passing backwards, the jaw increases in both depth and width. The alveolar border is fairly straight. A series of small nutrient foramina open on the outer surface of the dentary.

The coronoid is missing from the material at hand. Camp recognized this vestigial bone in *Machaeroprosopus* (= *Rutiodon*), loosely attached to the splenial and prearticular, but this element is usually lost in most specimens. The angular terminates beneath the glenoid. Dorsally the bone is excavated into a narrow longitudinal canal for lodging part of the meckelian cartilage. The surangular forms most of the lateral wall of the adductor fossa. The bone runs back, behind the glenoid, almost to the tip of the retroarticular process as a narrow end, where it is compressed between the articular and the angular.

The prearticular is preserved only by a fragment in our collection, and its relationships with the angular, coronoid, splenial, and articular are inferred from the sutural surfaces on the other bones. The articular is a short, compact bone, broadest at the glenoid region. The glenoid is not a single concavity, but it is rather saddle-shaped to receive the double keel of the quadrate condyle. This complex articulation must have limited the jaw to an essentially orthal movement. The glenoid is fairly deep, showing a general tilt towards the mesial side and is set transverse to the mid-line. From the glenoid, a flange of bone extends mesially as a narrow horizontal process and is pierced by a foramen for the chorda tympani branch of the facialis.

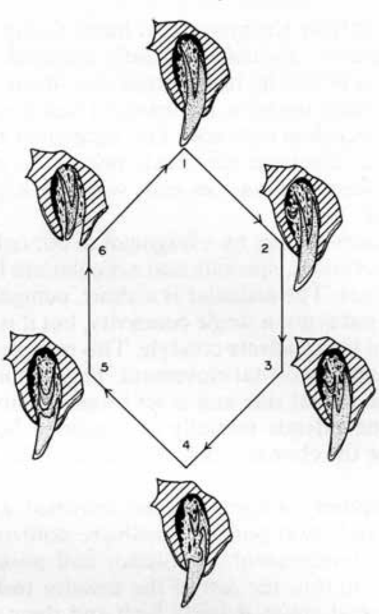
*Dentition*. This consists entirely of marginal teeth crowded in the premaxilla, maxilla, and dentary. The upper and lower posterior teeth are stout and elongate, compressed labio-lingually with the development of anterior and posterior carinae which are finely serrated. Contrary to this, the rest of the anterior teeth are slim, conical, and unserrated. The total dental count is fairly high and there appears to be forty-five teeth on either side of the skull, and about fifty-three teeth in each dentary. In a fully matured tooth, the relative length of the crown to the root is about 1:2·5.

Although repeated tooth-replacement activity has long been known to occur in parasuchians, our knowledge about the mode of replacing each individual tooth is, so far, poor. Fortunately, serial transverse sections of a tooth-bearing premaxilla in our collection exhibit all the various stages which would be expected in the replacement cycle of an individual tooth, and six stages are recognized (text-fig. 7).

Edmund (1960) described the wave-like replacement pattern of the relatively elongate conical teeth of parasuchians, the direction of this wave movement being apparently from back-to-front alternation in two series. The appearance of alternation in an 'odd' and 'even' series, however, is due to spacing of the impulses. A few excellent specimens in the ISI collections also show a clear sequence of back-to-front replacing waves, where the replacement teeth increase in size in alternate series towards the rear.

### *Post-cranial skeleton*

*Vertebral column*. This consists of 25 presacrals, 2 sacrals, and more than 25 caudals. The centra are weakly amphicoelous throughout the series. The lengths of the centra show minor variations along the column, ranging from 3·3 cm to 3·8 cm. Cervicals are somewhat elongated, followed by a shortening of the centra in the anterior dorsals and a lengthening in the posterior dorsals. A serial change in the general build, as well as in the position of the rib facets, can be seen along the column.



TEXT-FIG. 7. *Parasuchus hislopi* Lyd. Dentition. Tooth replacement cycle of an individual tooth. Semi-diagrammatic, based on serial sections of a premaxilla. 1, the tooth is fully erupted, and the root is set in a deep socket. 2, the first indication of replacement activity is the appearance of a small calcified tooth germ in a shallow pocket in the alveolus lingual to the functional tooth. 3, a small erosion appears at the lingual side of the root of the functional tooth and the tooth germ migrates through it. 4, resorption of part of the lingual and labial sides of the root of the old tooth, and the replacing tooth enters within the pulp cavity of the predecessor to grow directly beneath the old crown. 5, further resorption of the root continues and the old tooth at this stage has been so much destroyed that its crown is held in position by a thin shell on the labial aspect; the developing tooth increases in size. 6, the shedding of the old tooth; the new tooth takes its position, and grows in size quite considerably in the socket and ready for eruption.

*Atlas-axis complex*. The proatlas was not found, but the exoccipital and the atlantal arch show distinct facets for the reception of this little bone. No ossified intercentra are found posterior to the atlas and axis. The atlas intercentrum is larger than the posterior one and has a typical crescentic form with its two ends clipped off to form articular facets for the neural arches. The neural arch halves of the atlas lack the spines and do not meet dorsally.

The three components of the axis, odontoid (= atlantal centrum), intercentrum, and the axis proper, remain separate in the Maleri specimens, these probably being juvenile forms. The neural arch of the axis is very large and distinctive, hatchetshaped, and elongated antero-posteriorly. The powerful spine was presumably used as an area of attachment by the obliquus capitis magnus muscle and the nuchal ligament connected to the head and vertebral column. The dorsal edge of the spine is not horizontal but slopes anteriorly and shows a rudimentary 'spine table' (Ewer 1965) at the back. The prezygapophysis of the axis is a little projecting flange, close to the horizontal, and facing upwards and outwards, the opposite of the normal situation. The post-zygapophysis, on the other hand, is oriented as usual. The transverse process is weakly developed.

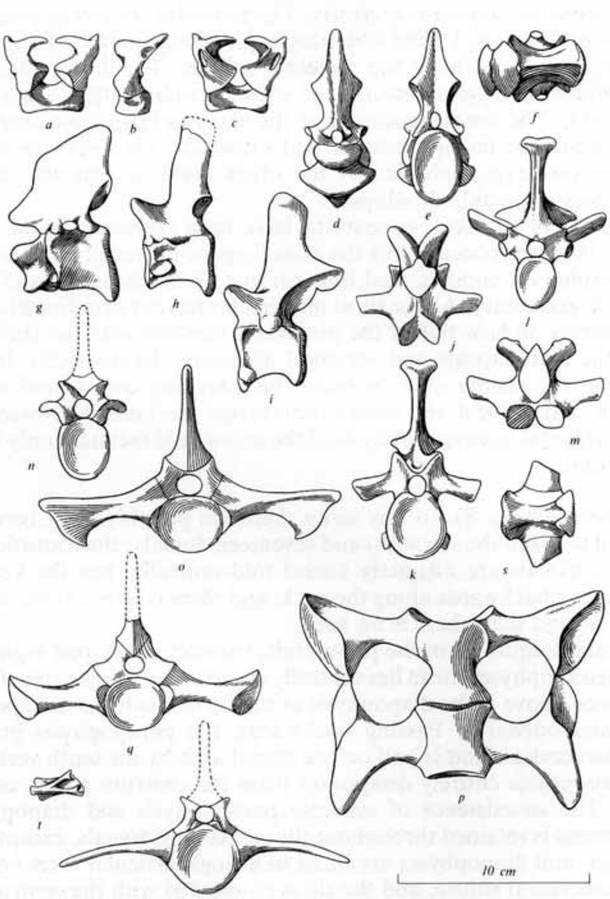
The movement of the skull appears to have been concentrated at the occipito-atlantal joint. Here the concavity of the atlas forms a universal ball and socket joint with the hemispherical condyle, and thus permits all the three types of movements: lateral, vertical, and rotary. All the three movements have approximately equal ranges but depend largely on how tightly the proatlas articulates with the skull, and on the elasticity of the joint capsule and vertebral ligaments (Evans 1939). In addition to this movement, the saddle joint between the atlas and axis would allow a good lateral motion, but vertical and rotary movements are limited. Moreover, the flat, practically horizontal, prezygapophysis of the axis would facilitate only lateral movement at this joint.

*Presacral series* (text-fig. 8). In this series there are possibly eight cervicals (whose ribs would fail to reach the sternum) and seventeen dorsals; the transition is gradual. The anterior cervicals are distinctly keeled mid-ventrally, but the keels gradually fade away moving backwards along the neck, and there is only a trace of them on the last cervical; behind that, there is no keel.

Rib facets are ubiquitous in the pre-sacrals, variably developed regionally. In the cervicals the parapophyseal facet lies ventrally close to the anterior rim of the centrum. A short distance above is the diapophysis at the tip of the transverse process, facing downwards and outwards. Passing backwards, the parapophysis gradually rises upwards in the cervicals and is half on the neural arch by the tenth vertebra. Behind this, the parapophysis entirely disappears from the centrum and is carried on the neural arch. The co-existence of separate parapophysis and diapophysis on the transverse process is retained throughout the succeeding dorsals, except the last one, where the para- and diapophyses are fused to a single articular facet (synapophysis) along the neurocentral suture, and the rib is co-ossified with the centrum.

The gradual shift of the diapophysis can also be seen. It is situated along the neurocentral suture in the cervicals, but gradually rises in the anterior dorsals and reaches the highest position in the mid-dorsal region, beyond which it descends again and ultimately lies on the neurocentral suture in the last two dorsals. The diapophyseal facet becomes enlarged from the anterior to mid-dorsal region, and the facet faces downwards in the anterior cervicals, slightly upwards in the anterior dorsals, and horizontally in the mid- and posterior dorsals.

The neural spine is compressed laterally and lies well towards the posterior half of the centrum. It is quite slim in the third vertebra, but further posteriorly the spines begin to elongate with a narrow base in the cervicals and posterior dorsals, but decline in height with a broad base in the anterior and mid-dorsal region. In the anterior dorsals, the spines become more and more expanded dorsally to form the spine



TEXT-FIG. 8. *Parasuchus hislopi* Lyd. (×0·30). Vertebral column. *a–c*, anterior, lateral, and posterior views of the atlas; *d–g*, anterior, posterior, ventral, and lateral views of the axis; *h*, lateral view of third vertebra; *i–k*, lateral, dorsal, and anterior views of eighth vertebra; *l*, *m*, anterior and dorsal views of fourteenth vertebra; *n*, anterior view of twenty-third vertebra; *o*, anterior view of first sacral; *p*, ventral view of the two sacrals; *q*, anterior view of second sacral; *r*, anterior view of twenty-eighth vertebra; *s*, ventral view of thirty-first vertebra; *t*, ventral view of thirty-ninth vertebra.

tables. Ewer (1965) suggested that the spine tables may be related to the attachment of muscles belonging to the transverso-spinalis system for raising the head.

The successive neural arches are jointed in amphiarthroses by zygapophyses of variable dimensions and orientations. In the cervicals from the third vertebra onwards, the prezygapophyses become greatly enlarged, and extend well forward beyond the anterior face of the centrum, but the facets again reduce in size in the dorsals. The slopes of the zygapophyses are generally close to 40° from the horizontal in the cervicals and anterior dorsals. Further backwards, the facets become more and more horizontally placed, but in the last presacral there is a sharp rise in the slope of the facets, similar to the cervicals.

*Sacrum.* The sacrum includes two separate vertebrae which are, in general, similar in build to those of the adjacent vertebrae, but possess distinctive large and wing-like ribs. Both the centra are equally long antero-posteriorly, and contact each other by almost flat surfaces. The zygapophyseal facets are moderately tilted. The neural spines are high and broad without any spine table. Rib facets are united to form the synapophysis, but the parapophysial and diapophysial facets can be distinguished, and are separated by the neuro-central suture. The parapophysis lies on the centrum and the diapophysis on the neural arch, facing each other at an obtuse angle.

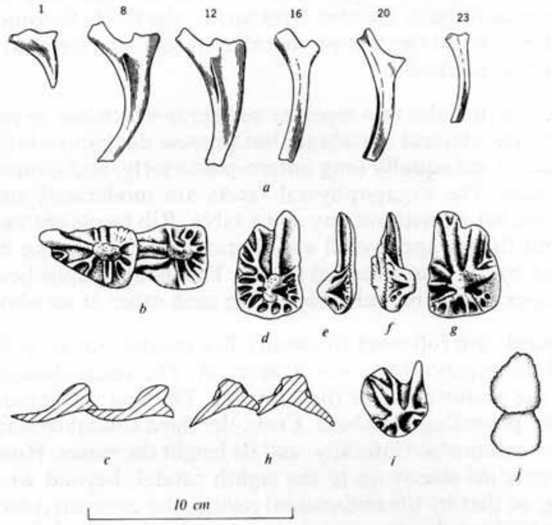
*Caudals.* The sacrals are followed by twenty-five caudals in the collection. Most of their spines and the zygapophyses are broken off. The serial changes in the caudals are reflected in the architecture of the centrum. The first two caudals are not very different from the preceding vertebrae. From the third caudal onwards, the centrum is more and more compressed laterally, and its height decreases. However, the length of the centrum remains steady up to the eighth caudal, beyond which the length is also diminishing, so that by the mid-caudal region, the centrum is narrow and spool-shaped. Further backwards, the caudals become slender and delicate.

The chevrons are Y-shaped and begin at the third caudal, and continue in gradually shortened form in the rest of the series. From the third caudal, each centrum bears a mid-ventral furrow, flanked by two strong ridges which terminate posteriorly in semicircular chevron facets.

*Ribs.* These are regionally differentiated (text-fig. 9). The cervical ribs are short and dichocephalous. Their heads remain close together in front, but the bifurcation of the head tends to increase posteriorly. The tubercular facet is larger than the capitular, but the latter is more prolonged medially. Just below the head a strong longitudinal ridge projects on the anterior surface of the shaft to which was presumably attached some of the medial bundles of the intercostal muscles.

The thoracic ribs are much longer and are curved. Each rib shaft is subtriangular proximally and subcircular distally. Proceeding backwards, the capitular attachment migrates upwards, and the heads tend to come closer to one another. In the posterior dorsals the two heads are united, but in the last dorsal, the rib is single headed and fused to the centrum.

The sacral ribs are immovably attached to the vertebrae, like the preceding dorsal and the succeeding caudals. Each rib is strong and stout, with a broad head, a short shaft, and a distal expansion applied to the inner surface of the ilium. The distal expansion is in the horizontal plane, and each rib extends towards its neighbour to make a slight contact at the tips. The first sacral rib takes the major share of the articulation with the ilium. The distal expansion of the second sacral rib is more prolonged antero-posteriorly; its posterior edge ends as a blade. A number of proximal caudals bear slightly curved short ribs, which are flattened dorso-ventrally and fused to the neural arches.



TEXT-FIG. 9. *Parasuchus hislopi* Lyd. (×0·33). *a*, anterior views of left presacral ribs of first, eighth, twelfth, sixteenth, twentieth, and twenty-third vertebrae. *b*, left paramedian dorsal scutes associated with fifth and sixth presacrals; *c*, the same, longitudinal section; *d*, left paramedian presacral scute, seventh; *e*, the same, mesial view; *f*, mesial view of right seventh presacral scute; *g*, the same, dorsal view; *h*, transverse section of the seventh paramedian pair; *i*, fifteenth presacral scute, left; *j*, left lateral scutes associated with seventh paramedian scute.

*Dermal armour*. Scutes are well preserved, having been found in almost their normal positions resting on their respective vertebrae. There are two rows of elongated paramedian scutes, supplemented laterally by small subcircular lateral scutes. The paramedian scutes are the better exhibited, extending throughout the column and undergoing various changes of size and shape (text-fig. 9).

The scutes are segmentally arranged; each vertebra bears a single paramedian pair, and each plate receives two lateral scutes. The lateral scutes are smooth and smaller in size than the paramedian. The length of the paramedian scute ranges from 2·5 cm to 5·0 cm. The cervical scutes, except the first one, are elongated, and the length decreases steadily in the posterior direction.

The paramedian scutes are coarsely sculptured dorsally. In each plate, there is an eccentric knob-like projection on the postero-medial quarter, from which an alternate series of ridges and furrows radiates towards the periphery. In the cervicals and anterior dorsals, each scute is triangular, but further posteriorly it is somewhat quadrate with a strong spine about 1·5 cm long, projecting anteriorly. The spine is abbreviated in the caudals.

Each scute overlaps its posterior successor. The ventral surface of the knob is deeply hollowed out to receive the tapering anterior portion of the succeeding scute. The juncture of the two scutes rests on the spine table.

The articulation between a paramedian pair is interesting. The left and right scutes in a pair are not perfect mirror images of one another; they differ considerably in the median hinge area. The mesial border of one of the pair is appreciably thickened as a flange, somewhat incised longitudinally. The mesial border of the antimere is sharp-edged and crenulated to fit into the incision of the flange. This groove-and-ridge joint permits a certain degree of movement, mainly flexion and extension along the hinge, but allowed no lateral movement. The ventral surface of the scute shows some scar marks.

There is an alternation of this interlocking device at the interval of two successive scutes. For example, in the first and second scutes, the flange develops on the left side, whereas the ridge is on the right side, but in the third and fourth, the reverse is the case, i.e. the flange develops on the right side and the ridge on the left side. This alternate pattern can be traced up to the eighteenth presacral, beyond which the scutes are somewhat fragmentary.

The ventral armour is unknown except in the throat region. Here a shield of small subcircular plates form a mosaic, interlocking by means of serrated borders or by overlapping. Each plate is 1·0–2·5 cm in diameter.

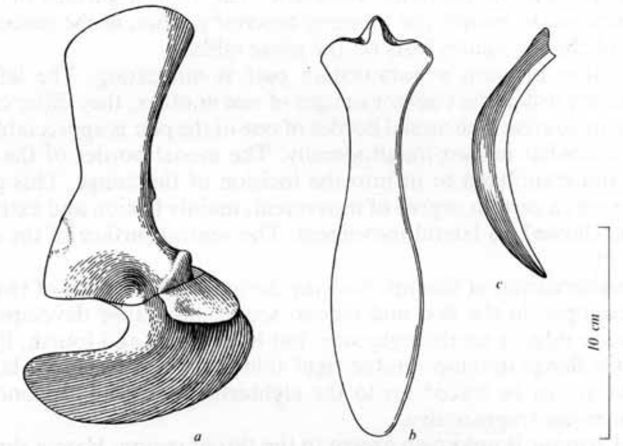
*Abdominal ribs.* A close-packed series of abdominal ribs was found in specimen ISI R 42, covering the posterior part of the belly. The abdominal ribs are arranged in a V-shaped form, just behind the interclavicle, in an overlapping series; the apex of the V points anteriorly. Each chevron is thick near the apex, where it is overlapped by its predecessor, but slim laterally where they are separate. The total count of the preserved part of the ribs may be as many as thirty.

*Shoulder girdle* (text-fig. 10). The scapula is curved so as to fit round the ribs. The main part of the blade is thin, but is appreciably thickened at the postero-lateral corner to form the glenoid. The glenoid lips face posteriorly and somewhat laterally, and diverge away from each other at an obtuse angle. A short distance above the glenoid is a prominence for the tendinous origin of the scapular head of the triceps muscle. At the anteroventral corner lies the acromion process to which the clavicle was connected by ligament.

The coracoid is a broad and short element, deeply emarginated anteriorly; the emargination was presumably closed in life by a bar of cartilage to form the coracoid foramen. Except for the glenoid region, the coracoid is otherwise thin, and fairly convex on the ventral surface.

The clavicle is a thin, crescentic bone. The dorsal end is a tapering process which abuts against the acromion process of the scapula. The shaft is curved, and bears a longitudinal ridge on the anterior surface. The distal end is thickened to a hook-like knob and shows the facet for the interclavicle.

The interclavicle is dagger-shaped; its anterior end is broad and trifurcated and bears antero-lateral notches in which the medial ends of the clavicles were lodged. The remainder of the bone is thin, slightly convex downwards, and tapers gradually posteriorly.

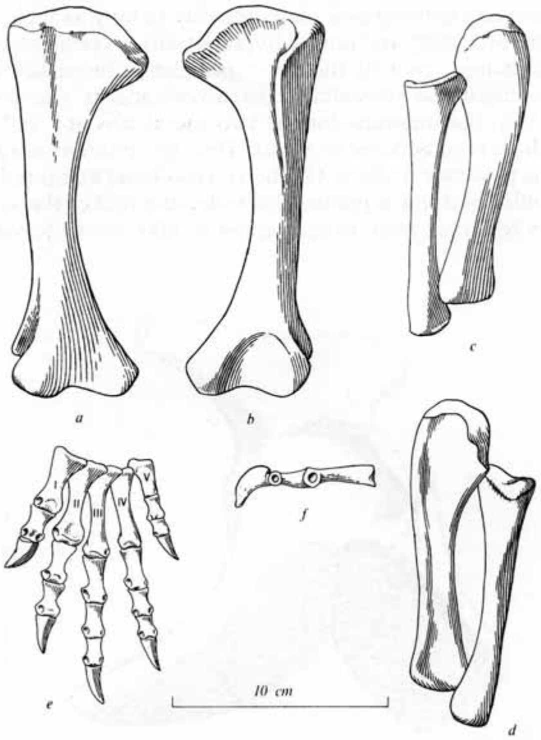


TEXT-FIG. 10. *Parasuchus hislopi* Lyd. (×0·33). Left shoulder girdle. *a*, scapulocoracoid, lateral view; *b*, ventral view of interclavicle; *c*, anterior view of clavicle.

*Fore-limb* (text-fig. 11). This is much shorter than the hind, the humerus being 76% of the length of the femur; when the lengths of the radius and tibia are added to the humerus and femur respectively, the same proportion is maintained. The propodials are distinctly longer than the epipodials; the length of the radius is 67% of that of the humerus, and the length of the tibia is 64% of that of the femur. The manus is considerably shorter than the pes; the first metacarpal is 60% of the length of the metatarsal.

The distal end of the humerus bears two convexities separated by a concave facet. The larger (anterior) convexity forms the capitellum, the concavity comprises the trochlea, and the smaller medial convexity affords an additional articular surface for the ulna. Near the capitellum lies the prominent epicondyle on the anterior border flanking a longitudinal groove for the passage of the radial nerve and the blood vessels.

The radius shows an oval and concave articular surface proximally to fit into the capitellum of the humerus, permitting a rotary motion. Laterally the head is prolonged as a lip to overlap the outer edge of the ulna, which is widely expanded proximally with a large olecranon process. The proximal articular end of the ulna slopes gently towards the radius to form a continuous surface for the articulation with the humerus. The distal end is swollen and oval in outline.

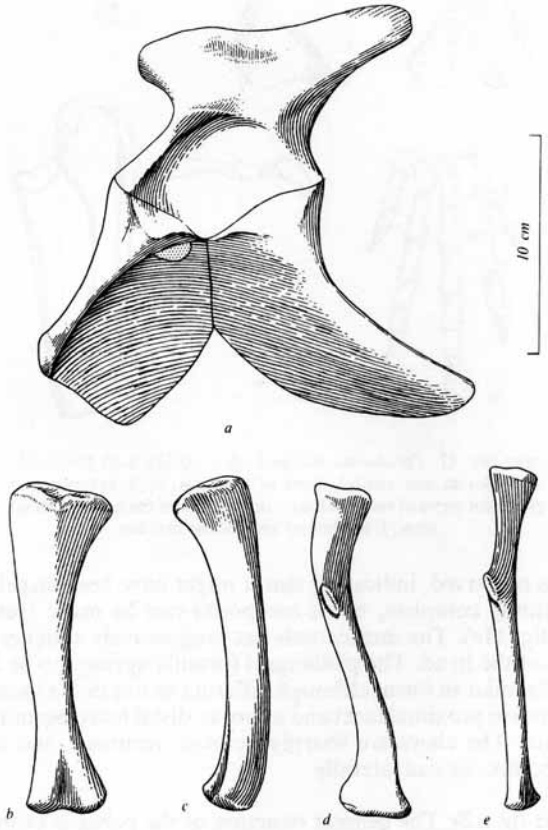


TEXT-FIG. 11. *Parasuchus hislopi* Lyd. (×0·33). Left fore-limb. *a, b,* dorsal and ventral views of humerus; *c, d,* anterior and posterior views of radius-ulna; *e,* restoration of the manus, dorsal view; *f,* left lateral view of the first toe.

No carpus was preserved, indicating that it might have been largely cartilaginous. No manus is entirely complete, but a composite can be made from the available specimens (text-fig. 11*e*). The metacarpals get progressively slimmer from the inner to the outer side of the hand. The phalangeal formula appears to be 2–3–4–5–3. The phalanges are all similar in form, although differing in size in the various digits. Each phalanx has a concave proximal facet and a convex distal facet, permitting a moderate amount of flexure. The claws are sharply pointed, recurved, and bilaterally compressed. They decrease in size laterally.

*Pelvic girdle* (text-fig. 12). The general structure of the pelvis is primitive and plate-like, V-shaped in cross-section, with an imperforate acetabulum. The median symphysis is rather straight, and is interrupted by a notch, presumably filled in life by symphyseal cartilage.

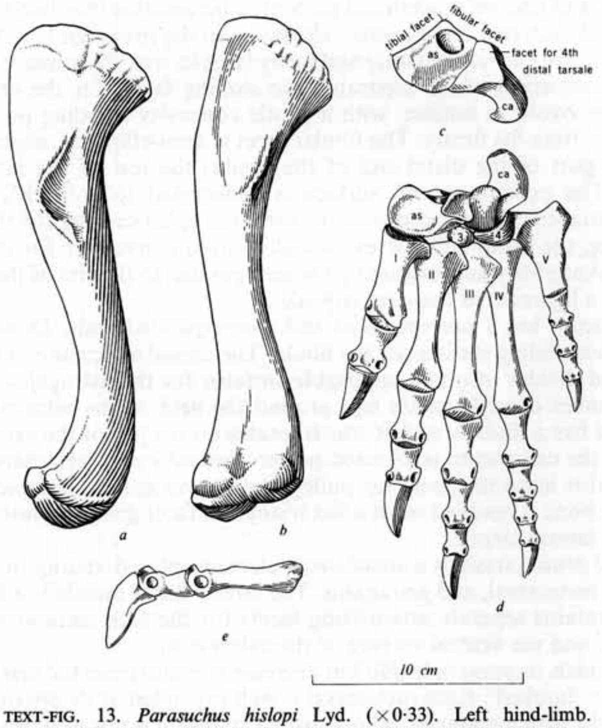
The ilium is an essentially vertical plate, roughly as long as high. The iliac crest is finely striated both externally and internally; the striations radiate out from the upper edge of the acetabulum towards the outer periphery. Internally the iliac crest is deeply concave lengthwise presumably to accommodate the longitudinal axial muscles. Below this, the incisions for the two sacral ribs are well marked. At the mid-height, the ilium is constricted to a neck. Here the anterior margin is appreciably thickened, but the posterior is sharp. On the antero-dorsal margin of the acetabulum, the supra-acetabular buttress is inflated laterally, and makes the acetabulum somewhat deep in the adjoining area, thus adapted to take strong forward thrusts from the femur.



TEXT-FIG. 12. *Parasuchus hislopi* Lyd. (×0·33). *a*, composite restoration of the left pelvis in side view; *b*, *c*, lateral and posterior views of left tibia; *d*, *e*, lateral and anterior views of left fibula.

The ischium is plate-like and extends posteriorly to the level of the prolongation of the ilium. The lamelliform anterior edge drops straight from the acetabulum to match the posterior edge of the pubis. The pubis is concave externally with an overhanging anterior rim. A large obturator foramen is located at the postero-dorsal corner through which the obturator nerve would pass to the muscles of the thigh. The pubic symphysis is short but deep.

*Hind-limb* (text-figs. 12, 13). The femur of *Parasuchus* is very reminiscent of that of a crocodilian. The bone is long and slender and shows a gentle sigmoid flexure. The proximal and distal expansions are rotated about 55° out of line with each other. The fourth trochanter rises as a ridge from the ventral surface of the femur, and is entirely confined to the proximal half of the femur. Medial to the fourth trochanter, a prominent muscle scar indicates the insertion of the coccygeo-femoralis longus. Distal to the fourth trochanter, a rugose projection can be seen on the postero-dorsal edge, more pronouncedly in specimen ISI R 42 (text-fig. 1). Camp (1930) interpreted this



TEXT-FIG. 13. *Parasuchus hislopi* Lyd. (×0·33). Left hind-limb. *a*, *b*, medial and ventral views of femur, composite restoration; *c*, antero-ventral view of astragalus-calcaneum; *d*, restoration of the pes, dorsal view; *e*, left lateral view of the first toe. Abbreviations: as, astragalus; ca, calcaneum; 3, 4, disal tarsals 3 and 4.

rugosity as a 'fifth trochanter' on which the ilio-femoralis possibly inserted by a tendon. The shaft is long and cylindrical and ovate in cross-section. Distally the two condyles are somewhat asymmetric, the lateral condyle is larger as well as extended farther distally than the medial one. The intercondylar groove is shallow.

The tibia has an expanded proximal end, triangular in section, and bears a weak cnemial crest. The distal end is slightly convex for the ankle joint and is ovate in outline. The fibula is a slim, antero-posteriorly compressed bone with slight sigmoid curvature. Both the proximal and distal ends are somewhat expanded transversely, connected by a twisted shaft. The prominent iliofibularis trochanter is an important landmark on the anterior face, running obliquely a little above the mid-height. Further distally the bone swells medio-laterally and becomes spatulate in shape. The distal end shows two separate facets for articulation with the tarsus; the medial one is apposed firmly to the upper surface of the astragalus, the lateral one is somewhat concave, and could move freely on a similar convex surface of the calcaneum.

The parasuchian tarsus, hitherto poorly known, is well represented in the Maleri specimens. It is of general crocodiloid pattern, differentiated into two rows, proximal and distal, and each row contains two elements. In the proximal row, the astragalus and calcaneum are entirely separate and fairly large in size. Proximally the astragalus rises as a dorsal apex, which separates two sloping facets for the crus. The tibial facet is larger, ovoid in outline, with a gentle concavity trending postero-medially into which the tibia fits firmly. The fibular facet is semi-elliptical, slightly depressed, and receives part of the distal end of the fibula; the rest of the latter meets the calcaneum. The postero-ventral surface is constricted to a 'neck', below which the lateral surface is slightly projected to form the spherical peg for the calcaneum. From the peg, the distal end curves medially into a convex arc for union with the metatarsals. Anteriorly an elongated pit is seen parallel to the rim of the fibular facet, probably for a ligament of the joint capsule.

The calcaneum has a narrow waist and two expanded ends. Dorsally the bone carries a convex sliding surface for the fibula. The mesial articular end is appreciably thickened and divides into two apposable surfaces for the astragalus. The anterior half has a convex condyle which laps around the neck of the astragalus, while the posterior half has a shallow socket which rotates on the peg of the astragalus. From this contact, the calcaneum is directed postero-laterally and terminates in a rugose tuber. The tuber lacks the posterior pulley-like groove as seen in typical crocodiles. Ventrally the bone is bevelled off at a flat triangular facet giving an intimate articulation with the lateral tarsale.

The medial distal tarsale is a small ovoid element, placed among the lateral distal tarsale, third metatarsal, and astragalus. The lateral distal tarsale is a large irregular bone, and contains separate articulating facets for the fifth metatarsal, the medial distal tarsale, and the ventral surface of the calcaneum.

The metatarsals increase in length but decrease in width from the first to the fourth, and the fifth is 'hooked'. Each metatarsal is well expanded at its proximal and distal ends, except the fifth metatarsal, whose distal expansion is not well pronounced. The fifth metatarsal is equal in length to the first one, and is Y-shaped. The medial branch of the Y bears a rectangular facet for articulation with the lateral distal tarsale. The lateral edge of the fifth metatarsal thickens ventrally to form the hamate process.

The phalangeal formula is 2–3–4–5–4. Each phalanx is expanded proximally and distally; the proximal surface is a shallow concave facet, the distal end forms a rolling hemicylindrical surface. Claws are present in all the digits, decreasing in length and proportion laterally. The length of the first claw is almost twice that of the fifth one. The medial surface of each claw is convex, the lateral surface bears a prominent longitudinal groove running almost the entire length.

The ankle joint of *Parasuchus*, although basically confirming to the crocodilian pattern, differs mainly on the nature of the astragalo-calcanear joint and the breadth of the tuber. The fit of the astragalus with the crus is so close and exact that it prohibits any movement between them. In *Parasuchus*, the initial phase in the evolution of the movable interlocking peg and socket joint between the astragalus and calcaneum can be seen. Here the astragalar peg is merely a gentle convexity and the calcanear socket is merely a shallow concavity. Nevertheless, this joint permits free rotary movements of the calcaneum on the astragalus. The astragalus forms part of the crus, whereas the calcaneum, distal tarsals, and the combined metatarsals move as a unit on astragalus and fibula. Thus the ankle joint is mesotarsal on the tibial side, and the crurotarsal on the fibular side.

Walker (1964) pointed out that the crocodiloid type of ankle joint seems to be a basic pattern in many thecodontians. Bonaparte (1971) recognized two distinct types of astragalo-calcanear joint among thecodontians, on the basis of the relative positions of peg and socket. One is 'crocodilian-normal' type, in which the peg is on the astragalus, and the socket on the calcaneum. The tarsus of *Parasuchus* is a good example of this pattern. The second category is the 'crocodilian-reversed' type, in which the peg is on the calcaneum and the socket on the astragalus. This pattern of ankle joint is found in *Riojasuchus*. It is interesting that both types of ankle joints allow rotary motion between astragalus and calcaneum, and both are well represented among the Late Triassic thecodontians.

## STANCE AND GAIT

Charig (1972) analysed stance and gait in the archosaurs from the structural evidence of the pelvis and the hind-limb, and he recognized three distinct types, namely 'sprawlers' (the earliest Proterosuchia), 'semi-improved' or 'intermediate' (other Thecodontia and Crocodilia), and 'fully-improved' or 'vertical' (dinosaurs). *Parasuchus* seems to have possessed almost all of the attributes of the 'semi-improved' type, listed by Charig. These are: (*a*) two sacral vertebrae; (*b*) weakly developed anterior process of the ilium and weak supra-acetabular buttress; (*c*) imperforate acetabulum; (*d*) elongated pubo-ischiadic plate; (*e*) inturned head of the femur with sigmoid curvature of the shaft; (*f*) weakly developed fourth trochanter and absence of internal trochanter; (*g*) untwisted tibia; (*h*) flexible tarsus of crocodiloid pattern with peg and socket articulation between astragalus and calcaneum; (*i*) presence of calcanear tuber; (*j*) plantigrade pes with symmetrical pattern of toes.

The femur of *Parasuchus* resembles that of crocodilians very closely. There is a striking similarity in the limb proportions between *Crocodylus porosus* and *P. hislopi*. In both cases the length of the fore-limb as percentage of hind-limb is close to 80%.

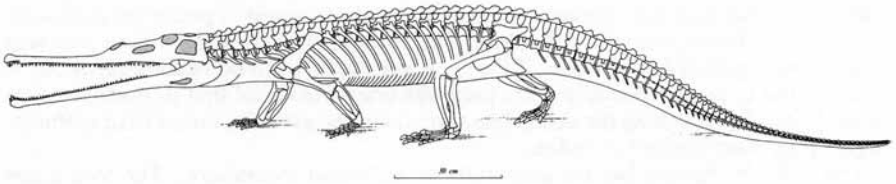
The crocodilians have three distinct gaits. There is a normal upright stance with body lifted off the ground, a gait most unlike the popular conception of a crocodile walking. When moving slowly, the body is dragged along the ground and the limbs are moved in a lizard-like fashion. More familiar is the tobogganing used when dashing into the water. The crocodile slides on its belly, using its legs as paddles. Cott (1961) observed an unusual method of locomotion by the young Nile crocodile, which gallops along with fore- and hind-limbs working together, like a bounding squirrel.

Walker (1970) pointed out that the elongated coracoids and the freeing of the shoulder girdle by the loss of the clavicles allow the lightly built juvenile Nile crocodile to gallop; but such locomotion could hardly have arisen in a large primitive thecodont like *Parasuchus*. Nevertheless all other crocodilian gaits were possibly used by *Parasuchus* without much difficulty. The ability of the crocodiles to raise the body off the ground may be associated with the extensive development of the pubo-ischio-femoralis externus and the adductor femoris (Romer 1923). These groups of muscles seem to have been well developed in *Parasuchus* also.

The limbs of *Parasuchus* are well built for terrestrial locomotion. Although the hind-limb is 24% longer than the fore-limb, its structure shows no bipedal adaptation. Unlike the archaic archosaurs, the humerus is but little twisted at its two ends. The glenoid lips face outwards and downwards, allowing the humerus to swing through an arc without dislocation. The humerus was swung in a rotary motion during a single stride, forwards and outwards, backwards and inwards.

The shaft of the femur is gently sigmoid, and its head, although it lies terminally, is turned inwards to some extent. The pelvis is V-shaped in end-view, where the median region of the elongated pubo-ischiadic plate recedes beneath the acetabulum. The articulation of the femur with the acetabulum indicates an oblique position of the femur. As Charig has pointed out, in this intermediate group (such as *Parasuchus*), the acetabulum, the sites of the origin of the protractor, and the retractor muscles and their insertion on the femur were no longer in the same plane. Hence, these groups of muscles not only pulled the femur anteriorly and posteriorly, but also towards the mid-line as a resultant component. The adduction of the femur would help the animal to raise the body off the ground, particularly during rapid progression. Thus *Parasuchus* was certainly incapable of adopting a vertical posture, but had improved its posture from the typical sprawling position to a great extent.

The 'twin' specimens of *Parasuchus*, being articulated, give valuable information as to the position and attitude of the different bones. The skull is 585 mm long, the presacral vertebral series in natural association is 900 mm, and the preserved part of the tail would also be 900 mm. The tail may have been somewhat longer, say about 1200 mm. The estimated snout to tail-tip length of the restored skeleton, representing an individual of the size of ISI R 42, would be about 2·7 m. Text-fig. 14 shows a restoration of the whole skeleton, with the animal using this suggested quadrupedal gait with the body off the ground.



TEXT-FIG. 14. *Parasuchus hislopi* Lyd. Restoration (×0·06).

## MODE OF LIFE

The active carnivorous habit of *Parasuchus* is reflected in the gastric contents of the 'twin' specimens, where both the hunter and the hunted were fossilized in the same block. Each specimen contains a small bipedal archosaur in the stomach, the bones of which are more or less articulated and well preserved, except for the cranial region. The left specimen (ISI R 42), in addition to this, shows a few skull bones of a rhynchosaur in its stomach. The general skeletal construction of *Parasuchus* must be considered in relation to this mode of life, and the habits of recent crocodilians could be taken as an analogy, assuming *Parasuchus* occupied an ecological niche like that of living crocodilians.

Most revealing of all anatomical evidence, of course, is the dentition. The numerous sharp-pointed conical and polyphyodont teeth are that of a formidable carnivore. The teeth do not meet at the tips, but interdigitate when the jaws are closed. The elongated jaws with sharp teeth and wide gape are well suited for prehension. The frontal position of the eyes close to the mid-line, with a fairly large degree of binocular vision must have a good correlation with predacity. The crocodilians have about 25° of binocular vision (Walls 1963), and *Parasuchus* would have had close to this value, as is inferred from the similar position of the orbit. Binocular vision offers good distance judgement which enables the killer to strike the prey more precisely.

With the eyes and nostrils set high in the skull, *Parasuchus* had a natural advantage over its prey at the water's edge, as it could lie totally submerged. Thus lying in the water, it could breathe, smell, and see. The development of a soft secondary palate would help air breathing while seizing prey under water. Once the jaws got a firm hold on the animal, the twist would be an effective way of overpowering the prey. The slender snout is a special device for catching swift-swimming fishes by a sidewise sweep of the head.

Like all other predators, the parasuchians also had powerful jaw muscles (Anderson 1936). The opening and closing of the jaw must be very rapid in a snapping action. The forwardly sloping pterygoideus allowed the lower jaw to snap shut rapidly from the fully open position, for seizing prey. When the prey was caught between the jaws, a strong bite would be essential to kill it. This was performed by the vertical temporalis muscle. These two sets of muscles must have been well developed in *Parasuchus*, as is evident from the architecture of the skull.

The food remains inside the stomach of *Parasuchus* give some clue as to its method of feeding. The skull bones of the medium-sized rhynchosaur are found somewhat scattered in the stomach, whereas the little bipedal archosaur is preserved almost in natural articulation, except for the skull. This evidence indicates that, if the prey was small, it was gulped down whole; if the prey was too large to be swallowed whole, it was reduced to pieces. Possibly small prey was orientated head first to make it easier to swallow, after crushing the skull. The animal hunted actively, rather than ambushing its prey from a place of hiding.

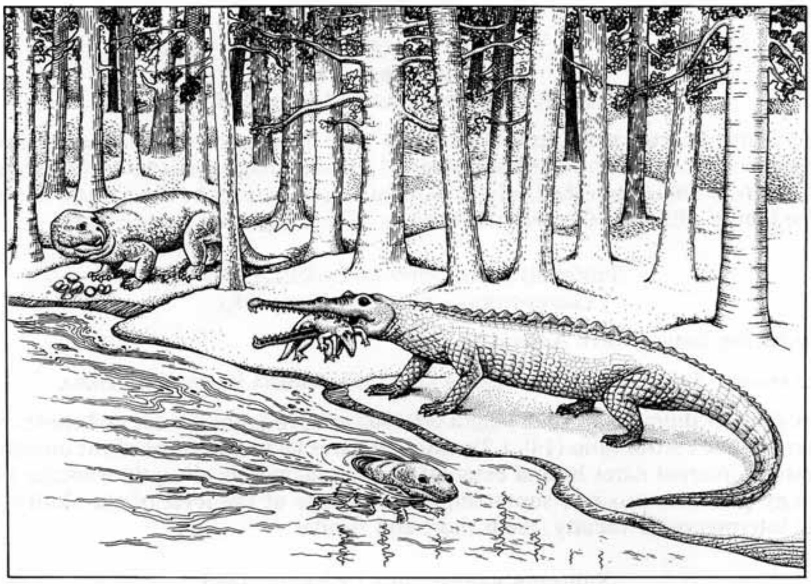
The limbs of *Parasuchus* are well built for terrestrial locomotion. The fore-limbs being slightly shorter than the hind, are well adapted for grasping and holding the prey with sharp claws. The animal was probably capable of a rapid chase for a short distance. The relatively large and spreading manus and pes may have helped to prevent the feet sinking into the swampy land which was the probable habitat. The throat and back of the animal are protected by a formidable shield of scutes, making it almost impregnable. The abdominal ribs provide reinforcement for the belly. During swimming, the limbs would probably be folded against the body and the powerful, compressed tail used for sculling through the water. The latter could strike an assailant a severe blow by a sidewise sweep.

What was the mode of life of *Parasuchus* in the Maleri ecosystem? The physical setting in which the animal lived seems to be broad flood plains of low relief with swamps and numerous large rivers. The climatic conditions were probably of monsoon type, marked by high rainfall with alternate wet and dry seasons (Robinson 1971). There are a few records of contemporary flora, mainly as fragments of *Dadoxylon*, *Araucarioxylon*, and *Mesembrioxylon* (Pascoe 1959, p. 971). The animal presumably lived for the most part in the water, seeking food and lowered body temperature, and making only occasional excursions on to the ground, particularly during egg-laying. Sunny banks would be a favourite spot for hunting the land-dwellers, particularly when the latter came to water for drinking or feeding. *Parasuchus* in the Maleri environment seems to have been the arch predator of his time, having little to fear from the enemies, and thus enjoyed a brief period of supremacy and success (text-fig. 15).

## DISTRIBUTION, EVOLUTION, AND RELATIONSHIPS OF THE PARASUCHIDAE

Parasuchian phylogeny is a good example of explosive evolution during the Late Triassic. The continental deposits of North America, Europe, and India have provided a variety of parasuchians with excellent cranial material and a number of relatively complete skeletons. Parasuchian remains from North Africa, China, and Madagascar are at present insufficiently known for comparative study or diagnosis. The great multiplicity of generic names for parasuchians has been reduced to a few after careful evaluation (Gregory 1962, 1969; Gregory and Westphal 1969). Gregory's classification is more simple and realistic, as parasuchians are a morphologically homogeneous group of limited stratigraphic range, in the sense that they have a restricted number of variations from a basic pattern.

Gregory recognized five valid genera: *Paleorhinus*, *Angistorhinus*, *Mystriosuchus*, *Nicrosaurus*, and *Rutiodon*. He considered *Francosuchus* as a subgenus of *Paleorhinus*, and *Parasuchus* as a synonym of *Nicrosaurus*. However, the present study, amplified



TEXT-FIG. 15. Restoration of the Upper Triassic Maleri landscape showing some of the characteristic tetrapods. In the water is the labyrinthodont amphibian *Metoposaurus*. Behind it is the predatory parasuchian *Parasuchus* holding a bipedal archosaur in its mouth. On the left, is the rhynchosaur *Paradapedon* eating mussels (unionids, *Tikhia*). In the background is shown *Araucarioxylon* forest. These animals lived in a lowland environment near the water's edge, in a subtropical climate with alternate hot and dry seasons, and a high rainfall.

by excellent material, indicates a somewhat different picture. In this study the generic status of *Parasuchus* and *Francosuchus* is revived, and *Paleorhinus* is considered as a subjective junior synonym of *Parasuchus*. The arguments for this revised classification will follow immediately after brief descriptions of the known parasuchian genera. The classification presented herein is based mostly on skull characters and will enable identification of skull material rather precisely (adapted from Case 1922, Camp 1930, and Gregory 1962). Differences certainly exist in the post-cranial structures, but their use in classification is severely hampered by lack of association of parts in most genera. Among various post-cranial characters, the nature of scutes (whether overlapping or not) is singled out as being of great phyletic significance.

### *Systematic Descriptions*

### Order THECODONTIA
### Suborder PARASUCHIA
### Family PARASUCHIDAE Lydekker, 1885

Long-snouted carnivorous reptiles from the Late Triassic continental sediments of Europe, India, and North America. A good familial diagnosis is given by Gregory (1962). *Mesorhinus* from the Early Triassic of Germany may be the earliest member of the family, although Gregory doubted its affinity, age, and provenance.

### Subfamily PARASUCHINAE Lydekker, 1885
### Genus PARASUCHUS Lydekker, 1885

*Distribution.* India, North America.

*Type species. Parasuchus hislopi* Lydekker, 1885; Maleri Formation, India.

Small to medium-sized, skull length 600–900 mm, rostrum slender and short without crest; low rostral ratio (1·0–1·2); external nares lie well in front of the antorbital fenestrae, internal nares behind external nares; squamosals abruptly truncate without any posterior process; supratemporal fenestrae at the level of the skull roof; large interpterygoid vacuity; teeth short and slender.

### Subgenus PARASUCHUS Lydekker, 1885

*Parasuchus hislopi* Lydekker, 1885; Maleri Formation, India.

Moderately deep skull, orbit directed outwards and upwards; post-temporal fenestrae moderate sized; teeth weakly heterodont; overlapping scutes.

### Subgenus PALEORHINUS Williston, 1904

*Paleorhinus bransoni* Williston, 1904; Popo Agie Formation, Wyoming, North America.

Low occiput, orbit directed more upwards than outwards; small post-temporal fenestrae; homodont dentition, non-overlapping scutes.

### Genus ANGISTORHINUS Mehl, 1913

*Distribution.* North America.

*Type species. Angistorhinus grandis* Mehl, 1913; Popo Agie Formation, Wyoming, North America.

Large-sized, skull length 900–1200 mm; moderately deep; external nares posterior, between the antorbital fenestrae; post-temporal arcade at the level of the skull roof; rostrum long and strong with prominent downturned tip and lacks crest; rostral ratio moderate (1·4–1·9); large infratemporal and post-temporal fenestrae; palate vaulted with small interpterygoid vacuity; squamosal process rounded and short, extended well behind the contact of the paroccipital process; orbits directed outwards as much as upwards; teeth weakly heterodont with compressed and enlarged posterior teeth; non-overlapping scutes.

### Genus NICROSAURUS Fraas, 1866

*Distribution.* Germany and North America.

*Type species. Nicrosaurus kapfi* (Meyer), 1860; Stubensandstein, Stuttgart, Germany.

Moderate to large sized, skull length 750–1400 mm; moderately deep; massive rostra with continuous rostral crest; rostral ratio low (average 1·2), independent of size; external nares posterior, between the antorbital fenestrae; squamosal process short and deep; narrow interpterygoid vacuity; post-temporal fenestrae large, supratemporal fenestrae depressed; strong heterodont teeth, overlapping scutes.

### Genus RUTIODON Emmons, 1856

*Distribution.* Europe and North America.

*Type species. Rutiodon caroliensis* Emmons, 1856; Cumnock Formation, North Carolina, U.S.A.

Large-sized, skull length 800–1200 mm, rostra vary from slender and uncrested in small skulls to moderately robust with large dorsal crests in the posterior half of the largest individuals; rostral ratio low to moderate (1·2–1·7); squamosal process slender and show phyletic elongation; external nares posterior, between antorbital fenestrae; supratemporal fenestrae depressed; interpterygoid vacuity narrow, large post-temporal fenestrae; orbits directed obliquely outwards and upwards; strongly heterodont teeth; non-overlapping scutes.

### Subfamily MYSTRIOSUCHINAE von Huene, 1915

### Genus FRANCOSUCHUS Kuhn, 1932

*Distribution.* Germany.

*Type species. Francosuchus broilii* Kuhn, 1932; Blasensandstein, Franconia, Germany.

Small-sized, skull length 600 mm; extremely low occiput; rostrum slender and long without crest; moderate rostral ratio (1·7); external nares anterior to antorbital fenestrae but more close to orbits than in *Parasuchus*; posterior squamosal process absent; orbit directed more upwards than outwards; large interpterygoid vacuity, post-temporal fenestrae small; supratemporal fenestrae at the level of the skull roof; homodont dentition; non-overlapping scutes.

### Genus MYSTRIOSUCHUS Fraas, 1896

*Distribution.* Germany.

*Type species. Mystriosuchus planirostris* (Meyer), 1863; Stubensandstein, Würtemberg, Germany.

Small to medium-sized, skull length 750–1050 mm, fairly deep; highly specialized posterior nares close to orbit resulting in high rostral ratio (2·2–2·7); rostrum low and slender with occasional dorsal swellings; greatly depressed supratemporal fenestrae close to paroccipital process; orbit directed more outwards than upwards; squamosal primitive, lacking posterior process; teeth slender and homodont; small interpterygoid vacuity; post-temporal fenestrae extremely reduced.

## GENERA INCOMPLETELY KNOWN

### Genus MESORHINUS Jaekel, 1910

*Type species. Mesorhinus fraasi* Jaekel, 1910; Buntsandstein, Germany.

Possibly the earliest parasuchian; low occiput; external nares lie well in front of the antorbital fenestrae; pineal foramen present; supratemporal fenestrae at the level of the skull roof; palate primitive with large interpterygoid vacuity.

Horizon, supposedly Lower Trias, highly dubious (Gregory 1962). The only specimen was lost during the Second World War.

### Genus PACHYSUCHUS Young, 1951

*Type species. Pachysuchus imperfectus* Young, 1951; Lower Lufeng Series, Yunnan, China.

Very fragmentary material, lacks diagnostic characters.

Good skeletons of parasuchians have recently been discovered from Triassic sediments of Morocco, North Africa. No descriptions or affinities are yet available.

### *Analysis of Characters*

Gregory (1962, Table 1) has analysed various skull characters in detail and tabulated to those, which, according to him, are of great systematic value. He did not include *Parasuchus*, as the Indian material was then poorly known. A slightly modified and more elaborate version of Gregory's scheme is given below (Table 3).

Some of the morphologic characters such as skull height, direction of the orbit, and size of the post-temporal fenestra, may be affected by crushing, and thus should be used with some caution. The following characters seem to be of great systematic value; some of the characters are indicative of grades of evolution, some are of phyletic affinity.

1. Position of external nares in relation to antorbital fenestrae; more precisely, the distance between the nares and the orbits.
2. Rostral ratio (pre-narial to post-narial length); nature of the rostrum, whether slender, robust, crested, or uncrested.
3. Posterior border of the supratemporal fenestrae at the level of the skull roof, or depressed.
4. Presence or absence of the posterior squamosal process.
5. Palate open or vaulted.
6. Teeth homodont or heterodont.
7. Scutes overlapping or non-overlapping.

*Parasuchus*, *Paleorhinus*, and *Francosuchus* share many of the primitive characters and represent more or less similar levels of organization. *Parasuchus* and *Paleorhinus* are so similar in form that their generic distinction is questionable. Of twelve cranial

TABLE 3. Tabular comparisons of diagnostic characters of parasuchid skulls.

| | *Paleorhinus* | *Francosuchus* | *Parasuchus* | *Angistorhinus* | *Mystriosuchus* | *Nicrosaurus* | *Rutiodon* |
|---|---|---|---|---|---|---|---|
| I. Position of external nares | Anterior | Anterior | Anterior | Posterior | Posterior | Posterior | Posterior |
| II. Position of orbit | Directed more upwards than outwards | Directed more upwards than outwards | Directed outwards as much as upwards | Directed outwards as much as upwards | Directed upwards and backwards | Obliquely more outwards than upwards | Obliquely more outwards than upwards |
| III. Nature of supratemporal fenestra | Level of the skull deck | Level of the skull deck | Level of the skull deck | Level of the skull deck | Greatly depressed | Depressed | Depressed |
| IV. Nature of infratemporal fenestra | Small, posterior to orbit | Small, posterior to orbit | Small, posterior to orbit | Large, at the level of the orbit | Small, posterior to orbit | Large, at the level of the orbit | Large, at the level of the orbit |
| V. Nature of post-temporal fenestra | Small | Small | Moderate | Large | Very small | Large | Large |
| VI. Pineal foramen | Present (only in *P. scurriensis*) | Absent | Absent | Absent | Absent | Absent | Absent |
| VII. Nature of interpterygoid vacuity | Large | Large | Large | Small | Small | Small | Small |
| VIII. Ratio of rostral length to postnarial length | 1·0–1·2<br>Low | 1·7<br>Moderate | 1·1<br>Low | 1·4–1·9<br>Moderate | 2·2–2·7<br>High | 1·05–1·37<br>Low | 1·2–1·7<br>Low to moderate |
| IX. Ratio of skull height to skull width | 0·37<br>Low | 0·30<br>Low | 0·57<br>Moderate | 0·44<br>Moderate | 0·63<br>High | 0·44<br>Moderate | 0·63<br>High |
| X. Posterior squamosal process | Absent | Absent | Absent | Rounded, short | Absent | Rounded, elongate | Rounded, elongate |
| XI. Plane of quadrate | Inclined, sloping posteriorly | Inclined, sloping posteriorly | Inclined, sloping posteriorly | Inclined, sloping posteriorly | Vertical | Vertical | Vertical |
| XII. Dentition | Homodont | Homodont | Weakly heterodont | Weakly heterodont | Homodont | Strongly heterodont | Strongly heterodont |

characters listed by Gregory as typical of *Paleorhinus*, eight are also found in *Parasuchus* (see Table 3). Four contrasting characters between these two forms are: (*a*) Skull-height, low in *Paleorhinus* but moderate in *Parasuchus*. (*b*) Size of the post-temporal fenestrae—small in *Paleorhinus* but moderate in *Parasuchus*. (*c*) Position of the orbit; directed more upwards than outwards in *Paleorhinus*, but in *Parasuchus*, it is directed outwards as much as upwards. (*d*) Dentition: homodont in *Paleorhinus* but weakly heterodont in *Parasuchus*.

Of these, the first three characters, as has already been pointed out, may easily be accounted by differential crushing and individual growth differences. It is thus seen that the only distinction between *Paleorhinus* and *Parasuchus* hinges mainly on the nature of the dentition. Otherwise *Paleorhinus* and *Parasuchus* are remarkably similar in all qualitative features of narial form and position and development of temporal arcades (text-fig. 16). The beginning of the differentiation of teeth in *Parasuchus* is a derived character and indicates that *Parasuchus* is just one step further forward than *Paleorhinus*. Uniting *Paleorhinus* and *Parasuchus* in a single genus stresses the close relationship between these animals; their separate identities at subgeneric level seem to be a useful compromise between two geographically separated populations. In this connection it is interesting to mention that the Indian metoposaur, *Metoposaurus maleriensis* from the same horizon, is extremely similar to those of North America and Germany, differences being at a specific level only (Roy Chowdhury 1965).

Although *Francosuchus* agrees well with *Parasuchus* (*Paleorhinus*) in most of the cranial characters, the outstanding feature of *Francosuchus* is its extremely long and slender snout. The high rostral ratio is weighted heavily in phyletic classification of parasuchians. This is why *Francosuchus* is kept separate as a distinct genus from *Parasuchus* (*Paleorhinus*).

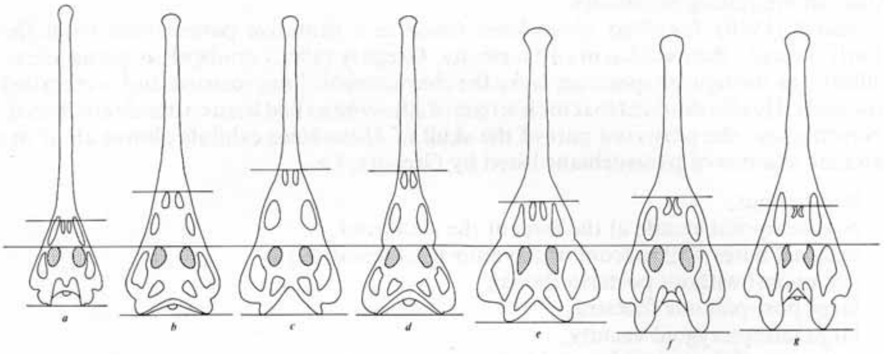
### *Phenetic Relationships*

The parasuchian genera, when arranged in order of chronology, show certain changes in cranial characters. From the primitive *Parasuchus* (*Paleorhinus*)-like animal, the morphologic changes shown by the Parasuchidae could have appeared by the following evolutionary developments:

1. Gradual posterior shift of the external nares in relation to antorbital fenestrae.
2. Change of the orientation of the orbit from upwards to more outwards.
3. Gradual depression of the supratemporal fenestra from the skull deck to the occipital region.
4. Progressive anterior enlargement of the infratemporal fenestra.
5. Gradual enlargement of the post-temporal fenestra.
6. Loss of the pineal foramen.
7. Reduction in size of the interpterygoid vacuity.
8. Gradual increase of the rostral ratio (correlated to 1).
9. Progressive increase of the height of the skull in relation to its width.
10. Gradual enlargement of the squamosal process posteriorly.
11. Swinging forward of the quadrate, the backwardly sloping quadrate becoming vertical.
12. Tooth differentiation, from homodont to heterodont.

One should take into account the morphological variations that result from differences in sex and age. It is not unlikely that some of the above changes could have been produced by these two factors. Nevertheless, the general pattern of evolution can be gathered from an analysis of these characters.

It appears from the Table 3 that the parasuchian genera tend to segregate into three different stages or grades of evolution from the primitive to the advanced condition. The primitive grade of greatest paleotelic weight includes the genera *Francosuchus* and *Parasuchus*. *Angistorhinus* is intermediate in grade as its nostrils have shifted fairly far back between the antorbital fenestrae, with the development of the posterior squamosal process. *Nicrosaurus*, *Mystriosuchus*, and *Rutiodon* are advanced, in that the supratemporal fenestrae greatly depressed below the skull roof (text-fig. 16).



TEXT-FIG. 16. Dorsal views of parasuchian skulls to show variations in the position of the external nares, antorbital fenestrae, supra- and infratemporal fenestrae, and posterior squamosal process; the skulls have been reduced to a unit length for comparisons. Orbit stippled. *a*, *Mystriosuchus planirostris* (after McGregor 1906); *b*, *Francosuchus broilii* (after Kuhn 1936); *c*, *Paleorhinus* sp. (after Gregory 1969); *d*, *Parasuchus hislopi*; *e*, *Angistorhinus megalodon* (after Gregory 1969); *f*, *Nicrosaurus kapfi* (after Gregory 1969); *g*, *Rutiodon adamanensis* (after Camp 1930).

## *Phylogenetic Relationships*

It is very difficult to derive the long-snouted parasuchian from any other families of Thecodontia, since intermediate forms are lacking. Walker (1968) suggested that *Proterochampsa* from the Ischigualasto Formation of Argentina is a primitive parasuchian. Romer (1971) also described a further two closely related forms, *Chanaresuchus* and *Gualosuchus* from the Chanares Formation of Argentina, and grouped them along with *Proterochampsa* and *Cerritosaurus* in the single family Proterochampsidae of the suborder Proterosuchia. Although the Proterochampsidae show many parasuchian affinities, the absence of the postfrontal bone in these forms raises a serious problem, as this bone is ubiquitous in all parasuchids. Moreover, the pineal foramen, being present in primitive species, such as *Paleorhinus* (= *Parasuchus*) *scurriensis*, ought to be present in the ancestral form. This is also lacking in the Proterochampsidae. Furthermore, the post-cranial skeleton of the Proterochampsidae does not show any positive relationship to that of parasuchids (Romer 1972). However, one important feature seen in these forms is the initiation of the movement of the external nares, as slit-like structures, well back on to the dorsal surface. This suggests that the parasuchians could be the direct descendants of the Proterosuchia by the process of moving the external nares back along the skull in a longirostral lineage. The Proterochampsidae must be regarded as an aberrant offshoot of the primitive proterosuchian stock (Romer 1971, 1972).

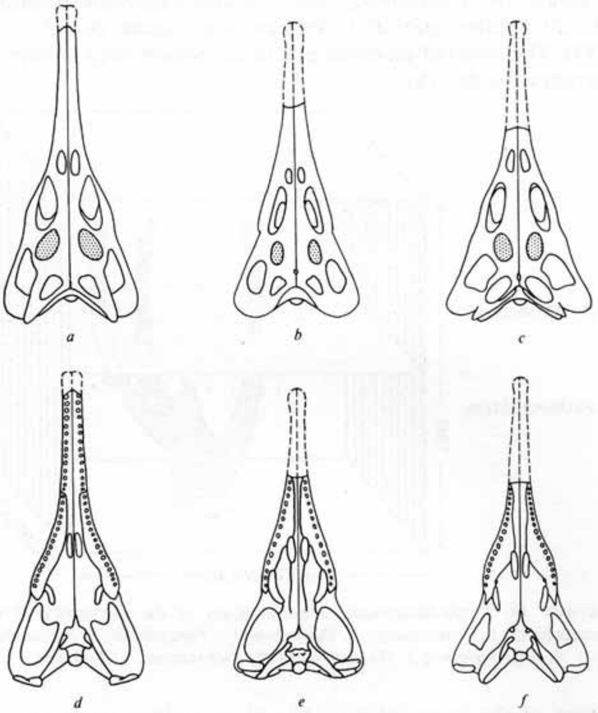
The skull of *Proterosuchus* shows some parasuchian traits (Gregory 1962). The general form of the skull (Cruickshank 1972) is elongate, with downturned premaxillae, indicating a tendency toward lengthening of the snout. It also possesses a postfrontal bone and a pineal foramen. But the gap between *Proterosuchus* and a typical parasuchian is so great as to make an assumption of relationship little more than an interesting possibility.

Jaekel (1910) described *Mesorhinus fraasi* as a primitive parasuchian from the Early Triassic Buntsandstein of Germany. Gregory (1962) doubted its parasuchian affinity, as the figured specimen lacks the characteristic long rostrum and is recorded too early. He also doubted that the horizon of *Mesorhinus* had been correctly attributed. Nevertheless, the preserved part of the skull of *Mesorhinus* exhibits almost all of the archaic features of parasuchians listed by Gregory, i.e.

low occiput;
post-temporal arcade at the level of the skull roof;
external nares well in front of the antorbital fenestrae;
squamosal without posterior hook;
large post-palatine fenestra;
large interpterygoid vacuity;
retention of the pineal foramen.

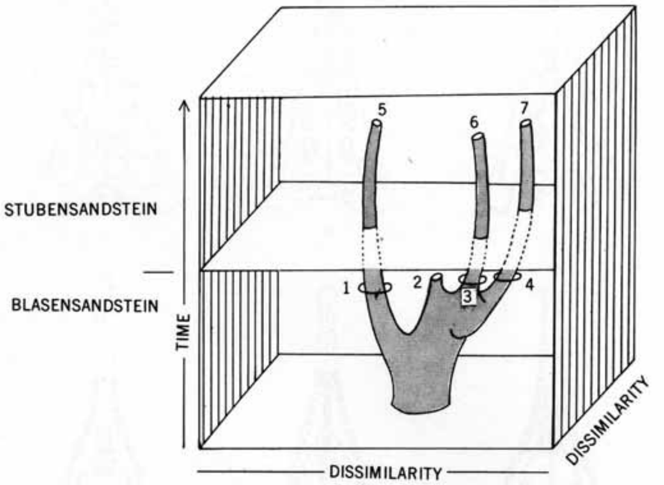
The close similarity of the skull *Mesorhinus* to those of primitive parasuchians such as *Paleorhinus* (= *Parasuchus*) *scurriensis* is very striking (text-fig. 17). There seems ample evidence for regarding *Mesorhinus* as a very primitive parasuchid. If *Mesorhinus* is truly a parasuchid and if it comes from the Early Triassic, it is by far the earliest member of the family. Unfortunately the only specimen of *Mesorhinus* was destroyed during the war in 1945 (Dr. Frank Westphal, pers. comm.), and further re-examination is therefore impossible. Future discovery of good material of *Mesorhinus* may help to solve this long-standing problem regarding the origin of parasuchians.

There seems to be two distinct phyletic lines in the parasuchian evolution, one containing *Francosuchus* and *Mystriosuchus*, the other containing *Parasuchus*, *Angistorhinus*, *Nicrosaurus*, and *Rutiodon*. *Mystriosuchus* is obviously an advanced genus, similar to *Nicrosaurus* and *Rutiodon* in its high occiput, depressed post-temporal arcade, and posterior external nares. It resembles *Francosuchus* in the absence of squamosal process, in retaining homodont dentition, and sharing characteristic long and slender rostrum. The similarity of high rostral ratio is suggestive of phyletic relationship between them. This trend towards a more elongate rostrum suggests that *Francosuchus* has diverged from the primitive stock (?*Mesorhinus*) in a separate phyletic line from the rest of the genera earlier than the Early Triassic, leading to *Mystriosuchus*. Furthermore, both *Francosuchus* and *Mystriosuchus* occur only in Germany, which supports this hypothesis. The subfamily Mystriosuchinae (*nom. transl. ex* Mystriosuchidae von Huene 1915) is proposed herein to include *Francosuchus* and *Mystriosuchus*.



TEXT-FIG. 17. A comparison of the skull in *Mesorhinus*, *Paleorhinus*, and *Parasuchus*. *a*, *d*, dorsal and ventral views of *Parasuchus hislopi* Lyd. (specimen ISI R 44); *b*, *e*, dorsal and ventral views of *Mesorhinus fraasi* (after Jaekel 1910); *c*, *f*, dorsal and ventral views of *Paleorhinus scurriensis* (after Langston 1949). In this figure the skulls have been reduced to a unit length in order to facilitate comparisons of proportions.

In the rest of the genera, the progressive evolution in another phyletic line can be seen. Gregory (1962) has pointed out that *Paleorhinus*, though approaching closely the structural ancestry for the parasuchians, must be regarded as slightly off the direct line of development that led to the more highly specialized genera, as this subgenus occurs in the same horizons as *Angistorhinus* and *Rutiodon*. The different subgenera of *Parasuchus* may represent the beginning of a divergence which led eventually to the later generic lines. The derivation of *Rutiodon* from the intermediate form *Angistorhinus* is rather straightforward, by the depression of the supratemporal fenestra and subsequent hooking of the squamosal. The presence of overlapping scutes in *Nicrosaurus* indicates an early separation from *Angistorhinus–Rutiodon* lineage. *Parasuchus*, however, develops overlapping scutes. Thus *Nicrosaurus* might have descended from a *Parasuchus*-like ancestor and acquired its similarities to *Rutiodon* independently. *Parasuchus*, *Angistorhinus*, *Nicrosaurus*, and *Rutiodon* are grouped here into another subfamily Parasuchinae (*nom. transl. ex* Parasuchidae Lydekker, 1885). The inferred phylogenetic relationships may be represented by the following diagram (text-fig. 18).



TEXT-FIG. 18. Three-dimensional representation of the phylogeny of the parasuchians. 1, *Francosuchus*; 2, *Paleorhinus* (= *Parasuchus*); 3, *Parasuchus*; 4, *Angistorhinus*; 5, *Mystriosuchus*; 6, *Nicrosaurus*; 7, *Rutiodon*.

The extinction of the parasuchians, like their sudden emergence, is a baffling phenomenon to comprehend. They disappeared suddenly at the close of the Triassic at a time coinciding with the first wave of reptilian extinction, and were replaced by the crocodilians. The parasuchians were excellently adapted for a predatory life in amphibious habitat, having little to fear from their enemies. Their extinction is not a case of competitive exclusion. Yet they disappeared, leaving no descendants, and after their disappearance, the crocodilians, hitherto small reptiles, grew large and occupied successfully the similar ecological niche. Why should the parasuchians have failed to survive beyond the Triassic, while their contemporaries, the crocodilians, still survive? The question remains unanswered.

## AGE AND THE CORRELATION OF THE MALERI FORMATION

The Maleri sediments are continental clastics of the Gondwana Group, highly variable in coarseness, grain size, and composition both along and across the strike of the formation. Three main lithological units are encountered: these are thick, unlithified red clays, fine-grained white sandstones, and pale-green lime-pellet rocks. The sediments are interpreted as fluviatile channel, interchannel, and back-swamp deposits (Sengupta 1966; Kutty 1971).

The flora is poorly documented in the Maleri sediments. The known fauna consists mostly of vertebrates, which are varied and well represented. The only invertebrate member so far discovered is the freshwater unionid. The occurrence of *Parasuchus* in the Maleri Formation is of particular significance as it may bear upon the age and the correlation of the sediments.

The Maleri vertebrates consist of three kinds of fishes, of a single amphibian genus, and of various reptiles. A complete list of the Maleri vertebrates, known to date, is given below (Table 4).

TABLE 4

| Faunal list | Stratigraphic affinities |
|---|---|
| *Fishes* | |
| Dipnoi—*Ceratodus hunterianus* | Mesozoic |
| Subholostei—unnamed genus and species | |
| Pleuracanths—teeth resembling *Pleuracanthus parvidens* | Triassic |
| *Amphibian* | |
| Metoposaurs—*Metoposaurus maleriensis* | Late Triassic (Carnian through Middle Norian) |
| *Reptiles* | |
| Rhynchosaurs—*Paradapedon huxleyi* | Late Triassic (Carnian through Middle Norian) |
| Parasuchians—*Parasuchus hislopi* | Late Triassic (Late Carnian to Early Norian) |
| Aetosaurs—scutes similar to *Typothorax* | Late Triassic |
| Thecodontosaurs—unnamed genus and species | Late Triassic |
| Traversodonts—similar to *Exaeretodon* | Late Triassic |
| Coelurosaurs—similar to *Coelophysis* | Late Triassic |

The better-known faunal elements in the above list are the amphibian *Metoposaurus* (Roy Chowdhury 1965), the rhynchosaur *Paradapedon* (Chatterjee 1974), and the parasuchian *Parasuchus*. The travesodont is very similar to *Exaeretodon* of the Ischigualasto Formation of South America. The lungfish *Ceratodus* is represented by isolated teeth, including vomerine teeth (Jain 1968), and has a long geological history. The rest of the fauna is insufficiently known at present, and as such its stratigraphic importance cannot be ascertained.

There has been a good deal of discussion in the past concerning the age of the Maleri Formation. Earlier workers tended to regard both the Maleri and the overlying Kota Formations as Liassic. Von Huene (1940) and Colbert (1958) suggested a Late Triassic age for the Formation, as the parasuchians and the metoposaurs are confined to the Late Triassic sequences of North America and Germany. Roy Chowdhury (1965) has shown that the Maleri metoposaur, *Metoposaurus maleriensis* is extremely similar to that of North America and Germany, the differences being on a specific level. In Germany the metoposaurs range in age from horizons equivalent to Schilfsandstein up to Blasensandstein. In North America they have a longer geological history and extend up to horizons equivalent to the Stubensandstein of Germany, but they show no stratigraphically useful varieties (Colbert and Imbrie 1956). On the evidence of the metoposaurs, Roy Chowdhury thus postulated a Carnian through Middle Norian age for the Maleri Formation.

Rhynchosaurs are fairly well distributed throughout the Trias. Chatterjee (1969) grouped the known rhynchosaur genera, on the basis of their morphologic characters, into three well-defined subfamilies representing three stages in rhynchosaur evolution, considered characteristic of the Early, Middle, and Late Triassic, respectively. The Maleri genus *Paradapedon* is included in the advanced subfamily Hyperodapedontinae, along with *Hyperodapedon* and *Scaphonyx*, and the Maleri Formation is equated with the Lossiemouth Beds of Scotland as well as with the Santa Maria and Ischigualasto Formations of South America.

The parasuchians, however, offer a more accurate dating of the Maleri Formation than do the metoposaurs and rhynchosaurs. Gregory (1956, 1962, and 1969) has attempted a palaeontological subdivision of the Carnian to Middle Norian faunas of North America and Germany on the basis of the parasuchians, as their skulls were undergoing rapid structural modifications through a limited geological time range. In Germany the primitive genus *Francosuchus* occurs in the Blasensandstein of the Middle Keuper, whereas the advanced genera such as *Mystriosuchus*, *Rutiodon*, and *Nicrosaurus* are common higher up in the Stubensandstein. A similar situation is observed in North America also. Here the primitive and intermediate genera such as *Parasuchus* (*Paleorhinus*) and *Angistorhinus* are restricted to beds probably equivalent to the Blasensandstein of Germany, whereas the advanced genera like *Rutiodon* and *Nicrosaurus* are abundant in horizons equivalent to the Stubensandstein. The primitive and advanced genera do not occur in the same stratum, except in Crosby County, Texas, where a primitive species of *Rutiodon* is found along with *Parasuchus* (*Paleorhinus*). The primitive and advanced genera represent successive stages in parasuchian evolution and occur in progressively younger deposits.

As the geological range of primitive parasuchians such as *Parasuchus* in North America and *Francosuchus* in Germany is known from Gregory's work, the upper limit of the Maleri and Tiki Formations can be fixed as Early Norian, equivalent to the Blasensandstein of Germany. The lower limit may extend down to the Schilfsandstein, as a doubtful record of a parasuchian jaw is known from this horizon (Gregory 1969). Thus the age range of the Maleri Formation is probably Late Carnian to Early Norian of the standard marine sequence, i.e. from the Schilfsandstein to the Blasensandstein of the German continental Trias. This is exactly the range of metoposaurs in Germany. A tentative correlation of the parasuchian-bearing sediments is given in the following table (adapted from Gregory 1956, 1969; Anderson and Anderson 1970).

TABLE 5. PROVENANCES OF THE PARASUCHIDAE.

| | Alpine facies | ......W. Europe..... | ......United States of America...... | | | | ......India...... | | W. China | North Africa |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Germanic facies | Atlantic coast (Nova Scotia-N. Carolina) Newark group | Texas + E. New Mexico Dockum group | Arizona (Colorado Plateau) | Wyoming | Pranhita-Godavari Valley | Son-Mahanadi Valley | (Shansi & Sinkiang) | (Morocco) |
| LATE TRIASSIC | RHAETIAN | Rhaetian*? (gen. indet.) | | | | | Dharmaram Formation | | Lufeng* Series (gen. indet.) | |
| | NORIAN | Knollenmergel | Brunswick Fm.* upper part (*N.*)<br>Portland Arkose<br>Meriden Fm. | Redonda Fm.* (undescribed) | CHINLE FORMATION<br>Wingate Fm.*? Moenave Fm. Owl Rock M. (gen. indet.) | | | | | |
| | | Stubensandstein* (*N.*, *M.*, *R.*) | New Haven Arkose* (*N.*)<br>Brunswick Fm. lower part<br>Lockatong Fm.* (*N.*)<br>Cumnock Fm.* (*R.*)<br>Stockton Fm.* (*N.*) | Upper fauna* (*N.*)<br>Middle fauna* (Tecovas Shale) (*N.*) | Upper fauna* (*N.*)<br>Lower fauna* (*R.*, *N.*)<br>Shinarump M.* (unnamed) | | | | | Morocco fauna* (undescribed, similar to *M.*) |
| | | Blasensandstein* + Lehrbergstufe (*F.*) | | Basal fauna* (*P.*, *A.*) | | Popo Agie M.* (Chugwater Fm.) (*P.*, *A.*) | Maleri Fm.* (*PS.*) | Tiki Fm.* (*PS.*) | | |
| | CARNIAN | Schilfsandstein*? (gen. indet.) | | | | | | | | |
| | | Lettenkohle | | | | | | | | |

* Parasuchid-bearing horizon

Abbreviations: *A.* = *Angistorhinus*; *F.* = *Francosuchus*; *M.* = *Mystriosuchus*; *N.* = *Nicrosaurus*; *P.* = *Paleorhinus*; *PS.* = *Parasuchus*; *R.* = *Rutiodon*

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